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ANTHROPOGENIC IMPACTS ON FRESHWATER BIODIVERSITY

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IMPACTS DES ACTIVITÉS ANTHROPIQUES SUR LA BIODIVERSITÉ DES ÉCOSYSTÈMES D'EAU DOUCE

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RÉSUMÉ

Comprendre les impacts anthropiques sur les écosystèmes est essentiel pour gérer les communautés naturelles et les services écosystémiques qu'elles fournissent. Les écosystèmes d'eau douce semblent particulièrement menacés par les impacts anthropiques. Une compréhension plus approfondie de ces impacts est nécessaire de toute urgence afin de gérer et de protéger efficacement la biodiversité des écosystèmes d'eau douce. Parmi les facteurs de stress anthropiques, les espèces invasives ont des effets dévastateurs sur la biodiversité des écosystèmes d'eau douce. Cependant, les effets à long terme des espèces invasives sont encore mal compris, ainsi que le potentiel que l'hétérogénéité environnementale naturelle dans la création de refuges contre l'invasion et atténuer l'impact de l'invasion sur les communautés résidentes. Un exemple de menace émergente pour la biodiversité des écosystèmes d'eau douce est l’augmentation mondiale des niveaux de sels observée au cours des dernières décennies dans différents types d’écosystèmes. De telles augmentations des niveaux de sel sont préoccupantes, et les premières recherches sur le sujet ont montré des effets négatifs sur la biodiversité. Cependant, de nombreux taxons et systèmes n'ont pas encore été étudiés, et les impacts sur les réseaux trophiques naturels sont encore mal compris.

Ma thèse explorera les questions suivantes : i) quels sont les effets à long terme d’un important poisson invasif, le gobie à tache noires (*Neogobius melanostomus*), le long d'un gradient de présence historique ? ii) comment les gradients naturels sous forme d'hétérogénéité environnementale peuvent-ils atténuer les impacts d’espèces invasives sur les communautés résidentes ? iii) quels sont les impacts de la salinisation sur les réseaux trophiques planctoniques d'eau douce, et si les recommandations pour la qualité de l'eau permettent de les prévenir ? Pour répondre aux questions 1 et 2, j’ai mesuré la diversité des communautés de macroinvertébrés et de poissons dans la rivière Saint-Laurent en relation avec les abondances de gobie à tache noires invasifs, le temps écoulé depuis l'invasion, et des gradients environnementaux naturels sous forme d’hétérogénéité environnementale émergeant de différences de conductivité à large échelles spatiale, et de milieux humides à échelle locale. Pour répondre à question 3, j’ai expérimentalement exploré les effets de la salinisation sur un réseau trophique planctonique à l'aide de mésocosmes in-situ et de méthodes génomiques.

Dans son ensemble, ma thèse souligne l'importance du suivi continu des espèces envahissantes pour mieux comprendre leurs effets à long terme sur les écosystèmes d'eau douce. Ma thèse souligne également l'importance de la conservation des refuges non envahis pour atténuer les impacts de l'invasion dans les écosystèmes d'eau douce, tels que les sites à faible conductivité, et les milieux humides dans les eaux à haute conductivité du fleuve St. Laurent. De plus, je souligne l'importance cruciale des milieux humides pour la biodiversité des eaux douces. Les zones humides sont gravement touchées par le développement urbain et agricole, et mes travaux montrent l'importance de protéger et de restaurer ces précieux habitats pour la biodiversité des eaux douces. Finalement, les effets de la salinisation que j'ai détectés impliqueraient un total effondrement de réseaux trophiques lacustres, si ces effets s'appliquent à l'échelle de l'écosystème. Mon étude souligne que les recommandations pour les concentrations de chlorure dans les eaux intérieures en vigueur au Canada et aux États-Unis ne protègent pas tout les écosystèmes d'eau douce, et que ces recommandations devraient prendre en considération les niveaux de sel ambiant locaux, l'historique de salinisation et la composition des communautés locales pour une gestion adéquate.

Mots clés : Écosystème d'eau douce, impactes anthropiques, biodiversité, espèces invasives, salinisation

ABSTRACT

Understanding the impacts humans have on ecosystems is critical to manage natural communities, and the ecosystem services they provide to human well-being. Freshwater ecosystems are particularly at risk from anthropogenic impacts. A deeper understanding of such anthropogenic impacts on freshwater biodiversity, and how they can be mitigated or moderated, are urgently needed in order to efficiently manage and protect freshwater biodiversity. Among anthropogenic stressors, exotic invasion is having devastating effects on freshwater biodiversity globally. However, little emphasis has been directed by most research in understanding long-term effects of invasive species, and how natural environmental heterogeneity may provide refuges against invasion that can help mitigate invasion impact on resident communities. An example of an emerging threat to freshwater biodiversity is salinization, in which worldwide continental increases of salts levels in all types of freshwater ecosystems have been observed over the past several decades. Such increases in salt levels are concerning, and early research has shown negative effects on freshwater biodiversity. However, numerous taxa and systems have not received much attention, and impacts on natural food webs are still poorly understood.

My PhD thesis addresses the following questions: i) what are the long-term effects of an important invasive fish species, the round goby (*Neogobius melanostomus*), along a gradient of historical presence? ii) how natural gradients in the form of environmental heterogeneity can mitigate invasive impacts on resident communities? and iii) what are the impacts of salinization on a pristine freshwater planktonic food web, and how do these impacts relate to water quality guidelines for chloride concentrations? To answer questions 1 and 2, I measured the diversity and structure of macroinvertebrates and fish communities in the Upper St-Lawrence River in relation with invasive round goby abundances, time since invasion, and natural gradients in the form of environmental heterogeneity from broad-scale conductivity and local-scale wetlands. To address question 3, I experimentally test the effects of salinization on a pristine freshwater planktonic food web using in-situ lake mesocosms and metabarcoding.

For question 1, I found that sites in the Upper St. Lawrence River with prolonged invasive presence from the round goby show first signs of reaching carrying capacity with diminished macroinvertebrate community resources. For chapter 2, I found that environmental heterogeneity in the form of a broad-scale conductivity gradient and local-scale wetlands provided refuges to resident macroinvertebrate and fish communities from the invasive Ponto-Caspian round goby fish, and that wetlands also had the effect of enhancing aquatic biodiversity in face of invasion in the Upper St. Lawrence River. For chapter 3, I observed major shifts in the composition and diversity of the planktonic food web as a response to freshwater salinization. Salinization greatly simplified the food web, and it impoverished the basal resources nutritional quality at salt levels deemed acceptable by water quality guidelines of both Canada and the United States.

Overall, my thesis highlights the importance of continued invasive species monitoring to better understand their long term effects in freshwater ecosystems. My thesis underlines the importance of conserving uninvaded refuges for mitigating invasion impacts in freshwater ecosystems, such as low-conductivity sites and wetlands within invaded, high conductivity waters within the Upper St. Lawerence River. Furthermore, I highlight the crucial importance of wetlands for freshwater biodiversity. Wetlands are being severely impacted by urban and agricultural development, and our work shows the importance of protecting and restoring these valuable habitats for freshwater biodiversity. Moreover, the effects of freshwater salinization that I detected would imply major collapse of entire food webs if the effects were to scale to whole lake ecosystems. My research indicates that water guidelines for chloride concentrations in inland waters in Canada and the United States are not protecting pristine freshwater ecosystems today, and that guidelines should take local ambient salt levels, history of salinization, and local community composition into consideration for adequate management.

Keywords : Freshwater, anthropogenic impact, biodiversity, invasive species, salinization

INTRODUCTION

0.1 Anthropogenic stressors and biodiversity loss

Humans are impacting their environment and threatening ecosystems on a global scale. Human impacts on the Earth system as a whole are so deep that scientists have advocated for our epoch to be referred to as the ‘Anthropocene’ (Crutzen, 2006). The ‘Anthropocene’ describes the recent rupture in earth’s history arising from human activities and their impacts on the Earth system, starting with the industrial revolution in the 1800’s (Steffen *et al.*, 2011 ; Waters *et al.*, 2016). Human impacts in the ‘Anthropocene’ are not limited to the disruption of atmospheric carbon cycles but also affect other biogeochemical cycles fundamental to life on Earth (eg. nitrogen, phosphorus and sulphur), they also deeply modify terrestrial water cycles through land-cover change, and driving loss of biodiversity (Steffen *et al.*, 2006). Human impacts on the functioning of the Earth system in the last centuries have been of such magnitude that they now rival some of the great forces of Nature (Steffen *et al.*, 2011). The major loss of biodiversity is one of the many consequences of human activities which have driven scientists to describe the current reduction of biodiversity as the sixth major extinction in Earth history (Ceballos *et al.*, 2015, 2017).

Biodiversity is the total, and the variability in space and time, of all microorganisms, plants, animals, and fungi on Earth; their phenotypic and genetic variation; and the communities and ecosystems from which they are a part (Dirzo et Raven, 2003). Concern about rates of species loss in natural ecosystems has been growing since the

1980’s and led to research showing the importance of organisms in engineering ecosystems (physical formation of habitats) (Jones et al., 1996), regulating biogeochemical cycles (Sterner et Elser, 2002), affecting the productivity of ecosystems (Power *et al.*, 1996). Such studies suggested that species loss could have important impacts on the structure and function of natural ecosystems. After several decades of research, it has now been established that biodiversity loss negatively impacts the efficiency of natural communities’ ability to capture essential resources, produce biomass, recycle and decompose nutrients (Cardinale *et al.*, 2012). Furthermore, more evidence of the negative impact of biodiversity loss on ecosystem functioning and productivity have accumulated over the years (Cardinale *et al.*, 2012). There is evidence that important ecosystem services, such as crop yield, stability of fisheries yield, and wood production, have a positive relationship with biodiversity (Cardinale *et al.*, 2012). Biodiversity is important not just for it’s intrinsic wonder and beautiful nature, but it is a key resource for present and future human societies. However, since the industrial revolution humans have had such profound effects on their environment that biodiversity is at risk. Freshwater ecosystem biodiversity is particularly endangered, and declines of freshwater biodiversity are far greater than the most affected terrestrial ecosystems (Albert et al., 2021 ; Sala et al., 2000 ; Strayer et Dudgeon, 2010) (Fig. 1).

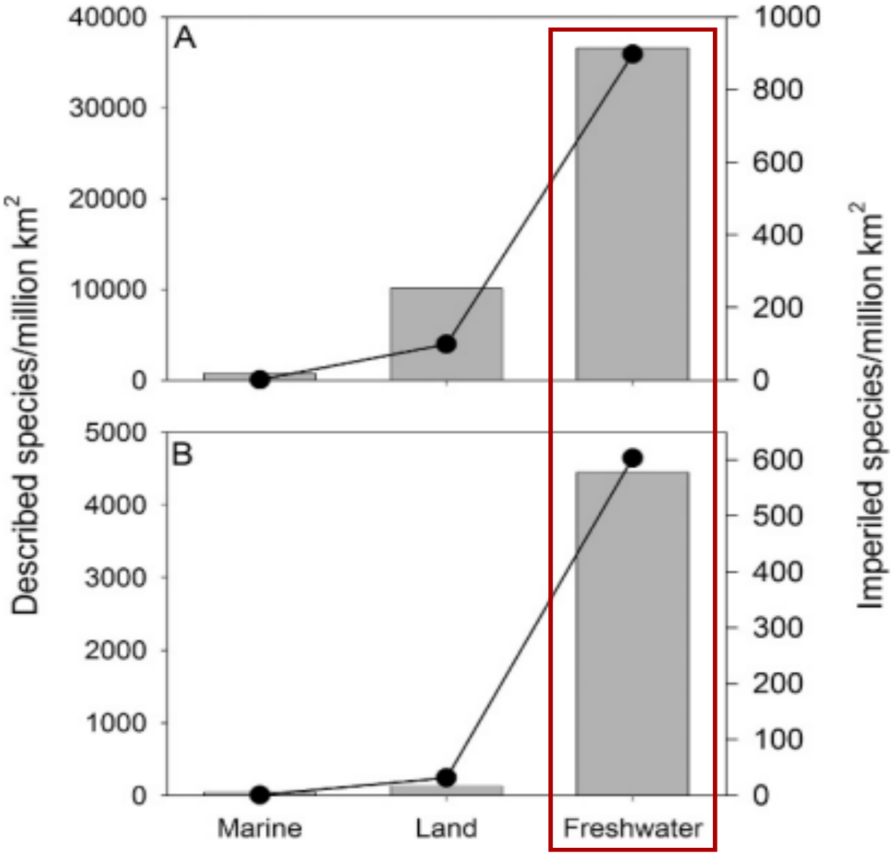

Figure 1. The number of described (bars) and imperilled species (lines) of eukaryotes (A) and chordates (B) in freshwaters is much higher than would be expected from the area of the globe covered by freshwater habitats. Modified from Strayer & Dudgeon 2010.

0.2 Threats to freshwater biodiversity

Freshwater environments comprise 0.01% of the water on Earth, covering 2.3% of the global land surface area (Lehner et Döll, 2004), but represent a disproportionate portion of plants and animal diversity with more that 40% of global fish diversity and a quarter of global vertebrate diversity (Dudgeon *et al.*, 2006). Furthermore, freshwater ecosystems provide key services contributing directly and indirectly to human well-being, such as recreation, water for consumptive use, and the maintenance of fisheries (Dodds *et al.*, 2013). The large majority of the world's population are serviced by freshwater ecosystems (Green *et al.*, 2015). Despite the central role of freshwater ecosystem in both human well-being and natural biodiversity, these ecosystems are particularly at risk. Threats on freshwater ecosystems by anthropogenic stressors have now been widely recognized and detailed for the past two decades, since the United Nations General Assembly proclaimed an International Decade for action "Water for life" in 2003. In 2006, a seminal review identified over-exploitation, water pollution, flow modification, species invasion and habitat degradation as five major threats to freshwater biodiversity (Dudgeon *et al.*, 2006). Despite the recognition and definition of important threats, freshwater biodiversity has continued to decline at alarming rates (Collen *et al.*, 2014). Conservation efforts continue to be biased toward terrestrial systems (Di Marco *et al.*, 2017), protection of freshwater aquatic life is insufficient with 84% of freshwater threatened megafauna range unprotected (Carrizo *et al.*, 2017), and freshwater ecosystem still representing hotspots of endangerment (Reid *et al.*, 2019). A more recent review identified over-exploitation, habitat degradation, and invasive species as persisting threats to freshwater biodiversity (Reid *et al.*, 2019). Furthermore, freshwater ecosystems are now facing emerging challenges putting more pressure on biodiversity and the ecosystem services these environments provide for human societies (Reid *et al.*, 2019).

Freshwater ecosystems are increasingly at risk by multiple emerging stressors at multiple spatial scales that lead to the loss of sensitive species, and an overall reduction of biodiversity (Gatti, 2016). Indirect changes of freshwater abiotic environments that threaten biodiversity are climate change, harmful algal blooms, and the global reduction of calcium inputs (Reid *et al.*, 2019). Climate change has concerning effects on freshwater ecosystems mainly through important change in water temperature and altered discharge (Ficke *et al.*, 2007 ; Heino *et al.*, 2009). For example, drying events in many freshwater systems have been rising in frequency and intensity (Datry *et al.*, 2016), which can have negative effects on biodiversity (Hastie *et al.*, 2003). The warmer temperature combined with eutrophication (Downing, 2014) and arid conditions have made favorable conditions for the surge of harmful algal blooms (Huisman *et al.*, 2018). Harmful algal blooms have direct toxicity and reduce water dissolved oxygen availability (Merel *et al.*, 2013), choking freshwater biodiversity. Human activities are indirectly changing freshwater ecosystems' biotic environment through new vectors of invasive species, and the rise of infectious diseases (Reid *et al.*, 2019). Invasive species are one of the primary threats to freshwater biodiversity, but developing vectors pose emerging conservation challenges. The surge of electronic commerce in plant and animal trade (Humair *et al.*, 2015), combined with the change in societal attitude towards unusual pets (Prokop et Randler, 2018) are posing new challenges for the monitoring and control of invasive species in freshwater ecosystems. The increased flow of exotic pets and wildlife is increasing the spread and transmission of infectious diseases, further facilitated by the aquatic medium preventing desiccation (Okamura et Feist, 2011). Introduced diseases can have dramatic impacts on native biodiversity by extirpation or local extinction of hundreds of species (Rödder *et al.*, 2009). Direct emerging anthropogenic habitat degradation and pollution are also threatening freshwater ecosystems (Reid *et al.*, 2019). Expanding hydrological power installations are restricting freshwater organismal movement, population connectivity, and dispersal (Juracek, 2015). Nanomaterials and microplastics are emitted at alarming rates in ecosystems which are ultimately consumed by organisms causing various deleterious effects to freshwater biodiversity (Geyer *et al.*, 2017 ; Stone *et al.*, 2010). Salinization of freshwater is occurring at an unprecedented rate and scale (Kaushal *et al.*, 2018). Salinization of freshwater has been shown to have negative effects on biodiversity but still lacks global synthesis and precise guidelines for conservation (Herbert *et al.*, 2015). Furthermore, the emerging stressors are interacting together and with existing stressors, and could have unexplored cumulative effects on freshwater biodiversity (Reid *et al.*, 2019). In my thesis, I will focus my attention on invasive species, an established threat to freshwater biodiversity, and salinization, an emerging threat to freshwater biodiversity (Reid *et al.*, 2019).

0.3 Impact of invasive species on natural ecosystems

Invasive species are a major threat to freshwater biodiversity and have been recognized as such for more than 15 years (Dudgeon *et al.*, 2006). Human influences have increased the transfer of species between regions faster and farther than ever before in the past (Ricciardi *et al.*, 2013). Invasive species have generally been documented to negatively affect the abundance and diversity native communities in their introduced range (Azour *et al.*, 2015 ; Barton *et al.*, 2005 ; Burkett et Jude, 2015 ; Hirsch *et al.*, 2016 ; Janáč *et al.*, 2016 ; Krakowiak et Pennuto, 2008 ; Kuhns et Berg, 1999 ; Lauer *et al.*, 2004 ; Lederer *et al.*, 2008). The loss of native species can result from the dominance of invasive species in invaded habitats (Daehler, 2003 ; Pysek *et al.*, 2007 ; Richardson *et al.*, 1989). To investigate community impacts of invasive species in the field, comparing invaded and uninvaded plots can allow identification of effects of invasive species and help provide relevant information for management and conservation of natural ecosystems (Manchester et

Bullock, 2000). Individual invasive species have different impacts on diversity and composition of native communities (Hejda *et al.*, 2009). Aquatic invaders have been found to generate a generalized negative impact on abundance and diversity of communities, especially on fish, zooplankton and macrophytes (Gallardo *et al.*, 2016). Several studies have emphasized that invaders impacts are context-dependent, and are variable between habitats and species (Ricciardi *et al.*, 2013 ; Ricciardi et Atkinson, 2004). For example, dreissenid mussels impacts are much more prevalent on fine sediment than rock habitats, because mussels patch allow quick colonization by fauna that is otherwise unable to establish on fine sediment habitats (Ward et Ricciardi, 2007). Multiple trophic levels can be impacted by the presence of invasive species and are associated with the trophic position, and the ability of the invader to modify its environment (Maggi *et al.*, 2015 ; Thomsen *et al.*, 2014). Trophic impacts can propagate up and down in the food web, or they can dissipate within functional level most likely through compensatory effects (Pace *et al.*, 1999). Invasive species have also been documented to totally disrupt community assembly or even disassemble communities by rendering local community structure random and weakly aggregated (Sanders *et al.*, 2003). Such drastic changes in local communities triggered by invasive species can affect important processes at the ecosystem scale.

Invasive species inflict serious impacts on fundamental ecosystem processes for human well-being, defined as security, freedom, secure livelihoods, health and good social relations (Pejchar et Mooney, 2010). Changes caused by invasions can have global consequences on human societies (Douglas, 2018), these impacts include alteration or loss of goods (forest and agricultural products, fisheries) and services (recreation, clean drinking water, pollination, climate stabilization and culture) (Aitkenhead-Peterson et al., 2010). The economic impacts of invasions are wide ranging but astoundingly high, for example estimated to 14.45 billion US$ in China (Xu *et al.*, 2006), and ranging from 131 billion US$ cumulative to 128 billion US$ annually in the USA (Pimentel *et al.*, 2005). Ecosystem impacts of invasive species can be classified as both direct and indirect. Direct ecosystem impacts of invasive species can be defined as differences in stocks and variations in energy and materials appearing solely as a result of invasive presence and/or activities (Gutiérrez *et al.*, 2014). For example, zebra mussels filter feeding activity has a direct biotic effect on production and phytoplankton biomass (Vidal *et al.*, 2004). Indirect ecosystem impacts develop when invasive species changes the abundance or the activity rates of other species that itself alter ecosystem function (Gutiérrez *et al.*, 2014). The filter feeding activity of zebra mussel on phytoplankton increased water clarity, which in turn increased macrophyte production (Strayer *et al.*, 1999 ; Zhu *et al.*, 2006). Ecosystem impacts of invasive species have important consequences for natural communities and human societies. These consequences can develop rapidly but some effects can appear on longer time scales.

Invasive species impacts on natural communities and ecosystems can substantially change over time (Strayer *et al.*, 2006). With time, the magnitude of impacts can be modified by environmental changes, ecological or evolutionary dynamics in the community, and the accumulation of novel natural enemies by invasive species (Flory et D'Antonio, 2015 ; Karatayev *et al.*, 2018 ; Ricciardi *et al.*, 2013 ; Strayer *et al.*, 2006). Invaders can display changes through both non genetic responses including shifts in morphology, physiology, gene expression, and resource allocation within the lifespan of individuals (Strayer *et al.*, 2006). Such acclimatization can strongly modify community and ecosystem processes (Eviner et Chapin III, 2003), and might be especially important in invasive species which tend to be highly plastic (Daehler, 2003). Invasive species can also evolve to match locale environmental conditions (Hodgins *et al.*, 2018), avoid local enemies (Wolfe *et al.*, 2004), or use local species as food resources (Sammons *et al.*, 1997). Adaptation of invasive species through genetic responses can increase their local population size or range, and in turn their ecological effects (Strayer *et al.*, 2006). The time needed for genetic changes could explain the lag often observed between invader arrival and sharp increase in its population growth (Crooks, 2005). Changes in the community that has been invaded can also modulate invasive species impacts. Diseases, parasites and predators of the invasive can arrive and proliferate by taking advantage of the new resource the invader provides to them (Petrie et Knapton, 1999). The resident community composition can shift toward more resistant species after long term presence of an invasive species which can moderate the initial severe impacts over time (Sharp et Whittaker, 2003 ; Vanderploeg *et al.*, 2011). Analogous to changes in invasive species, resident species can display genetic or phenotypic changes after invasion, adapting to better use invasive as food or habitat (Hare, 1990), or better resist the invader (Callaway *et al.*, 2005 ; Phillips et Shine, 2004). Lastly, natural or invasive induced abiotic changes have the potential to modify invasive impacts over time (Beekey *et al.*, 2004 ; Schwindt *et al.*, 2004). Understanding long term effects of invasive species is therefore crucial to better predict and manage their impacts over long periods of time. However, in spite of the potential for invasive species to change in abundance and in impact over time, most studies lack temporal context and have focused on the early stages of invasion (Flory et D'Antonio, 2015 ; Hirsch *et al.*, 2016 ; Ricciardi *et al.*, 2013 ; Strayer *et al.*, 2006).

Ponto-Caspian species (originating from the Azov, Black and Caspian Seas, and adjoining estuaries and rivers) have invaded numerous brackish and freshwater habitats of the Laurentian Great Lakes – St. Lawrence River region, and North and Baltic Seas in the past few decades (Casties *et al.*, 2016 ; Pauli *et al.*, 2018). Interestingly, North and Baltic Seas, and the Great Lakes – St. Lawrence River region represent very different habitat types, with the North and Baltic Seas being mostly marine and brackish environments, while the Great Lakes – St. Lawrence River region is mostly freshwater (Antonov *et al.*, 2006). Invasion by Ponto-Caspian species have occurred at much higher rates than expected from commercial shipping exchanges and local environmental conditions (Casties *et al.*, 2016). The particular success of Ponto-Caspian species has been linked to their salinity tolerances and capability to rapidly adapt to a large range of salinity (Casties *et al.*, 2016). The Ponto-Caspian region has a wide range of salinity with a long and complex geologic evolution involving periodic connections of large lakes with salt water, and a succession of inter-bassin connection and isolation (Reid et Orlova, 2002). Ponto-Caspian species have therefore experienced habitats with freshwater, brackish, and marine characteristics. The complex and diverse nature of Ponto-Caspian species evolutionary history seem to have resulted in euryhaline (broad salinity tolerance) faunal groups with important adaptive capabilities (Reid et Orlova, 2002). More than 90% of of Ponto-Caspian invaders are found in freshwater habitats, and the majority of Ponto-Caspian invaders occupy freshwater and brackish habitats In their native region (Pauli et Briski, 2018). Furthermore, experimental selection on marine amphipods showed that adaptation to lower salinity was more successful than to higher salinity, pointing towards freshwater origin of some Ponto-Caspian invaders which could explain their success in freshwater habitats (Pauli *et al.*, 2018).

Ponto-Caspian invaders are very successful in the Great Lakes – St. Lawrence River region with 70% of invasion discovered since 1985 being native to fresh and brackish waters of the Ponto-Caspian region (Ricciardi et MacIsaac, 2000). The recent influx of Ponto-Caspian species in the region has been related to both their euryhalinity, and increasing success in European ports in the past decades (Leppäkoski *et al.*, 2002). The widely cited ‘biological resistance model’ states that species-rich communities are more resistant to invasion because resources are more completely utilized, and competitors and predators are more likely to be present compared to species poor communities (Elton, 2020). However, different Ponto-Caspian invaders have had great success in the Great Lakes – St. Lawrence River region, and successfully invaded a broad range of communities which challenges the biological resistance model. For example, the planktonic crustacean *Ceropagis pengoi* became established in Lake Ontario (MacIsaac *et al.*, 1999) which has the highest rate of planktivory among the Great Lakes (Mills *et al.*, 1995). Similarly, despite the presence of competitors the amphipod *Echinogammarus* rapidly colonized the Great lakes (Dermott *et al.*, 1998). The pattern of invasion despite relatively rich native communities suggest that the Great lakes – St. Lawrence region is experiencing an 'invasional meltdown' (Ricciardi, 2001). 'Invasional meltdown' happens when successive invasions facilitate further invasions by repeated perturbation of the invaded system, and providing interaction between co-evolved invaders (Simberloff et Von Holle, 1999). This phenomenon might explain the success of the round goby facilitated by the establishment of large populations of zebra mussels on the invasive fish prey in its native range (Ricciardi, 2001). In the Upper St. Lawrence River, Ponto-Caspian invaders seem to be less successful compared to the Great Lakes. The reduced success of dreissinid mussels, the round goby and *Echinogammarus* has been attributed to several factors, such as substrate characteristic for dreissinid mussels (Kipp *et al.*, 2012), and water conductivity for the round goby and *Echinogammarus* (Iacarella et Ricciardi, 2015 ; Kestrup et Ricciardi, 2010). Despite potential facilitation between Ponto-Caspian invaders, such study show that environmental heterogeneity is capable of modifying species distributions and interactions in highly impacted habitats like the Upper St. Lawrence river.

0.4 Environmental heterogeneity and freshwater invasions

Environmental heterogeneity is regarded as one of the most important factors promoting diversity (Stein *et al.*, 2014). Environmental heterogeneity benefits biodiversity through multiple mechanisms. First, by increasing the amount of habitat types, resources, and complexity in the environment, environmental heterogeneity should increase the available niche space which should allow more species to thrive (Tews *et al.*, 2004). Second, areas with environmentally heterogeneous conditions are more likely to provide shelter and refuges from adverse environmental conditions, such as climate change and invasive species, which can in turn benefit species persistence (Fjeldså *et al.*, 2012 ; Kallimanis *et al.*, 2010). Lastly, the probability of speciation arising from adaptation or isolation to diverse environmental conditions should be greater in more heterogeneous landscapes (Antonelli et Sanmartín, 2011 ; Hughes et Eastwood, 2006). Environmental heterogeneity can impact connectivity between populations (Bricker *et al.*, 2011 ; Godhe *et al.*, 2016 ; Nanninga *et al.*, 2014 ; Peterman et Semlitsch, 2013) which can in turn affect genetic diversity (Bachmann *et al.*, 2019 ; Botigué *et al.*, 2013 ; Epps *et al.*, 2005 ; Pavlova *et al.*, 2017). With environmental heterogeneity in a variety of environmental dimensions (temperature, conductivity, salinity, substrate types…), the intraspecific genetic and phenotypic variation in species is likely to be increased, and this can determine how organisms respond to selection pressure (Hendry *et al.*, 2011).

In the context of invasive species, environmental heterogeneity could potentially allow communities to buffer invasive impacts through ecological and evolutionary processes by providing increased inter- and intraspecific variation. Environmental heterogeneity can promote the coexistence between native and invasive species (Melbourne *et al.*, 2007 ; Strauss *et al.*, 2006), which is crucial for potential adaptation of native species to exotic invasion because community interactions need to be maintained so that evolutionary diversification in native species can occur (Haloin et Strauss, 2008). Furthermore, by enhancing biodiversity, environmental heterogeneity can increase the diversity of responses that communities can provide to ecological changes caused by exotic invasion, which can in turn enhance the capacity of communities to buffer environmental change through compensation and compensatory dynamics (Gonzalez et Loreau, 2008). Environmental heterogeneity is therefore likely to be important in enhancing biodiversity, and limiting negative impact in invaded ecosystems by providing habitats refuge that limit the spread of invasive species (Melbourne *et al.*, 2007 ; Ricciardi *et al.*, 2013 ; Vander Zanden *et al.*, 2017).

Refuges to invasion can be defined as discrete or continuous habitats with lower abundance of invasive species relative to surrounding areas. Environmental heterogeneity can create refuges from biological invasion by interacting with invasive species habitat preferences and ecological tolerances (Anton *et al.*, 2014 ; Tamme *et al.*, 2010). Wetlands are good examples of how environmental heterogeneity can provide refuges from biological invasions. Wetlands contribute to shoreline aquatic habitats environmental heterogeneity (Krieger, 1992) by providing structurally complex and highly productive habitats (Wetzel, 1990). Wetlands are known to increase freshwater biodiversity (Céréghino *et al.*, 2008 ; Thiere *et al.*, 2009), and can disproportionately support regional biodiversity compared to other water-body types (Williams *et al.*, 2004). Furthermore, wetlands have been shown to be unfavorable environments for aquatic invaders such as zebra mussels (Bowers et Szalay, 2004) and round gobies (Cooper *et al.*, 2007, 2009 ; Young *et al.*, 2010). Another factor limiting the abundance of invasive species and creating refuges in freshwater is water conductivity, which seem to be particularly important for certain Ponto-Caspian invaders (Iacarella et Ricciardi, 2015 ; Jones et Ricciardi, 2005 ; Kestrup et Ricciardi, 2010 ; Whittier *et al.*, 2008). The exact mechanisms by which low water conductivity limits Ponto-Caspian invaders are still not clear, however several studies have proposed that low calcium could be one of the important limiting ion (Iacarella et Ricciardi, 2015 ; Jones et Ricciardi, 2005 ; Whittier *et al.*, 2008). Calcium ion is especially important for shelled organisms such as mussels (Jones et Ricciardi, 2005), but is also for crustaceans (Kestrup et Ricciardi, 2010 ; Palmer et Ricciardi, 2004) and fish invaders (Baldwin *et al.*, 2012). The low water conductivity limitations of Ponto-Caspian invaders has been related to their euryhalinity and brackish water evolutionary history (Baldwin *et al.*, 2012 ; Iacarella et Ricciardi, 2015 ; Jones et Ricciardi, 2005). However, other ions can limit the growth and reproduction of aquatic organisms (Griffith, 2017), and calcium might not be the only limiting ion in low conductivity freshwater habitats.

Water conductivity is a measure of the ease of electrical current flow in a solution which generally increases with the number of ions, and reflects ion concentrations

(Williams et Sherwood, 1994). For limnologists, salinity is regarded as the total concentration of the major ions in terms of mass per unit of volume (Wetzel, 2001). Therefore, water conductivity is one the most widely used measure of salinity, but it is an indirect measure, and relationships between salinity and conductivity are not straight forward (Williams et Sherwood, 1994). The relationships between conductivity and salinity are non-linear, and depend on the ions present in the water, their concentration, and the temperature (Niekerk *et al.*, 2014). Conductivity can therefore give reasonable estimates of freshwater salinity in regions with some homogeneity in water ionic composition. Freshwater salinity is usually defined as lower than 0.5 parts per thousand (ppt) of dissolved salts (Hammer, 1978), and lower than 1 ppt by other sources (Dugan *et al.*, 2017b). Rivers and lakes have a wide range of salinity, from less than 0.01 ppt (Eilers *et al.*, 1990) to 1 ppt depending of the definition of freshwater and brackish water (Dugan *et al.*, 2017b). Salinity is a key environmental factor for aquatic organisms that need to regulate their ion content for different physiological mechanisms, and maintain adequate concentration within cells (Griffith, 2017). Salinity gradients in aquatic ecosystems are considered one of the most important abiotic factors shaping species geographical distribution (Rahi *et al.*, 2018). Osmoregulation is the main function for maintaining the ionic balance between body fluids and the environment (McNamara *et al.*, 2015). The ability for osmoregulation of organisms is greatly influenced by evolutionary history, and past environmental salinity conditions experienced by populations (Lee *et al.*, 2011). Local and regional environmental salinity levels, and historical condition can therefore greatly influence species and communities (Arnott *et al.*, 2020 ; Moffett *et al.*, 2021 ; Reid et Orlova, 2002). Recently, freshwater ecosystems have experienced global increases in concentrations of different salts (Dugan *et al.*, 2017a ; Stets *et al.*, 2020), which are having important negative consequences on the composition and diversity of aquatic communities (Velasco *et al.*, 2019).

0.5 Impact of Chloride on freshwater biodiversity

Natural salt and minerals provide major ions contained in freshwater but a dramatic increase in salt ions is occurring across local, regional, continental, and global scales (Kaushal *et al.*, 2021) (Fig. 2). All types of freshwater ecosystems, lakes, wetlands, streams and rivers, are affected by human induced salinization, and this issue is a growing threat for these valuable ecosystems. Approximately 1/3 of freshwater bodies are affected by salinization, and this number is expected to increase in the future due to human induced environmental change (Cañedo-Argüelles, 2020).

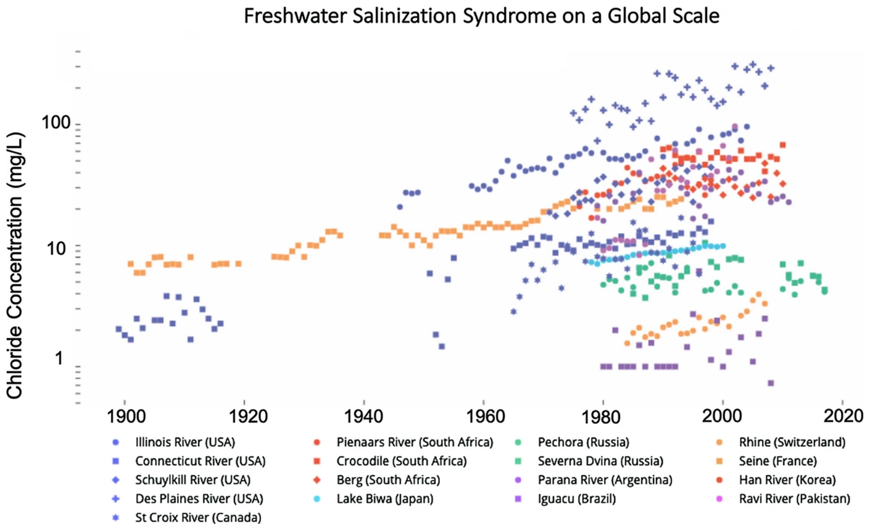

Figure 2. Increasing Cl− trends in freshwaters globally. From Kaushal et al., 2021

Salinization of freshwater ecosystem has several sources such as mining, agriculture, vegetation clearance, sea level rise, regulation of river hydrology and the application of road deicing salts (Albecker et McCoy, 2017 ; Herbert *et al.*, 2015 ; Hintz et Relyea, 2019 ; Schuler *et al.*, 2019). Impacts of human induced salinization are not limited to small ecosystems and local scales; some of the largest bodies of freshwater, such as Lake Constance in Europe, have had salinity levels more than double in the past 40 years (Müller et Gächter, 2012). There is evidence for widespread impacts of freshwater salinization on a global scale (Cañedo-Argüelles *et al.*, 2013 ; Herbert *et al.*, 2015). The complex interactions and relationships between salt ions and chemical, biological, and geologic factors, and consequences on the environment is called the Freshwater Salinization Syndrome (Kaushal *et al.*, 2018, 2019). Increasing salinization of freshwater environments has been occurring for over a century without recognition or regulation despite its adverse effects on freshwater environments (Kaushal *et al.*, 2021). However, freshwater salinization has received more attention in the past two decades and studies have found that salinization causes deleterious effects to the fitness and survival of many aquatic organisms (Cañedo-Argüelles, 2020).

An increase in salinity levels can have devastating impacts on every trophic level constituting freshwater food webs, from basal primary producers to top predators. Increasing levels of salt in freshwater ecosystems strongly reduces biodiversity (De Castro-Català *et al.*, 2015 ; Vander Laan *et al.*, 2013), and one of the stressors with the highest potential impacts on aquatic life (Velasco *et al.*, 2006). The negative effects of salinization on freshwater biodiversity are occurring at both taxonomic and functional levels (Suárez *et al.*, 2017 ; Szöcs *et al.*, 2014). Biodiversity reduces rapidly with increasing salt levels, and most freshwater organisms are extirpated over 4 g/L but this threshold varies greatly between taxa (Cañedo-Argüelles, 2020). Most freshwater ecosystems have salt levels below the Canadian (160 mg/L) (Environment

Canada and Climate Change, 2011) and US (230mg/L) (US EPA, 1988) thresholds, and ecological impacts have been shown to occur at lower concentrations (Hintz et Relyea, 2019). Furthermore, ecosystem pollution occurring through application of road salt in colder regions is not slowing, and concentration are still rising (Dugan *et al.*, 2017b ; Kaushal *et al.*, 2018). Higher trophic levels such fish species exhibit relatively high tolerance with negative sub-lethal effects at concentrations of 3,000 mg/L (Hintz et Relyea, 2017), and tolerance to very high concentrations (15,200 mg/L) (Nordlie et Mirandi, 1996). However, basal trophic levels, such as phytoplankton and zooplankton have been found to be more sensitive (Hintz et Relyea, 2019). Furthermore, phytoplankton and zooplankton are playing key functional roles in freshwater ecosystems for the production and transfer of energy to higher trophic levels consumers. Changes in the basal composition and diversity of freshwater ecosystems could have important consequences on ecosystem structure and functioning, leading to partial or total collapse of their food webs (Ledger *et al.*, 2013 ; Rooney et McCann, 2012 ; Tylianakis et Morris, 2017). It is therefore crucial to understand how phytoplankton and zooplankton communities are impact by salinization in order to efficiently manage freshwater ecosystems, and conserve the important resources they represent for human well-being.

Both positive and negative impacts of salinization have been reported on phytoplankton diversity and composition (Hintz et Relyea, 2019). However, salinization has been reported to negatively impact abundance, growth and diversity of certain phytoplankton groups such as diatoms (Porter-Goff *et al.*, 2013). Different phytoplankton groups have varying nutritional values, and highly nutritious phytoplankton, such as diatoms, are important food sources for higher trophic levels because of their particular fatty acid profiles (Taipale *et al.*, 2013). The quality and quantity of fatty acids provided by phytoplankton is crucial for the condition, development, reproduction and resilience of higher trophic levels organisms (Isanta-Navarro *et al.*, 2021 ; Taipale *et al.*, 2013). However, despite their crucial importance in freshwater food webs our understanding of salinization impacts on phytoplankton is still deficient (Hintz et Relyea, 2019).

Transferring the energy of primary producers is a crucial role played by zooplankton in freshwater ecosystems. Salinization has negative effects on the survival and reproduction of the three major zooplankton groups (cladocerans, copepods and rotifers) (Corsi *et al.*, 2015 ; Ives et Lawrence, 2018 ; Searle *et al.*, 2016). However, the different zooplankton groups seem to exhibit quite a lot of variation in their sensitivity to salinization. Cladocerans have been identified as fairly resistant to increased salt concentrations (Lind et Jeyasingh, 2018 ; Moffett *et al.*, 2021 ; Sarma *et al.*, 2006 ; Searle *et al.*, 2016), with *Daphnia* populations resisting to 860 mg/L of chloride (Hintz et Relyea, 2017). However, other *Daphnia* populations have shown greater sensitivity with increased mortality at 5-40 mg/L of chloride (Arnott *et al.*, 2020). The variability in resistance to high salt concentrations is also present in copepods. Cyclopoids seem more resistant maintaining high abundance over 500 mg/L (Moffett *et al.*, 2021 ; Van Meter et Swan, 2014), while calanoids decreased in abundance at 200 mg/L (Evans et Frick, 2001 ; Moffett *et al.*, 2021). More research is therefore needed to investigate resistance to salinization in more taxa within zooplankton groups, and elucidate the factors influencing the variability that has already been uncovered. Recent studies on zooplankton have advocated that resistance to elevated salt concentration in freshwater was probably linked to local and regional conditions, and previous exposure to salt in zooplankton populations (Arnott *et al.*, 2020 ; Moffett *et al.*, 2021). Investigating salinization effects on zooplankton is therefore crucial to have a better understanding of zooplankton sensitivity to salinization, and the impacts that could cascade to higher trophic levels (Hintz et Relyea, 2019). Overall, salinization affects freshwater biodiversity at all trophic levels, but the concentrations at which impacts are reported are highly variable, and more studies are needed to better understand this global threat that salinization represents to freshwater ecosystems and human well-being.

0.6 Thesis objectives

This thesis addresses the overarching question: How anthropogenic stressors impact aquatic biodiversity and the structure of communities in freshwater ecosystems ? (Fig 3) To understand the community consequences of anthropogenic stressors, both experimental and natural gradients can be powerful tools, especially to understand what can be the long term effects on natural communities (Fukami et Wardle, 2005). Contributing to the knowledge on biodiversity responses to anthropogenic stressors and how natural gradients can mitigate impacts is crucial to inform efficient conservation and management of freshwater ecosystems. To help improve our understanding of anthropogenic impacts on freshwater biodiversity, this thesis has three main objectives. The three objectives will be detailed in three separate chapters, in the form of three scientific manuscripts:

i What are the long term effects of an invasive species along a gradient of historical presence ? (referred to in text as Astorg et al. 2020)

ii How can natural gradients in the form of environmental heterogeneity mitigate invasive impacts on resident communities ? (referred to in text as Astorg et al. *in review*)

iii What are the impacts of salinization on pristine freshwater planktonic food webs, and how do they relate to water quality guidelines ? (referred to in text as Astorg et al. *Submitted*)

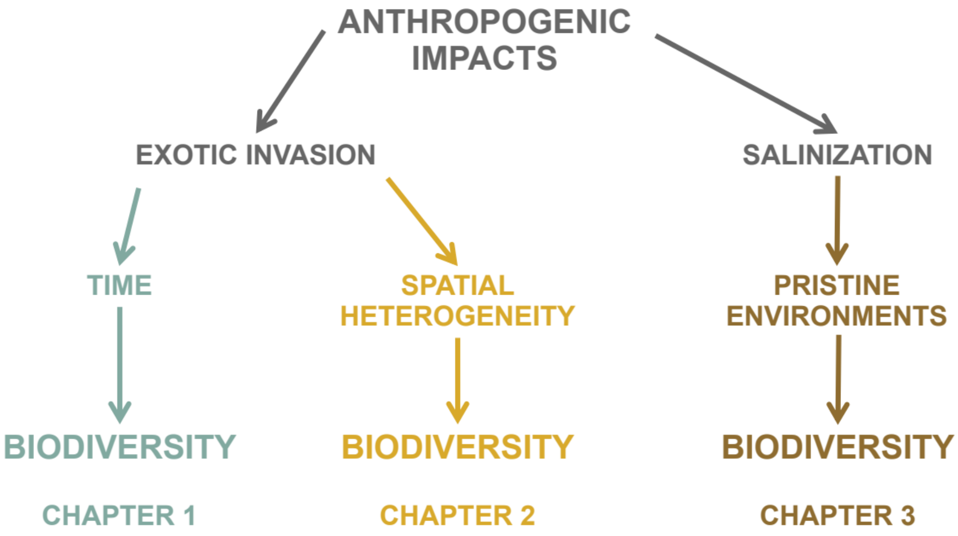

Figure 3. Thesis chapters conceptual diagram

0.7 Study system

0.7.1 The invasion of exotic round goby fish in the Upper St-Lawrence River

In CHAPTER 1 and CHAPTER 2, I will focus my attention on the St. Lawrence River, Canada, in the upper stretch from upstream of the City of Cornwall, Ontario to the City of Montréal at Lake St-Louis, Québec. The St. Lawrence River – Great Lakes system is the second largest river network in North America (Thorp *et al.*, 2005), and is an socially, economically and ecologically important river-lake system. The importance of this river – lake system stems from the amount of freshwater it holds, with roughly 18% of global freshwater (Botts et Krushelnicki, 1987). In this system, the St. Lawrence River main stem is ranked among the top 16 rivers in the world with regard to annual discharge, and the second highest flow in North America (Thorp *et al.*, 2005). Historically, the St. Lawrence River has been very important for first nations culture, transportation and livelihood, which have been established along the river since 1100 (Thorp *et al.*, 2005). Today millions of peoples in both Canada and the United States live near the St. Lawrence River, with important city centers such as Ottawa, Montreal and Quebec City on its banks. The St. Lawrence River is critical for the economy of Canada and the United States, with tens of thousands of commercial vessels trip every year, and millions on metric tons of goods passing through the Lake Ontario-Montreal section of the river each year (MacFarlane, 2014). Today, the commercial exchanges between Canada and the United States going through the St. Lawrence River represent 30% of combined Canadian and United States economic activity and employment (Kavcic, 2018). The St. Lawrence River is equally remarkable for its biological features, and is listed as continentally outstanding (Abell *et al.*, 2000). The ecological significance of the St. Lawrence River resides in its extreme diversity of wetlands and fish habitats, and rich fauna and flora (Thorp *et al.*, 2005). However, the St. Lawrence River is on the most invaded freshwater system in the world (Ricciardi, 2006). Transoceanic shipping important traffic, and release of exotic species through ships ballast waters is one of the main vectors of exotic invasion in the St. Lawrence River and the Great Lakes (Pagnucco *et al.*, 2015). Since the opening of the Great lakes – St. Lawrence Seaway, a new non-native species has been identified every 8 month on average (Ricciardi, 2006). A number of non-native species have been demonstrating negative community and ecosystem impacts, such as the Spiny waterflea (*Bythotrephes longimanus*), Zebra mussel (*Dreissena polymorpha*), Quagga mussel (*Dreissena bugensis*), Round goby (*Neogobius melanostomus*) and many others (Pagnucco *et al.*, 2015).

0.7.2 Round goby invasion

Round goby invasion in the St. Lawrence River – Great Lakes system has had devastating impacts on the abundance and diversity of both macroinvertebrate and fish communities (Brownscombe et Fox, 2013 ; Burkett et Jude, 2015 ; Kipp *et al.*, 2012 ; Raby *et al.*, 2010). The round goby was first reported in Lake St. Clair in 1990 and quickly spread to all five Great Lakes of North America (Charlebois *et al.*, 2001). The round goby was first detected in the St Lawrence River near Cornwall, ON in 2004 (Hickey et Fowlie, 2005). Round gobies then progressed rapidly down the Upper St-Lawrence River (Morissette *et al.*, 2018). Round goby populations quickly increased in abundance at sites where they had colonized (Morissette *et al.*, 2018). In the St. Lawrence River, invasive round goby fish have been reported to negatively impact benthic macroinvertebrate community diversity and biomass (Kipp et Ricciardi, 2012), with a particularly pronounced effect on molluscs (Kipp *et al.*, 2012). Fish communities are also impacted by round gobies, in particular benthic fish species such as the tessellated darter (*Etheostoma olmstedi*); these negative effects are likely occurring through competitive exclusion (Morissette *et al.*, 2018). However, some fish species have seen their abundance increasing as a result of relaxed competition and predation on the round goby (Morissette *et al.*, 2018). Round goby abundances in the St. Lawrence river are lower compared to the Great Lakes which has been attributed to sub-optimal habitat, lower dreissinid mussel densities and hydraulic conditions (Astorg *et al.*, 2021 ; Kipp et Ricciardi, 2012). Sub-optimal habitats in the Upper St. Lawrence River created a wide range of sites Time Since Invasion (TSI) among sites in this system (Kipp et Ricciardi, 2012). Furthermore, the confluence of the Upper St. Lawrence River and the Ottawa River at Lake St. Louis (N45220 12, W73490 12), a lacustrine widening of the St. Lawrence River, has created a conductivity gradient in which the north side of Lake St. Louis receives low conductivity water (10–15 mg/L of calcium) from the Ottawa River whereas the south side receives high-conductivity water (30–40 mg/L of calcium) from the St.

Lawrence River (Hudon et al., 2003). The invasive round goby are absent from areas that receive low conductivity water (10–15 mg/L of calcium) from the Ottawa River (Iacarella et Ricciardi, 2015 ; Kestrup et Ricciardi, 2010). Within these both the Ottawa and St-Lawrence River water masses, wetland are present. Wetland reduce round goby abundances in the Great Lakes (Cooper *et al.*, 2009 ; Young *et al.*, 2010) but it's potential to generate refuges for resident communities in high conductivity water of the Upper St-Lawrence River has not been investigated.

0.7.3 Experimental Salinization

In CHAPTER 3, I will discuss how a gradient of water chloride concentration impacts pristine planktonic food webs using an in-situ lake mesocosm experiment which was performed with water and biological communities from Lake Croche (Station Biologique des Laurentides). Lake Croche is a remote experimental lake that is naive to increased salinity and has very low ambient chloride (18 mg/L). Therefore, Lake Croche planktonic food web is totally naive to salinization stress. Local responses of aquatic communities and populations seem to be highly variable between taxa and regions (Cañedo-Argüelles, 2020 ; Hintz et Relyea, 2019). Recent studies have shown that local conditions, history of salinization and ambient chloride could be important in understanding the local response of aquatic organisms to salinization (Arnott *et al.*, 2020 ; Moffett *et al.*, 2021). However, the full spectrum of ambient chloride levels has not been explored, and few studies have investigated low ambient chloride ecosystem community responses to salinization. Canadian surface waters have a broad range of chloride concentration from less than 1 mg/L to more that 300 mg/L, but most Canadian watersheds have ambient chloride concentration under 20 mg/L, except watersheds including major urban centers or saline lakes (Mayer *et al.*, 1999). The experiment followed a regression design spanning nominal salt concentrations of ambient chloride (18 mg/L) to a highest concentration of 1100 mg/L. The mesocosm experiment was based on a protocol designed to test the effects of a single stressor, sodium chloride. The mesocosm experiment was completed during summer 2018 over six weeks during which I monitored chloride levels and the planktonic food web.

CHAPTER I

TWO DECADES SINCE FIRST INVASION : REVISITING ROUND GOBY IMPACTS ON NEARSHORE AQUATIC COMMUNITIES IN THE UPPER ST. LAWRENCE RIVER

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N.B. References cited in this chapter are presented at the end of the thesis

1.1 Abstract

Time Since Invasion (TSI) at invaded sites is an important factor that can moderate invasive species abundances and their ecological impacts on resident communities, and yet it remains rarely addressed by invasion studies. We revisit the ecological impacts of round goby invasion in the Upper St. Lawrence River (Canada) on macroinvertebrate and fish communities, by taking into consideration the effects of TSI since initial invasion 20 years ago. Our objectives were to: 1) test the effect of TSI and invasion status on round goby abundance, and 2) investigate the effects of TSI, invasion status, and round goby abundance on macroinvertebrate and fish communities. Round goby abundance displayed a strong positive relationship with TSI. Environmental conditions, especially substrate and water conductivity were found to reduce round goby TSI and characterize uninvaded sites and >12 years TSI sites. However, we detected first potential signals of a reduction in round goby abundance at sites with TSI of 17-19 years compared with sites having 13-16 years TSI which had similar environmental conditions. Nonetheless, round gobies continued to have enduring impacts on total macroinvertebrate diversity, even at sites with TSI of 17-19 years, likely as a result of ongoing predation. This observation was supported by a negative association of round goby TSI on the abundance of dominant macroinvertebrate taxa at sampling sites in the Upper St Lawrence River, as well as dietary stomach content data. The fish community was less sensitive to round goby TSI than macroinvertebrate communities. Our study highlights lasting effects of round goby invasion on macroinvertebrate and fish communities in the Upper St. Lawrence River, and the importance of integrating TSI with environmental conditions to improve our understanding of invasive species impact on resident communities over longer time periods.

Keywords: Invasion, Time Since Invasion, *Neogobius melanostomus*, round goby, St. Lawrence River

1.2 Introduction

The effects of invasive species on resident communities can substantially change over time because of evolutionary processes in both invasive and resident populations, shifts in resident community species composition, and changes to abiotic variables in the environment (Ricciardi et Macisaac, 2010). Over time, invasion impact can increase or decrease in magnitude because of environmental changes, ecological or evolutionary changes in the recipient community, and accumulation of natural enemies (Flory et D'Antonio, 2015 ; Karatayev *et al.*, 2018 ; Ricciardi *et al.*, 2013 ; Strayer *et al.*, 2006). However, a review by Strayer et al. (2006) found that only 40% of invasion studies state the amount of time since first invasion; most invasive species studies to date still lack a temporal context (reviewed in the following papers: Strayer *et al.,* 2006; terrestrial plants, Flory et D'Antonio, 2015; round gobies, Hirsch et al., 2016). Our study goal was to address the longer-term ecological impacts of the invasive round goby fish goby (*Neogobius melanostomus*) on resident aquatic communities, after two decades of TSI, in the Upper St. Lawrence River, Canada.

Invasive round gobies have generally been documented to negatively affect the abundance and diversity of aquatic resident communities of macroinvertebrates and fish in their introduced range, both in Europe (Azour *et al.*, 2015 ; Hirsch *et al.*, 2016 ; Janáč *et al.*, 2016 ; Ojaveer *et al.*, 2015) and North America (Barton *et al.*, 2005 ; Brownscombe et Fox, 2013 ; Burkett et Jude, 2015 ; Krakowiak et Pennuto, 2008 ; Kuhns et Berg, 1999 ; Lauer *et al.*, 2004 ; Lederer *et al.*, 2008 ; Raby *et al.*, 2010). Round gobies have therefore been extensively studied, and their impacts on both macroinvertebrates and fish communities investigated before and after arrival or along invasion fronts. However, the vast majority of round goby impact studies were undertaken within 5 years after first detection, and very few studies have investigated longer-term (over 10 years) effects of round goby invasion on resident communities (Gorman, 2021 ; Hirsch *et al.*, 2016). In Europe, one study describing sites with 16 years TSI found that crustaceans and molluscs were favored by round gobies for their diet, but this study did not relate the effects of round gobies on the macroinvertebrate or fish communities (Oesterwind *et al.*, 2017). In North America, only a handful of studies have addressed round goby TSI effects on resident aquatic communities (Great Lakes: Bailey, 2015, 2015; Burkett et Jude, 2015); two of these studies were done in the Upper St. Lawrence River (Kipp et Ricciardi, 2012 ; Morissette *et al.*, 2018). In the St. Clair River of the Lower Great Lakes, round goby abundance decreased since their initial invasion in 1990, between 1994-2011, and yet there was no consistent reduction in their impact in decreasing macroinvertebrate abundance (Burkett et Jude, 2015). In Lake Ontario, both composition and diversity changes in benthic communities were found to be greater after the invasion of round goby than other invaders, and resident gastropods and clams were lost (Bailey, 2015 ; Barrett *et al.*, 2016). In the Upper St. Lawrence River, Kipp and Ricciardi (2012) found that macroinvertebrate community composition varied significantly among samples grouped by TSI stage, but that macroinvertebrate diversity (Shannon) and dominance by large-bodied taxa declined with increasing TSI. Fish species were both negatively and positively affected by round goby invasion respectively through competitive exclusion and predation relaxation (Morissette *et al.,* 2018). However, over time and with longer TSI, there is the possibility that ecological impacts of round gobies stabilize following the removal of the most vulnerable species from resident communities, and as round goby abundances stabilize in relation to available resources (Karatayev *et al.*, 2018). Our study therefore revisits longer-term effects of round goby TSI in the Upper St. Lawrence River over two decades of invasion.

In this paper, we revisit the ecological impacts of round goby invasion in the Upper St. Lawrence River on macroinvertebrate (Kipp et Ricciardi, 2012) and fish (Morissette *et al.,* 2018) communities, by taking into consideration the effects of among-site variation in TSI since initial invasion 20 years ago. Our objectives were to: 1) test the effect of TSI on round goby abundance, and 2) round goby TSI would have a negative effect on macroinvertebrate community abundance and diversity, and 3) round goby TSI would have a negative effects on nearshore fish community abundances and diversity. To disentangle if round goby impacts were the result of the presence of round gobies rather than the time since they were first present at sites, we integrated both TSI effects and before/after invasion effects of round goby invasion. To do this, sites with null round goby abundance at the time of field collection in 2018 were considered uninvaded sites and sites where round gobies were captured were considered invaded sites (hereafter referred to as 'invasion status'). It is important to regularly assess invasion impacts for informing management measures, since invasive species such as round gobies have complex impacts on freshwater communities (Burkett et Jude, 2015), and the ecological impacts of invasive species can be maintained or change over time (Flory et D'Antonio, 2015 ; Strayer *et al.*, 2006).

1.3 Materials and Methods

1.3.1 Study System and Time Since Invasion (TSI)

The round goby was first reported in Lake St. Clair in 1990 and quickly spread to all five Great Lakes of North America (Charlebois *et al.*, 2001). Round gobies then progressed into the Upper St. Lawrence River, and were first recorded in Cornwall in 2004 (Hickey et Fowlie, 2005). Between 2004-2008, round goby populations were detected downstream of Cornwall to Lake St. Louis, where uninvaded locations remained in the Upper St. Lawrence River. Round goby invasion in the Upper St. Lawrence River was slower than in the Great Lakes, which has been attributed to sub-optimal habitat and hydraulic conditions (Astorg *et al.*, 2021 ; Brodeur *et al.*, 2011 ;

Kipp *et al.*, 2012). The confluence of the Upper St. Lawrence River and the Ottawa River at Lake St. Louis (N45220 12, W73490 12) creates a conductivity gradient from the north side of Lake St. Louis receiving low conductivity water (10–15 mg/L of calcium) to the south side receives high-conductivity water (30–40 mg/L of calcium) from the St. Lawrence River.

TSI for each sampling site was estimated using historical data, geographic position of the site, dominant substrate and round goby abundance. Historical data for round goby presence/absence were provided from Kipp et al. (2012) and Morissette et al. (2018). A total of 53 sites were sampled for this study (Fig. 1.1). Uninvaded sites were defined as sites with an absence of round gobies as detected by our sampling efforts. Sites that were not invaded in Lake St. Louis in the last surveys of the area (Kipp *et al.,* 2012; Morissette *et al.,* 2018) were identified as having TSI<12 years. Based on site-specific TSI provided by these two previous studies, sites upstream from Lake St. Louis and downstream of Cornwall were identified as having TSI between 13-16 years and sites upstream from Cornwall were identified as having TSI between 17-19 years. Between spring and fall of 2017-2020, we collected macroinvertebrate and fish community composition and abundance data from nearshore sites in the Upper St. Lawrence River (Lake St. Francis, Ontario and downstream), and in Lake St. Louis (Québec), Canada (Fig. 1.1).

1.3.2 Environmental site characteristics

Dissolved oxygen (DO; mg.L^{-1}), water temperature (ºC), and water conductivity (µS.cm-2) were measured using a Professional Plus Model YSI multi-parameter sonde (model 10102030; Yellow Springs Inc.). We also collected water samples to quantify total phosphorus (TP: µg.L^{-1}) and total nitrogen (TN; mg.L^{-1}). Detailed analytical methods for measured water chemistry variables are provided in ANNEX A. The dominant substrate was recorded at each site as recommended by the Ontario Benthos Biomonitoring Network (OBBN; Jones et al., 2006) (ANNEX A). We provide a Principal Coordinate Analysis (PCoA) to visualize how TSI groupings relate to environmental characteristics of the study sites (Fig. 1.2). PCoA of environmental variables were performed using Bray-Curtis dissimilarity matrix and the environmental matrix was squared to avoid negative eigenvalues.

Dreissenid mussels were collected for 27 of 53 sampling sites between 2018 and 2020. Three random quadrats of 0.25 m^2 were thrown on the substrate at each site. All individual dreissenids (quagga and zebra mussels combined) were hand-picked and counted per quadrat to determine site densities, which were calculated as the average of densities calculated for the three quadrats per site.

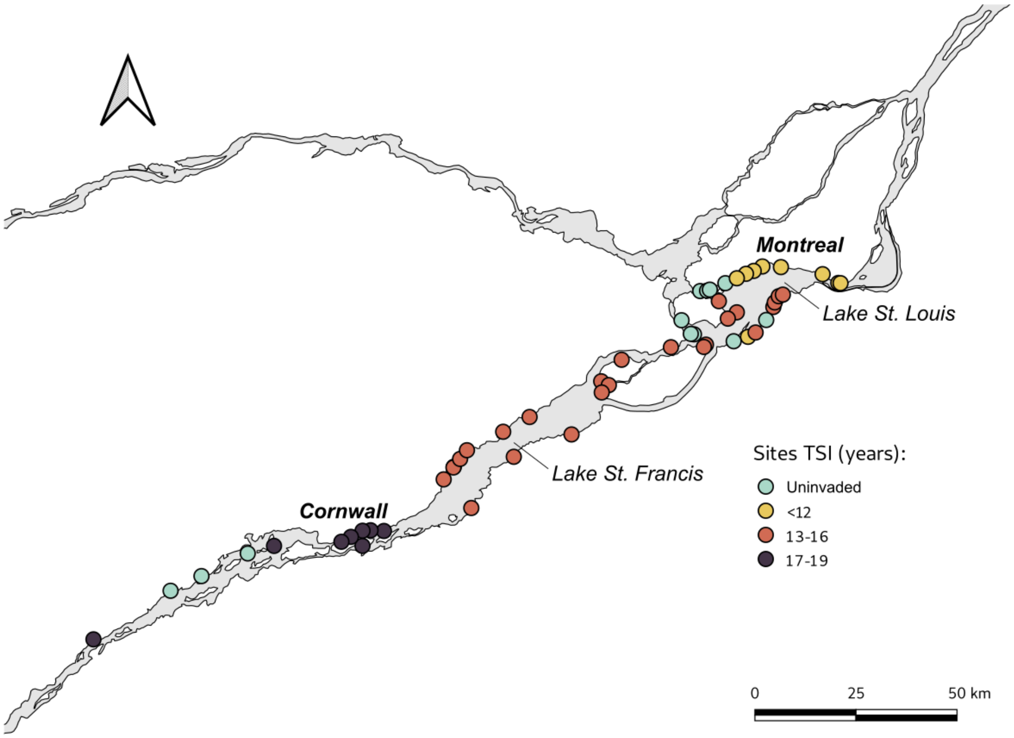

Figure 1.1: Map of Upper St. Lawrence River and sites of sample collection. The different symbols indicate sites with different Time Since Invasion (TSI): blue: Uninvaded; yellow: <12 years; orange: 13-16 years; purple: 17-19 years.

1.3.3 Community data collection

For nearshore macroinvertebrate community collection, all 53 sites were sampled between July and September on one single occasion. Three transects were randomly established to collect three samples at each site. Sampling was performed by the sweep method ("Kick and Sweep") running from the water's edge to 1 m depth with a 500 µm "D-net" as recommended by the Ontario Benthos Biomonitoring Network (Jones *et al.*, 2006). The collected samples were either preserved immediately in the field with 95% ethanol and the preserved samples were brought back to the laboratory at the Université du Québec à Montréal (UQAM), or live samples were brought back to the laboratory at the St. Lawrence River Institute for Environmental Sciences (River Institute). For each sample, we removed a measured portion (subsample) of the sample and each subsample was fully counted until no more invertebrates were found. If the 100th individual was not reached within the initial subsample, an additional subsample was counted. When the 100th individual was reached, the remaining part of the subsample was counted, and the total subsampled volume calculated. A ratio was then calculated between the total subsampled volume and the sample total volume to estimate the taxon-specific abundance of macroinvertebrates. The abundance in each site was estimated using the mean abundance of the three samples collected at every site. All macroinvertebrate samples were identified using SZX10 stereo microscopes (Olympus) with varying magnification (x6.3 – x10). In the laboratories at UQAM and the River Institute, identification was done up to the Order or Family level using a combination of information in OBBN protocol (Jones *et al.*, 2006), and following methods described in Merritt et Cummins, (1996), Moisan (2010), and Morse et al. (Eds) (2020).

For nearshore fish community collection, all sites were sampled between July and September on one single occasion. Each site was seined with three passes, with short (less than one hour) intermission periods between seining times. Fish were either placed into bins, identified and released after the three hauls or identified, counted, and released after each haul. A standardized beach seine net (30 feet long X 6 feet deep and 1/8 mesh) was used for sampling the nearshore littoral habitats (depth <1.5 m) on a distance of 10m. Species identifications were done according to Bernatchez et Giroux (2000).

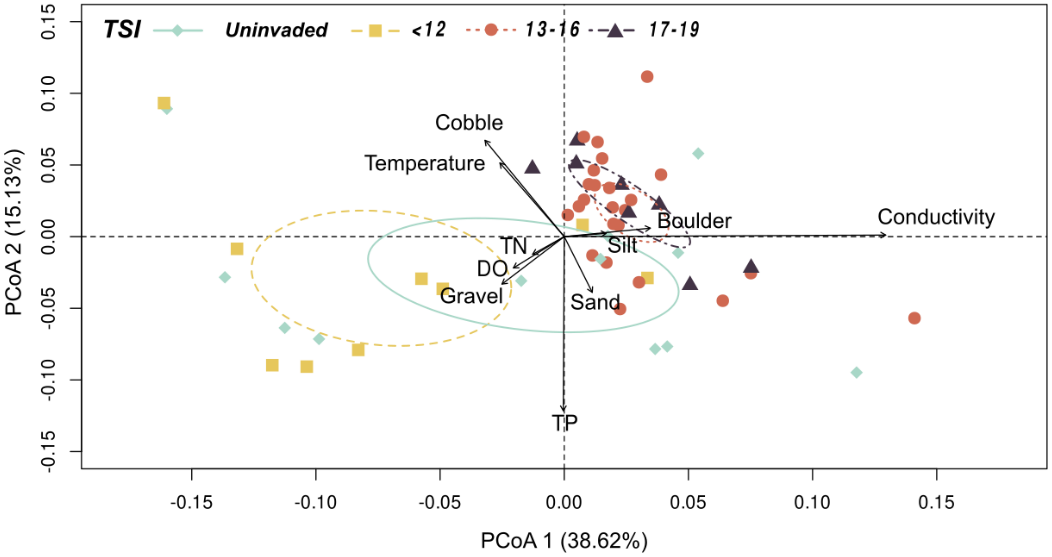

Figure 1.2: Environmental characteristics among sites with different Time Since Invasion (TSI) according to PCoA, with Bray Curtis dissimilarity matrix of squared macroinvertebrate taxon abundance. Blue diamond symbols represent uninvaded sites, yellow square symbols represent sites with TSI < 12, orange circle symbols represent sites with TSI between 13-16 years, and purple triangle symbols represent sites with TSI between 17-19 years. Vectors are the cosine directions of the squared environmental variables, scaled by their correlation with PCoA site scores. The ellipses are 95% confidence interval ellipses for the different TSI groups. The solid line ellipse represents uninvaded sites, the dashed line ellipse represents sites with TSI < 12 years, the dotted line ellipse represents sites with TSI between 13-16 years, and the dotted dash line ellipse represents sites with TSI between 17-19 years.

1.3.4 Round goby stomach contents

A total of 149 fish were collected from Lake St. Francis (N= 69) and Lake St. Louis (N=80) between July and September from 2018 to 2020. Individuals (9 to 18 per site) were sampled using the seining method at a subset of 13 out of the 53 study sites across Lake St. Francis (N=6) and Lake St. Louis (N=7). Upon capture, fish were immediately euthanized, measured, and brought back to the laboratory. Fish collected had a total length ranging from 39 mm to 110 mm. Since round gobies do not feature a distinct stomach, the entire digestive tract was removed and preserved in 95% ethanol for contents identification and enumeration under a dissection microscope. Items were identified according to the OBBN 27 taxa groups (Jones *et al.*, 2006) or when possible to the lowest taxonomic level. A minimum of nine stomach contents were analyzed per site.

For all fish size, the frequency of occurrence (%F) were calculated as follows (Hynes, 1950):

$$\% F = \frac{f_i}{\sum f} x 100$$

where $\boldsymbol{f_i}$ is the number of stomachs in which each prey item $\boldsymbol{i}$ occurs and $\sum \boldsymbol{f}$ is the total number of stomachs analyzed.

1.3.5 Data analyses

Diversity indices

Diversity indices were calculated using total abundances for the macroinvertebrate and fish community assemblages separately. We calculated taxon richness, Shannon diversity (Shannon, 1948) and Pielou’s evenness (Pielou, 1969). These diversity indices and total abundances were included as response variables in different generalized linear models that tested the influence round goby time of presence since invasion in each model (see section below). Local Contribution to Beta Diversity (LCBD) was computed from a percentage difference dissimilarity matrix for each site for both macroinvertebrate and fish in order to distinguish sites that contributed the most to overall beta diversity. LCBD represents the degree of uniqueness of a site in terms of species composition (Legendre, 2014).

Generalized Linear Models

For objective 1, we tested the effect of TSI and invasion status on round goby abundance using generalized linear models. We used negative binomial distribution since Poisson distribution showed signs of over-dispersion. The equi-dispersion hypothesis of Poisson models was tested using the AER package in R 3.6.3 (R Core Team 2020). For objective 2, we investigated the effect of TSI, invasion status, and round goby abundance on macroinvertebrate and fish community diversity indices (Shannon index, taxon richness and Pielou’s evenness, and LCBD) as well as on the total abundance for each of these communities. For all generalized linear models, we selected which variable best fitted each diversity index using AIC values (Aho *et al.*, 2014). Models were selected if they had 2 AIC units lower than competing models (ANNEX A Table 1). For Shannon index, taxon richness and Pielou’s evenness, and LCBD that are positive continuous variables, we used Gamma distributions that best fitted the data. Total abundance for each of the macroinvertebrate and fish communities were tested using negative binomial distribution since Poisson distribution showed signs of over-dispersion. When TSI was selected with generalized linear models, we further investigated these relationships using an alternative method of ANOVA for factors with ordered levels using mixed model methodology (Gertheiss, 2014). We also investigated if TSI grouping had different dreissenid mussel densities using a generalized linear model with negative binomial distribution for the 27 sites for which we had data for dreissenid densities.

Ordinally scaled independent variables

ANOVA with ordinally scaled factors, such as site TSI using F-Test is not the most powerful method to infer relationships (Gertheiss, 2014). Therefore, when TSI or invasion status were selected using generalized linear models, we used a mixed effects formulation of the usual factorial ANOVA model (with main effect only) while penalizing (squared) differences of adjacent means. This method assumes that ordinal factor levels take values 1,2,....,max, where max denotes the highest level of the respective factor observed in the data. Testing for equal means across factor levels is done by restricted likelihood ratio testing (RLRT). For each test, 1000000 values were simulated from the null distribution. We performed tests for ordinally scaled factors using the ordPens package in R 3.6.3 (R Core Team, 2020).

Principal coordinate Analysis (PCoA)

The effects of TSI, invasion status, and round goby abundance on taxon-specific responses in macroinvertebrate and fish communities were investigated using principal coordinate analyses (PCoAs). Both macroinvertebrates and fish community PCoA site scores were calculated using Bray-Curtis dissimilarity matrix. Community matrices were squared to avoid negative eigenvalues. Macroinvertebrate taxa and fish species abundances were fitted on PCoA site scores and the significance of the fitted vectors were assessed by permutation (999). We also tested the effect of TSI on PCoA site scores using a PERMANOVA with 9,999 permutations with vegan package in R 3.6.3 (R Core Team, 2020). PCoA site score coordinates and species vector fitting were plotted using the cmdscale and ape packages in R 3.6.3 (R Core Team, 2020).

Redundancy Analysis

Redundancy analysis (RDA) is a canonical ordination procedure that examines relationships among response variables and predictor variables in multivariate space (ter Braak et Verdonschot, 1995). The resulting RDA diagrams summarize the major environmental variables structuring biological communities while showing the approximate species composition for the different samples (Blanchet *et al.*, 2014). We used RDA to parse out environmental variables, TSI and the effects of dreissenid mussel density (at sites with available information) on macroinvertebrate and fish assemblages. We used forward selection to determine which environmental variables were related to response metrics. Forward selection (Blanchet *et al.*, 2008) of the explanatory variables was achieved using the ordistep{vegan} function in R 3.6.3 (R Core Team 2020) (α = 0.05). Prior to RDA, community data was Hellinger transformed to down-weight the influence of rare species (Legendre et Gallagher, 2001). RDAs were performed on the full data set of 53 sites for both macroinvertebrates and fish communities, as well as for macroinvertebrate communities at the 27 sites for which dreissenid mussel densities were available. All statistical analyses were performed in R 3.6.3 (R Core Team 2020).

1.4 Results and Discussion

Our study highlights lasting effects of round gobies on macroinvertebrate and fish communities, and the importance of integrating Time Since Invasion (TSI) to improve our understanding of invasive species impact. First, we found that sites with differing TSI had different environmental characteristics, mainly water conductivity and dominant bottom substrate (Fig 1.2). Uninvaded sites had soft bottom sand as the dominant substrate and intermediate water conductivity level (mean water conductivity of 252.22 $\mu S.cm^{-2}$), while more recently invaded sites with <12 years TSI had gravel as the dominant substrate and relatively low water conductivity (mean water conductivity of 176.01 $\mu S.cm^{-2}$). While recently invaded sites with TSI <12 years had mean water conductivity of 176.01 μS.cm^{-2}, sites with longer TSI (13-16 and 17-19) had mean water conductivity of 319.42 μS.cm^{-2} and 310.85 μS.cm^{-2}, respectively. Secondly, we found that round goby abundance had a positive relationship with TSI (Table 1.1, Fig. 1.3). However, there were potential first signals of round goby abundance declining at TSI of 17-20 years after reaching a peak at TSI of 13-16 years (Fig. 1.3).

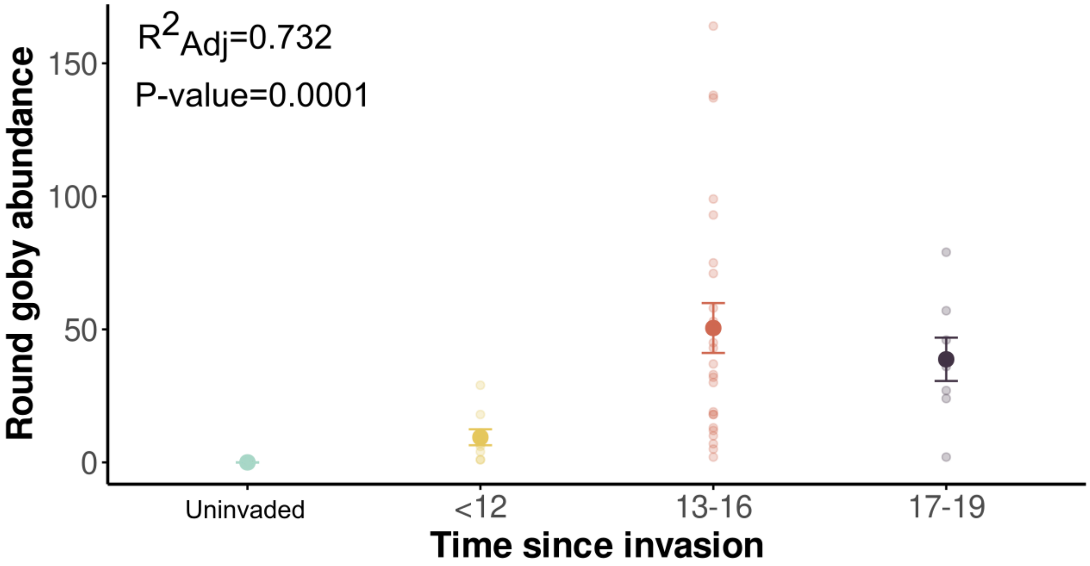

Figure 1.3. The positive influence of Time Since Invasion (TSI) on round goby abundance. Error bars refer to standard error. The reported *P*-value is from the ANOVA with ordinally scaled factor (Table 1.2).

Thirdly, we detected evidence of enduring impacts of round gobies on total macroinvertebrate taxon richness, which was reduced at sites with 17-19 years TSI (Fig. 1.4). This may be explained by round goby predation on Amphipoda, Gastropoda, and Chironomidae as evidenced by stomach contents collected from fish (ANNEX A, Fig. 1). Indeed, round goby TSI was negatively related with dominant macroinvertebrate taxa such as Amphipoda, Gastropoda and Chironomidae abundance in the macroinvertebrate communities (Fig. 1.5). Furthermore, TSI was statistically forward-selected along with certain environmental variables (water nutrients (TP and TN), conductivity, and temperature, as well as dominant bottom substrate) as significantly influencing macroinvertebrate communities (displayed in RDA ANNEX A, Fig. 2). Fourthly, we found that fish communities showed a shift in composition between uninvaded sites where round gobies were absent and more recently invaded sites (<12 years TSI) compared to sites with longer TSI (sites between 13-16 years and between 17-19 years TSI) (Fig. 1.6). However, the RDA on fish communities revealed these differences between sites were mainly driven by variations in water conductivity (ANNEX A, Fig. 3). Otherwise, the responses of resident nearshore aquatic communities to round goby abundance, invasion status, and TSI were inconsistent and did not present an overall uniform pattern of negative ecological impact across community diversity indices or taxa. We contribute lacking yet important information on the state of round goby impacts on aquatic nearshore communities after 20 years of invasion in the Upper St. Lawrence River, a culturally, socioeconomically, and ecologically important yet heavily invaded large-river ecosystem.

Table 1.1. Generalized linear model results for the influence of TSI on round goby abundance and the influence of round goby TSI, abundance or invasion status as predictors of resident community diversity indices: Shannon diversity, Pielou Evenness, taxon or species richness, Local Contribution to Beta Diversity (LCBD), and total abundance of macroinvertebrate and fish communities. Invasion status was defined by round goby absence (Uninvaded) versus presence (Post-invasion) as detected by our sampling efforts between 2017-2020, and it was confirmed by historical reports in other studies (Kipp *et al.*, 2012; Morissette *et al.*, 2018). In each model, variables and interactions were selected using AIC values. Bold *P*-values are <0.05. n describes the number of sites used in the model and df describes the degrees of freedom of residual deviance.

Round goby abundance			Distribution = Negative binomial		***n = 53*** ***df = 49***
Predictors	***Estimates***	***F-value***	***CI***	***p-value***	**Adjusted R^2**
					0.732
TSI <12 (intercept)	9.44	7.324	5.18 – 17.22	**2.4e-13**	
TSI 13-16	5.35	4.73	2.67 – 10.71	**2.25e-06**	
TSI 17-19	4.1	3.241	1.75 – 9.63	**0.001**	
TSI Uninvaded	0	-0.005	0.00 – Inf	0.996	
Macroinvertebrate Shannon index			Distribution =Gamma		***n = 52*** ***df = 50***
Predictors	***Estimates***	***t-value***	***CI***	***p-value***	**Adjusted R^2**
					0.075
Post-invasion	1.89	30.382	1.82 – 1.97	**<2e-16**	

(Intercept)					
Uninvaded	0.92	-2.175	0.85 – 0.99	**0.034**	
Macroinvertebrate taxon richness			Distribution =Gamma		***n = 53*** ***df = 49***
Predictors	***Estimates***	***F-value***	***CI***	***p-value***	**Adjusted R^2**
					0.21
TSI <12 (intercept)	1.100	11.961	1.08 – 1.11	**3.81e-16**	
TSI 13-16	1.000	-0.115	0.98 – 1.02	0.909	
TSI 17-19	1.040	2.655	1.01 – 1.07	**0.011**	
TSI Uninvaded	0.990	-0.656	0.97 – 1.01	0.515	
Macroinvertebrate Pielou’s evenness			Distribution =Gamma		***n = 52*** ***df = 50***
Predictors	***Estimates***	***t-value***	***CI***	***p-value***	**Adjusted R^2**
					0.02
Post-invasion (Intercept)	4.350	37.753	4.03 – 4.70	**<2e-16**	

Uninvaded	0.910	-1.109	0.78 – 1.07	0.273	
Macroinvertebrate total abundance			Distribution =Negative binomial		***n = 52*** ***df = 50***
Predictors	***Estimates***	***t-value***	***CI***	***p-value***	**Adjusted R^2**
					0.001
Post-invasion (Intercept)	683.890	52.498	541.08 – 881.65	**<2e-16**	
Uninvaded	1.050	0.116	0.63 – 1.83	0.868	
Macroinvertebrate LCBD			Distribution =Gamma		***n = 53*** ***df = 51***
Predictors	***Estimates***	***F-value***	***CI***	***p-value***	**Adjusted R^2**
					0.0001
(Intercept)	52.639	11.361		**1.39e-15**	
Round goby abundance	1.010	0.104	0.85 – 1.24	0.917	
Fish Shannon index			Distribution =Gamma		***n = 52***

					df = 50
Predictors	***Estimates***	***t-value***	***CI***	***p-value***	**Adjusted R^2**
					0.004
Post-invasion (Intercept)	2.130	18.688	1.97 – 2.31	**<2e-16**	
Uninvaded	1.050	0.573	0.89 – 1.26	0.569	
Fish species richness			Distribution =Gamma		***n = 53*** ***df = 51***
Predictors	***Estimates***	***t-value***	***CI***	***p-value***	**Adjusted R^2**
					0.002
Post-invasion (Intercept)	0.127	16.669	1.12 – 1.15	**<2e-16**	
Uninvaded	0.006	0.385	0.98 – 1.04	0.702	
Fish Pielou’s evenness			Distribution =Gamma		***n = 52*** ***df = 50***

Predictors	***Estimates***	***t-value***	***CI***	***p-value***	**Adjusted R²**
					0.008
Post-invasion (Intercept)	4.53	23.776	4.02 – 5.15	**<2e-16**	
Uninvaded	1.11	0.726	0.85 – 1.47	0.471	
Fish total abundance			Distribution =Negative binomial		***n = 53*** ***df = 51***
Predictors	***Estimates***	***t-value***	***CI***	***p-value***	**Adjusted R²**
					0.033
Post-invasion (Intercept)	182.150	40.393	142.92 – 237.1	**<2e-16**	
Uninvaded	1.330	1.063	0.80 – 2.33	0.288	
Fish LCBD			Distribution =Gamma		***n = 53*** ***df = 49***
Predictors	***Estimates***	***t-value***	***CI***	***p-value***	**Adjusted R²**

					0.05
TSI <12 (intercept)	0.021	18.51		**<2e-16**	
TSI 13-16	-0.002	1.748	0.94 – 1.08	0.087	
TSI 17-19	-0.004	-2.328		**0.024**	
TSI Uninvaded	-0.001	-1.178		0.244	

1.4.1 Relationship between TSI and round goby abundance

TSI, with sites ranging in invasion history over the last 20 years, had a strong positive relationship with round goby abundance (Fig. 1.3; Table 1.1). Our finding is consistent with a previous study in the Upper St. Lawrence River with TSI of up to 7 years (Kipp *et al.,* 2012). Uninvaded sites were sites where round gobies were not detected and sites with <12 years TSI had a low abundance of round goby. However, sites with differing TSI also had different environmental characteristics, mainly water conductivity and dominant bottom substrate (ANNEX A – Fig 1). Low conductivity water has been shown to exclude round gobies and create refuges for resident macroinvertebrate species (Astorg *et al.*, 2021 ; Baldwin *et al.*, 2012 ; Iacarella et Ricciardi, 2015). The most probable explanation for reduced success of round gobies in low conductivity water in the Upper St. Lawrence River system is low water calcium, which has been found to reduce foraging, growth, and survival of this invasive fish (Baldwin *et al.*, 2012 ; Iacarella et Ricciardi, 2015). Calcium is an essential element for fish physiological function, and whereas other native fish species are abundant across the conductivity/calcium gradient (Sanderson *et al.*, 2021), the round goby is rarely detected in calcium poor waters of the Upper St Lawrence River. The lower conductivity detected at uninvaded sites and at recently-invaded sites having <12 years TSI could therefore explain the late invasion and low round goby abundances at these sites. Moreover, uninvaded sites and recently invaded sites (<12 years TSI) were also represented by suboptimal bottom substrate for round gobies (sand and gravel). Round gobies preferentially colonize, and are found in greater densities, on rock and cobble substrates (Ray et Corkum, 2001 ; Young *et al.*, 2010). Soft-bottomed substrates appear to be less hospitable for this invasive fish in the Lower Great Lakes (Cooper *et al.*, 2007 ; Coulter *et al.*, 2015). Substrate characteristics (sand and gravel) and lower water conductivity could therefore potentially explain the absence and low abundance of round gobies at uninvaded and <12 years TSI sites. Indeed, environmental characteristics at sites with longer invasion exposure (from 13-16 years TSI and 17-19 years TSI sites) were fairly similar and consisted of rocky and cobble substrate, as well as higher water conductivity (Fig. 1.2). There was no relationship between round goby TSI and dreissenid mussel density (P-value = 0.485).

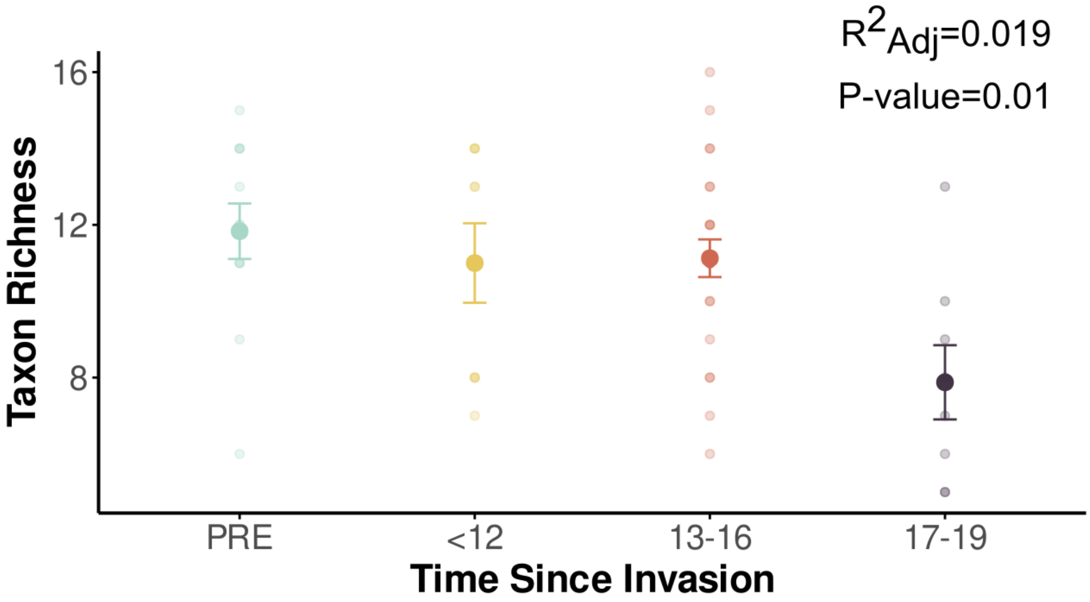

Figure 1.4. The influence of Time Since Invasion on total macroinvertebrate taxon richness. Error bars refer to standard error. The reported *P*-value is from the ANOVA with ordinally scaled factor (Table 1.2).

Our results are suggestive of potential first signals of round goby abundance declining at TSI of 17-19 years after reaching a peak at TSI of 13-16 years (Fig. 1.3). Reductions or stabilizing round goby abundances at sites with longer TSI (Fig. 1.3) could be indicative that the interactions between the resident communities and the invasive round goby have changed over time. Invasive species abundance can change over time as a result of evolutionary mechanisms such as phenotypic plasticity or evolution in the invader, changes in the community that is been invaded through species evolution or community shift toward resistant species, cumulative change in the invader environment, and interactions between invader and other controlling variables (Doody *et al.*, 2017 ; Flory et D'Antonio, 2015 ; Menke *et al.*, 2018 ; Strauss *et al.*, 2006 ; Strayer *et al.*, 2006). However, with adaptive adjustments such as population genetic change or phenotypic plasticity in round gobies, we would have expected increased or no change in round goby abundance with greater TSI, but this was not the case. Instead, the reduced abundance of round gobies at sites with longer TSI of 17-19 years was most likely the result of ecological changes in the invaded communities or environmental change.

Table 1.2. ANOVA with ordinally scaled factors results. Dependent variables for which the best independent variable selected by AIC were tested for equal means across factor levels is done by restricted likelihood ratio testing (RLRT). For each test, 1000000 values were simulated from the null distribution. Bold *P*-values are <0.05. Significant findings are summarized in Fig. 1.3 round goby abundance and Fig. 1.4 for macroinvertebrate community diversity indices.

	RLRT	**p-value**
Round goby		
TSI	12.615	**0.0001**
Macroinvertebrate taxon richness		
TSI	4.395	**0.01**
Fish LCBD		
TSI	0.648	0.139

Invaders can directly or indirectly modify their environments through their feeding or engineering activities, and such changes can take many years to play out (Crooks, 2002, 2005 ; Ehrenfeld, 2010 ; Emery-Butcher *et al.*, 2020 ; Ricciardi *et al.*, 2013). It is possible that this is the case in the Upper St. Lawrence River; other research has suggested that an invasional meltdown of the food web occurred in the Great Lakes as a result of sequential Ponto-Caspian invasions at multiple trophic levels that re-engineered food web pathways and energy flow (DeRoy et MacIsaac, 2020 ; Hogan *et al.*, 2007 ; Ricciardi, 2001 ; Simberloff, 2006 ; Wallace et Blersch, 2015). Given that invasive species abundances cannot continue to indefinitely increase exponentially at invaded sites because of per capita limiting resources (Benkwitt, 2013 ; Raby *et al.*, 2010), we would expect eventual reductions of round goby abundance at sites with longer TSI. Our results may have detected the start of this pattern in the Upper St. Lawrence River at sites with TSI of at least 17-19 years, and continued monitoring is essential for understanding i) if a trend in site-specific stabilizing round goby abundances continues with the passage of time and ii) the longer-term ecological consequences of round goby invasion in relation to resident aquatic communities.

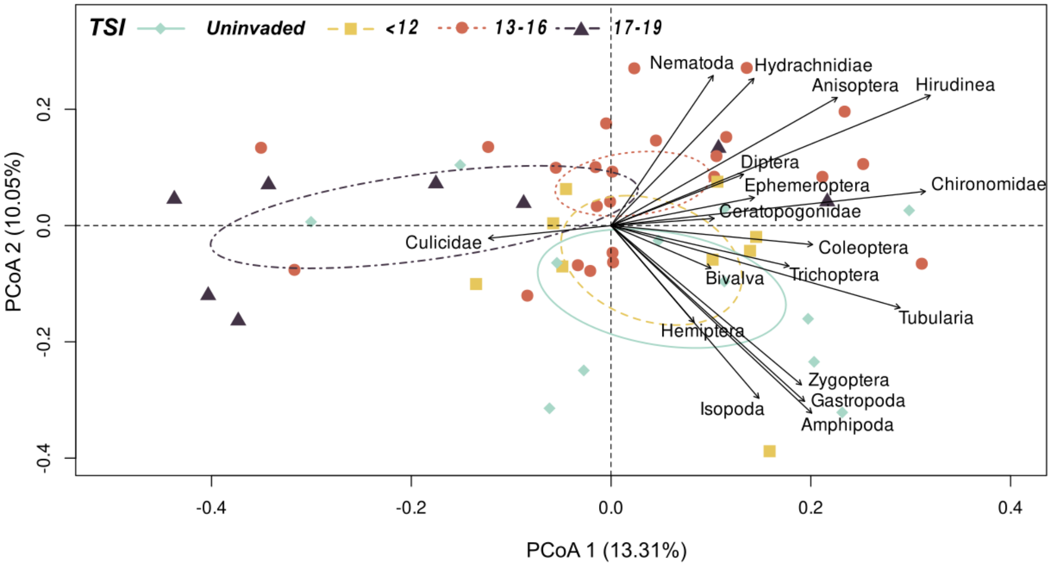

Figure 1.5. The response of macroinvertebrate communities to differences among sites in Time Since Invasion (TSI) according to PCoA with Bray Curtis dissimilarity matrix of squared macroinvertebrate taxon abundance. Blue diamond symbols represent uninvaded sites, yellow square symbols represent sites with TSI < 12, orange circle symbols represent sites with TSI between 13-16 years, and purple triangle symbols represent sites with TSI between 17-19 years. Vectors are the cosine directions of the squared macroinvertebrate taxon abundance, scaled by their correlation with PCoA site scores. The ellipses are 95% confidence interval ellipses for the different TSI groups. The solid line ellipse represents uninvaded sites, the dashed line ellipse represents sites with TSI < 12 years, the dotted line ellipse represents sites with TSI between 13-16 years, and the dotted dash line ellipse represents sites with TSI between 17-19 years.

1.4.2 Effects of round gobies on macroinvertebrate communities

Round gobies had enduring impacts on macroinvertebrate communities over the range of sites with different TSI. Macroinvertebrate taxon richness had a negative relationship with TSI; low macroinvertebrate taxon richness was detected at sites with TSI of 17-19 years (Fig. 1.4; Table 1.2). TSI explained differences in macroinvertebrate taxa abundance among sites in the Upper St. Lawrence River (effect of TSI on PCoA site scores, Permanova P-value = 2e-04), especially for Trichoptera, Coleoptera, Isopoda, Chironomidae, Amphipoda, Hydrachnidiae, Zygoptera, Hemiptera, Tubularia, Nematoda, Hirudinea, Anisoptera and Gastropoda (Fig. 1.5). Uninvaded sites with no round gobies and sites with TSI < 12 years had macroinvertebrate communities that strongly overlapped in composition, and had higher abundances of Amphipoda, Gastropoda, Isopoda, Hemiptera, Coleoptera, Tubularia, Chironomidae and Zygoptera. Sites with TSI between 13-16 years had higher abundance of Hydrachnidiae, Hirudinea, Anisoptera and Nematoda. Sites with TSI between 17-19 years had low abundance of all the above stated macroinvertebrate taxon. Amphipoda, Gastropoda, and Chironomidae have been reported as dominant taxa of macroinvertebrate communities in the Upper St. Lawrence River (Kipp *et al.,* 2012). The round goby diet consists mainly of macroinvertebrates (Kornis *et al.,* 2012), especially molluscs (Barton *et al.*, 2005 ; Kipp *et al.*, 2012 ; Kipp et Ricciardi, 2012 ; Kornis *et al.*, 2012 ; Lederer *et al.*, 2008), which was a finding also supported by our study, as well as for Chironomidae, Gastropoda, Ostracoda, Amphipoda and Chydorydae (ANNEX A, Fig. 1).

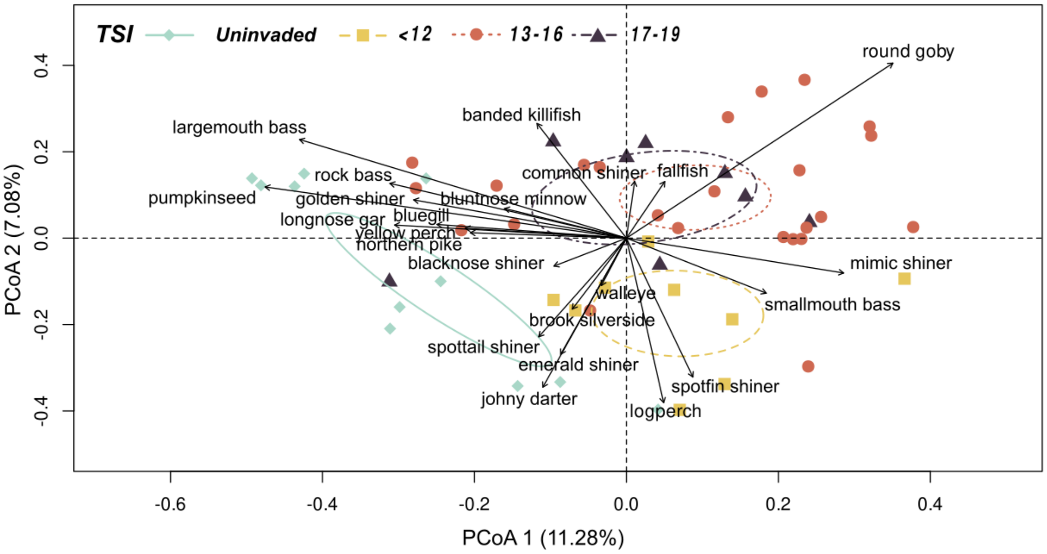

Figure 1.6. The response of fish communities to differences among sites in Time Since Invasion (TSI) according to PCoA with Bray Curtis dissimilarity matrix of squared fish species abundance. Blue diamond symbols represent uninvaded sites, yellow square symbols represent sites with TSI < 12, orange circle symbols represent sites with TSI between 13-16 years, and purple triangle symbols represent sites with TSI between 17-19 years. Vectors are the cosine directions of the squared macroinvertebrate taxon abundance, scaled by their correlation with PCoA site scores. The ellipses are 95% confidence interval ellipses for the different TSI groups. The solid line ellipse represents uninvaded sites, the dashed line ellipse represents sites with TSI < 12 years, the dotted line ellipse represents sites with TSI between 13-16 years, and the dotted dash line ellipse represents sites with TSI between 17-19 years.

Amphipods, chironomids and cladocerans have also been shown to be the most important prey items for round goby diet in the Great Lakes (Brush *et al.*, 2012). The negative relationship of round goby TSI to differences in macroinvertebrate taxon richness among sites could therefore reflect the effects of round goby predation on these communities. While differences in environmental conditions between sites can also have impacts on macroinvertebrate communities, our study showed that sites TSI between 13-16 years and sites with TSI between 17-19 years had no major environmental differences (Fig. 1.2). Using forward selection and RDA (ANNEX A,

Fig. 2), we found that TSI was a structuring factor of the macroinvertebrate community along with environmental characteristics (water nutrients (TP and TN), conductivity, temperature, and dominant bottom substrate). Therefore, it is likely that macroinvertebrate community differences between TSI site groupings reflect both long term effects of round goby predation and environmental effects. We, however, found no relationships between TSI, invasion status and round goby abundance on macroinvertebrate community Pielou's evenness, and LCBD; Shannon diversity showed a relationship with invasion status (Table 1.1). In the Upper St. Lawrence River, dreissenid mussels show similar invasion patterns as round gobies (Bailey, 2015 ; Ward et Ricciardi, 2007, 2010). Dreissenid mussels are known to have strong effects on macroinvertebrate communities (Bailey, 2015 ; Horvath *et al.*, 1999 ; Karatayev *et al.*, 2015 ; Ricciardi *et al.*, 1997 ; Ward et Ricciardi, 2007, 2010), which could have also contributed to patterns we observed in the Upper St. Lawrence River. However, we found no statistical support to suggest that dreissenid mussels were a major structuring agent of macroinvertebrates at the 27 study sites where dreissenid mussels were sampled. An RDA on the 27 sites for which we sampled dreissenid mussels indicated that TSI structured macroinvertebrate communities more strongly than environmental variables and dreissenid densities (ANNEX A, Fig 4).

Other studies have also found strong negative effects of round goby invasion on macroinvertebrate diversity in Europe (Hirsch *et al.*, 2016 ; Ojaveer *et al.*, 2015) and North America (Barton *et al.*, 2005 ; Burkett et Jude, 2015 ; Lederer *et al.*, 2008). Similar to a study that was conducted in the St. Clair River following 16 of years since invasion (Burkett et Jude, 2015), we found that round goby impacts were strong and lasting even when round gobies showed signs of declining abundances. Strong negative effects on macroinvertebrate community composition and diversity were also consistent with previously reported round goby impacts (Azour *et al.*, 2015 ; Barton *et al.*, 2005 ; Brownscombe et Fox, 2013 ; Burkett et Jude, 2015 ; Hirsch *et al.*, 2016 ; Janáč *et al.*, 2016 ; Krakowiak et Pennuto, 2008 ; Kuhns et Berg, 1999 ;

Lauer *et al.*, 2004 ; Lederer *et al.*, 2008 ; Ojaveer *et al.*, 2015 ; Raby *et al.*, 2010). Our study uniquely highlights that TSI can have important consequences on macroinvertebrate composition and diversity; scarce have implicitly integrated TSI into understanding the ecological impacts of round gobies on resident communities (Bailey, 2015 ; Barrett *et al.*, 2016 ; Burkett et Jude, 2015 ; Kipp et Ricciardi, 2012 ; Morissette *et al.*, 2018 ; Oesterwind *et al.*, 2017), underlining the importance of considering temporal context when studying the impacts of invasive species.

Predation from round gobies may have cumulative effects on resident prey communities over the years, leading to less abundant macroinvertebrate communities at sites with longer TSI. Other research has found evidence for cumulative ecological effects of invasive species over time: e.g., altered communities of aquatic plants by invasive benthivorous fish (Bajer *et al.*, 2016); modified benthic habitats by invasive bivalves (Bódis *et al.*, 2014); invasive macrophyte affecting wetland sediment properties (Bai et Shang, 2017). The accumulation of long-term ecological effects of invasive species on resident communities is most likely prevalent when the impacted taxa have strong ecosystem engineering effects (Crooks, 2002, 2005 ; Emery-Butcher *et al.*, 2020). Dreissenid mussels, which also occur in the Upper St. Lawrence River (Ricciardi *et al.*, 1997), have been reported to strongly engineer benthic communities (Bailey, 2015 ; Ward et Ricciardi, 2007, 2010), and so could have influenced the effects we detected. However, our analysis showed that round goby TSI was a better predictor of macroinvertebrate community compositional patterns than dreissenid mussel density. Since macroinvertebrates engineer freshwater habitats by influencing energy flow and nutrient cycling in aquatic ecosystems (Covich *et al.*, 1999), the cumulative effects of round goby predation on macroinvertebrate communities over time could potentially lead to important ecosystem changes - but this remains to be verified by further research.

1.4.3 Effects of round gobies on fish communities

TSI explained differences in fish species abundances among sites in the Upper St. Lawrence River (effect of TSI on PCoA site scores, P-value = 1e-04; Fig. 1.6). This was especially the case for bluegill (*Lepomis macrochirus*), emerald shiner (*Notropis atherinoides*), golden shiner (*Notropis atherinoides*), johnny darter (*Etheostoma nigrum*), banded killifish (*Fundulus diaphanus*), largemouth bass (*Micropterus salmoides*), logperch (*Percina kathae*), longnose gar (*Lepisosteus osseus*), mimic shiner (*Notropis volucellus*), pumpkinseed (*Lepomis gibbosus*), rock bass (*Ambloplites rupestris*), smallmouth bass (*Micropterus dolomieu*), spotfin shiner (*Cyprinella spiloptera*), spottail shiner (*Notropis hudsonius*), and round goby (Fig. 1.6). Uninvaded sites were associated with higher abundance of pelagic fish such as bluegill, pumpkinseed, largemouth bass, longnose gar, golden shiner, emerald shiner and spottail shiner (Fig. 1.6). While direct competitive interactions between the three species of shiners, pumpkinseed, bluegill and round goby are unlikely (Johnson *et al.*, 2015), pelagic fish can experience negative impacts from round goby competition at early life stages (Crane *et al.*, 2015) or can experience egg predation (Kornis *et al.*, 2012). Pelagic piscivorous species (e.g., largemouth bass, rock bass and longnose gar) were also associated with uninvaded sites, which could be the result of the abundance of pelagic prey described above at uninvaded sites. Benthic fish like johnny darter and logperch have been found at uninvaded and <12 years TSI sites. Benthic fish have been shown to experience direct competition for food resource and space by round goby (Balshine *et al.*, 2005 ; Bergstrom et Mensinger, 2009 ; Kornis *et al.*, 2012 ; Lauer *et al.*, 2004 ; Leino et Mensinger, 2017 ; Piria *et al.*, 2016). Round goby, smallmouth bass and mimic shiner were positively associated with invaded site groups (TSI <12, 13-16 and 17-19) (Fig. 1.6). The positive relationship between smallmouth bass and round goby could be the result of piscivorous predators shifting their diet to round goby, which could subsequently relax predation pressure other native fish prey such as the mimic shiner (Crane et Einhouse, 2016 ; Johnson *et al.*, 2015 ; Wallace et Blersch, 2015).

We did not detect any relationships between TSI and fish community diversity indices (Table 1.1). Consistent with another study that had some overlapping sites as our study (Morissette *et al.*, 2018), we also detected no relationships between invasion status and round goby abundance on fish community diversity using Shannon index, Pielou's evenness, taxon diversity, abundance and LCBD (Table 1.1). The ecological responses of certain fish species abundances to round goby TSI were therefore most likely a result of changing food web pathways at different trophic levels. Given that environmental gradients among sites are associated with TSI site groupings (Fig. 1.2), and that TSI was not important for structuring overall fish community composition among sites (Fig. 1.6), round goby impacts on resident fish communities were likely mostly indirect and were difficult to differentiate from environmental preferences. For our study, uninvaded and recently invaded sites (<12 years TSI) presented suboptimal round goby habitat with lower water conductivity and with sand and gravel bottom substrate. The uninvaded and recently invaded (<12 years TSI) sites shared more similar fish communities compared with sites with cobble/rocky bottom substrates and with higher water conductivity and longer history of round goby invasion (13-16 years TSI and 17-19 years TSI) (Fig. 1.2 and 1.6). Furthermore, RDA results suggested that water conductivity was the main structuring factor for fish communities at our sampling sites (ANNEX A, Fig. 3). We therefore suggest that environmental conditions were more important for differences in fish community composition among sites with different round goby TSI, and that round goby had localized effects on the abundances of certain fish species that were difficult to tease apart from site-specific environmental differences in our study.

1.5 Caveats

We found that time since invasion has the potential to be a valuable parameter to address long term impacts of invasive round gobies in aquatic ecosystems, but that temporal changes in site characteristics may confound the effects of invasion on macroinvertebrate and fish communities. Therefore, it is difficult to ascribe relatively depauperate macroinvertebrate communities solely to long-term round goby presence. Moreover, it is possible that the identification of macroinvertebrates to the Order and Family levels could have interfered with our capacity to detect round goby impacts on macroinvertebrate community diversity. We could not test for the effect of TSI on round goby diet because not enough sites were represented for the <12 and 17-19 years TSI. We also recognize that our subsampling technique for macroinvertebrate counting could have led to an underestimation of shelled individuals, mainly Bivalves and Gastropods. However, we detected strong impacts of round gobies time since invasion on macroinvertebrate taxon richness (Fig. 1.4) and composition (Fig. 1.5). Identification of macroinvertebrates to the Family level would have reduced our ability to detect round goby impact, but it would not have enhanced nor biased our ability to detect effects. Therefore, in light of our findings, we conclude that round gobies continue to have lasting impacts on macroinvertebrate community composition and diversity in the Upper St. Lawrence River, even 20 years after first contact.

1.6 Conclusion

With the passage of time, the continued increase in round goby abundances would be expected to decline at invaded sites, in relation to available resources. However, it may be that historical and continuing ecological impacts of round gobies on resident prey resources could endure despite a decline in round goby abundances at local sites. Research on the ecological effects of other invasive species in other ecosystems around the world has shown support for enduring ecological effects of exotic invasion on resident communities (Cane toads: Doody *et al.,* 2017; Argentinian ants: Menke *et al.,* 2018). Continued research is essential for tracking the long-term changes, and potential signs of decline, of invasive round goby abundances in relation to resident macroinvertebrate prey resources and nearshore fish communities.

CHAPTER II

DIFFERENT REFUGE TYPES DAMPEN EXOTIC INVASION AND ENHANCE DIVERSITY AT THE WHOLE ECOSYSTEM SCALE IN A HETEROGENEOUS RIVER SYSTEM

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N.B. References cited in this chapter are presented at the end of the thesis

2.1 Abstract

Refuges that result from environmental heterogeneity within ecosystems have an important yet under-appreciated role in maintaining native community diversity in face of exotic invasion. The objective of our study was to determine if different refuge types constrain invasion impacts on native biodiversity at the whole ecosystem-scale of the Upper St. Lawrence River. We focused on the voracious round goby fish as a sentinel exotic species whose spatial distribution within this ecosystem is also representative of the species distributions of several other Ponto-Caspian invaders. We first explored if wetlands were acting as unknown refuges in reducing the local abundance of the round goby fish. We then tested the relative influence of a known broad-scale conductivity gradient compared with local wetlands on structuring the composition, diversity, and abundance of native macroinvertebrate and fish communities inside and outside each of these refuge types. We found that the two types of refuges, broad-scale conductivity gradient and local wetlands, limited round goby abundances at the whole ecosystem scale, and structured macroinvertebrate and fish community diversity. The broad-scale conductivity refuge was twice stronger than wetlands in limiting round goby abundance. Although wetlands were effective in constraining round goby abundance, the direct effect of wetlands rather than their indirect effects through limiting round goby abundance, were more powerful in explaining maintenance of macroinvertebrate and fish community diversity in invaded high conductivity waters. Our findings underscore the important role of environmental heterogeneity in producing different types of refuges that buffer invasion effects in freshwater ecosystems, and we advocate the preservation of wetlands as a part of this process.

Keywords : Invasion Environmental heterogeneity Biodiversity Refuges Freshwater ecosystem Wetlands

2.2 Introduction

Environmental heterogeneity, variation in physical and ecological landscape characteristics, is well known for influencing biodiversity (Cardinale *et al.*, 2012 ; Stein *et al.*, 2014) and ecosystem resilience to stressors (Levine *et al.*, 2016 ; Oliver *et al.*, 2015). Among anthropogenic stressors, biological invasions are one of the major factors that have contributed to species endangerment and extinction globally (Pejchar et Mooney, 2009 ; Wilcove *et al.*, 1998). Environmental heterogeneity has potential to play an important role in the preservation of native species diversity and abundances in invaded ecosystems by providing habitat refuges that by limit the spread of biological invasions and constrain invasion impacts on native communities (Melbourne *et al.*, 2007 ; Ricciardi *et al.*, 2013 ; Vander Zanden *et al.*, 2017). In this context, refuges can be continuous or discrete habitats with a reduced abundance of invasive species relative to native species, compared with the surrounding environment. Refuges from invasion might be especially beneficial for native biodiversity when different refuge types limit invader abundance at the whole ecosystem level. Yet, we are not aware of empirical studies that have explicitly considered the effects of environmental heterogeneity in refuge type especially within large, continuous ecosystems characterized by high connectivity and thus high potential for invasive species spread, in buffering invasion impacts on native biodiversity.

Environmental heterogeneity can generate refuges for native species in face of biological invasion by interacting with ecological tolerances and habitat preferences of the invasive species (e.g., Anton et al., 2014 ; Kestrup et Ricciardi, 2009 ; Tamme et al., 2010). For example, refuges can occur when environmental conditions restrict the abundance and impact of invaders because of limits in their ecological tolerances (Iacarella et Ricciardi, 2015 ; Kestrup et Ricciardi, 2009 ; Latzka *et al.*, 2016). Moreover, when abiotic heterogeneity limits invasive species survival (Iacarella et Ricciardi, 2015) or competitive ability (MacDougall *et al.*, 2016), it can contribute to biotic resistance to invasion (Elton, 2020) through enhanced native species richness (Stein *et al.*, 2014) and native predation pressure on exotic prey (Meynard *et al.*, 2013 ; Stein et Kreft, 2015 ; Yang *et al.*, 2015). Maintaining environmental heterogeneity, by conserving a variety of habitat types, can also potentially create refuges for native species in invaded landscapes, which become important for native species persistence (Dias, 1996) and biodiversity preservation (Stein *et al.*, 2014) at the whole-ecosystem scale. Most of the research on the importance of environmental heterogeneity in invaded environments has been done in terrestrial ecosystems; knowledge about refuges in environmentally heterogeneous freshwater ecosystems is relatively scarce (exceptions: Iacarella et Ricciardi, 2015 ; Kestrup et Ricciardi, 2009 ; Latzka et al., 2016), despite that freshwater environments are among the most invaded ecosystems in the world (Richardson et Pyšek, 2008).

At the same time, refuges can also enhance the persistence of native species that are adapted to these environments (Derry *et al.*, 2013 ; Gelbard et Harrison, 2003 ; Gram *et al.*, 2004 ; Kobza *et al.*, 2004). For example, wetlands are structurally complex highly productive aquatic habitats (Wetzel, 1990) and contribute to environmental heterogeneity of shoreline aquatic habitats (Krieger, 1992). Wetlands are known to promote freshwater diversity in shallow freshwater environments (Céréghino *et al.*, 2008 ; Gee *et al.*, 1997 ; Robson et Clay, 2005 ; Scheffer *et al.*, 2006 ; Thiere *et al.*, 2009 ; Williams, 1997) and seem to contribute disproportionately to regional biodiversity than other water-body types (Williams *et al.*, 2004). Factors that increase biodiversity within wetlands are linked to the highly individual nature of physio-chemical characteristics of wetlands compared to rivers and large streams (Williams *et al.*, 2004). In particular, structuring effects of vegetation in wetlands can create environmental conditions suitable for diverse assemblages of macroinvertebrates (Scheffer *et al.*, 2006). The periodic flooding of certain wetlands can enhance biodiversity through the presence of egg banks that supply different macroinvertebrate species assemblages under various environmental conditions (Brendonck et Williams, 2000). Furthermore, inundation of wetlands can favor genetic diversity by increasing dispersal and connectivity of wetland organisms (Rundle *et al.*, 2002). Wetlands are highly productive environments because they host high rates of primary production, which in turn support high secondary production with rates that can exceed terrestrial ecosystems (Turner, 1977). Moreover, there is a compelling yet limited number of studies that suggest that wetlands have unfavorable substrate and hydrology for certain key aquatic invaders, including exotic zebra mussels (Bowers et Szalay, 2004) and round gobies (Cooper *et al.*, 2007, 2009 ; Young *et al.*, 2010).

The objective of our study was to address if the effects of different refuge types can reduce invasion impacts on native freshwater biodiversity. We focused on the voracious round goby fish (Neogobius melanostomus) as a sentinel exotic species whose spatial distribution within the Upper St. Lawrence River is also representative of several other Ponto-Caspian invaders in this ecosystem (Echinogammarus ischnus amphipods:, Kestrup et Ricciardi, 2009; dreissenid mussels: Neary et Leach, 1992; Jones et Ricciardi, 2005). We investigated the effects of environmental heterogeneity created by a broad-scale conductivity gradient and local wetlands in providing refuges to native fish and macroinvertebrate communities in face of Ponto-Caspian invasion in the Upper St. Lawrence River. Ponto-Caspian invaders are re-engineering littoral food webs of the Lower Great Lakes (Campbell *et al.*, 2009), but invasion impacts on native biodiversity have been reported to be more attenuated in the Upper St. Lawrence River compared to the Lower Great Lakes (Iacarella et Ricciardi, 2015 ; Kestrup et Ricciardi, 2009). One mechanism that has been proposed to explain this difference in invasion impact is a broad-scale conductivity gradient from the joining of separate water masses from two major rivers in the Upper St. Lawrence with different calcium concentration, which has been shown to restrict Ponto-Caspian invaders (Iacarella et Ricciardi, 2015 ; Jones et Ricciardi, 2005 ; Kestrup et Ricciardi, 2009 ; Whittier et al., 2008; Fig. 2.1). Conductivity is known to be a strong limiting factor of round goby invasion of freshwater habitats (Baldwin *et al.*, 2012), likely because of their evolutionary history in brackish water and physiological constraints that result in reduced fitness and performance at low freshwater conductivity, especially when calcium is limiting (Iacarella et Ricciardi, 2015). However, much less is known about the role of wetlands in providing refuges for native macroinvertebrate and fish communities from this exotic fish (Cooper *et al.*, 2007, 2009 ; Young *et al.*, 2010). We first explored if wetlands were acting as unknown refuges to reduce the local abundance of the round goby fish in invaded, high conductivity water of the Upper St. Lawrence River. We then tested the relative influence of the broad-scale conductivity gradient and wetlands on structuring the composition, diversity, and abundance of native macroinvertebrate and fish communities inside and outside of these refuges. We provide one of the few freshwater studies to date to address the unexplored yet important role of environmental heterogeneity in buffering invasion effects on native biodiversity. More specifically, our study provides support for the importance of preserving different refuge types, including wetlands, for their effects in dampening the negative impacts of exotic invasion on freshwater biodiversity.

2.3 Materials and methods

2.3.1 Study system

At a broad, river-wide scale in the Upper St. Lawrence River, Canada (Fig. 2.1), Ponto-Caspian invaders such as the round goby fish are limited to areas that receive high conductivity water (30–40 mg/L of calcium) flowing from the Great Lakes (Baldwin *et al.*, 2012 ; Iacarella et Ricciardi, 2015 ; Kestrup et Ricciardi, 2009). The confluence of the Upper St. Lawrence River and the Ottawa River at Lake St. Louis (N45220 12, W73490 12), a lacustrine widening of the St. Lawrence River, has created a conductivity gradient in which the north side of Lake St. Louis receives low conductivity water (10–15 mg/L of calcium) from the Ottawa River whereas the south side receives high-conductivity water (30–40 mg/L of calcium) from the St. Lawrence River (Hudon *et al.,* 2003) (Fig. 2.1). The Ponto-Caspian invasive exotics are absent from areas that receive low conductivity water (10–15 mg/L of calcium) from the Ottawa River (Iacarella et Ricciardi, 2015 ; Kestrup et Ricciardi, 2009). Within these water masses and along the conductivity gradient in the Upper St. Lawrence River, wetlands provide productive aquatic habitats that are structurally complex compared to adjacent shoreline habitats and contribute to environmental heterogeneity of shoreline aquatic habitats (Krieger, 1992 ; Wetzel, 1990). The environmental heterogeneity created by wetlands has the previously unexplored potential to generate numerous local refuges for native species in the face of exotic invasion within the high conductivity water of the Upper St. Lawrence River.

Between spring and fall of 2017 and 2018, we collected macroinvertebrate and fish community data, as well as environmental data, from wetland sites and from open-water (non-wetland) shore sites in the Upper St. Lawrence River (Lake St. Francis and upstream), Ottawa River (Lac des Deux Montagnes), and in Lake St. Louis in

Québec and Ontario, Canada (Fig. 2.1). Wetland sites were identified and chosen using information from Ducks Unlimited Canada (Powers *et al.*, 2012) and Land Information Ontario (LIO). A total of 27 sites were sampled for this study: 9 wetland sites and 17 open-water shore sites (Fig. 2.1). Of the 27 total sampling sites, eight sites were located in low conductivity water and 19 sites were in high conductivity water; the purpose of sampling a greater number of high conductivity sites was to focus the effort on the potential yet unknown attenuating effects of wetlands on biological invasion for native freshwater biodiversity in invaded areas of the Upper St. Lawrence River. The importance of low conductivity water in limiting round goby abundance has already been established by other previous studies (Baldwin *et al.*, 2012 ; Iacarella et Ricciardi, 2015 ; Kestrup et Ricciardi, 2009).

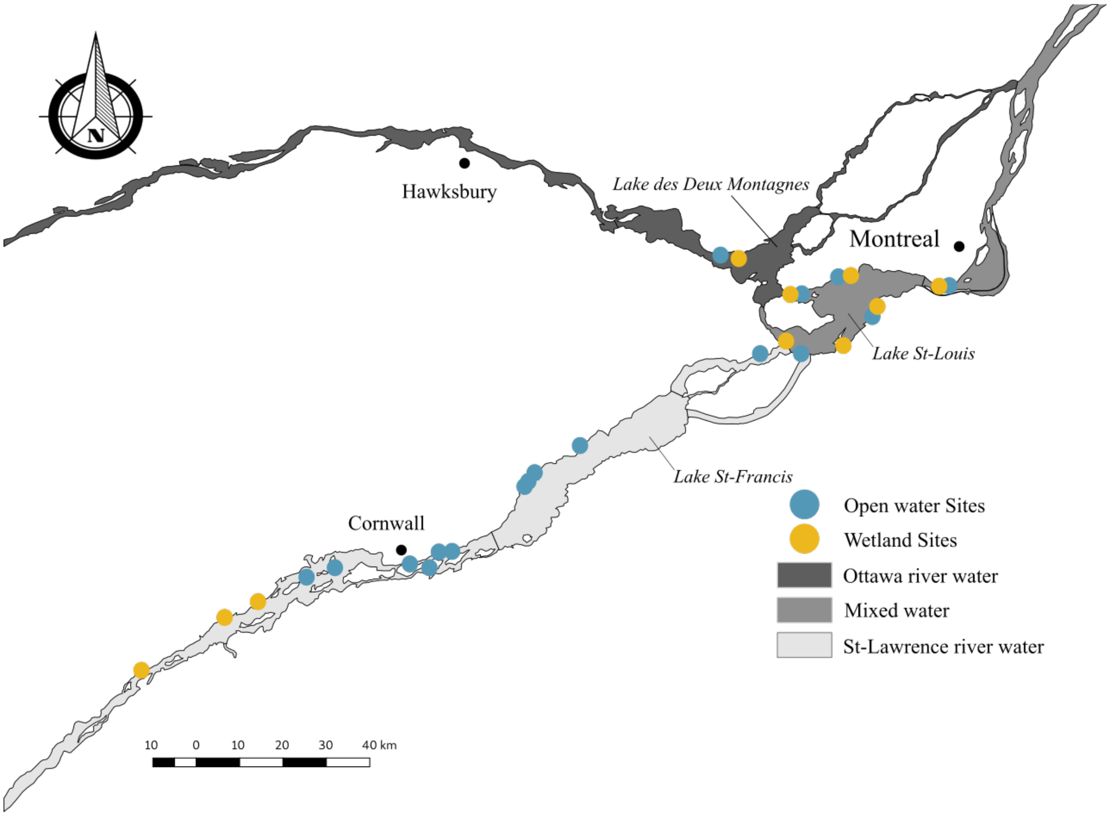

Figure 2.1. Map of the sampled area in the Upper St. Lawrence River. White background represents land, the light grey color is high conductivity water from the St. Lawrence River, and the dark grey color represents low conductivity water from the Ottawa River. The intermediate grey color represents an area of mixing of water masses. Note that the water mixing is not homogeneous in the mixing zone; water near the shore is less mixed. The blue circles represent open-water shore sampling sites while yellow circles represent wetland sampling sites.

Of the 27 sampling sites, 12 were located in Lake St. Louis (Fig. 2.1). Wetlands along each of the north and south shores of Lake St. Louis were sampled for a total of 6 wetlands and 6 open-water shore sites. In the low conductivity water refuge in Lake des Deux Montagnes, which receives low conductivity water from the Ottawa River that prevents round goby invasion (Iacarella et Ricciardi, 2015), we sampled 1 wetland site and 1 open-water shore site. In the highly invaded high conductivity waters of Lake St. Francis, we sampled 4 open-water shore sites. In the St. Lawrence River upstream of Lake St. Francis, we sampled 3 wetlands and 6 open-water shore sites. The selection of wetlands for sampling was based on maximizing the number of accessible wetlands while keeping a sampling design as balanced as possible.

2.3.2 Community data collection

For macroinvertebrate collection, three transects were randomly established to collect three samples at each site. Sampling was performed by the sweep method (''Kick and Sweep'') with a 500-µm ''D-net'' as recommended by the Ontario Benthos Biomonitoring Network (OBBN; Jones et al., 2006). The collected samples were stored in 100% ethanol and brought back to the laboratory at the Université du Québec à Montréal (UQAM) for identification. Identification was done up to the Family level using Moisan (2010). For each sample, 100 mL sub-sample was taken and counted until the 100th individual was reached. If the 100th individual was not reached within the initial 100 mL, an additional 100 mL was counted. When the 100th individual was reached, the remaining part of the sub-sample was counted, and the total sub-sampled volume calculated. A ratio was then calculated between the total sub-sampled volume and the sample total volume to estimate the taxon-specific abundance of macroinvertebrates. The abundance in each site was estimated using the mean abundance of the three samples collected at every site. All macroinvertebrate samples were identified using SZX10 stereo microscopes (Olympus) with varying magnification (96.3– 910). For fish collection, each site was seined three times consecutively for replication, with short (>1 h) intermission periods between seining times. The dimensions of the seine were 114 cm by 407 cm with 5 mm mesh. After seining, all fish were placed into bins, sorted by species according to Bernatchez et Giroux (2000), and counted for species-specific abundance.

2.3.3 Environmental data collection

Dissolved oxygen (DO; mg.L^{-1}), pH, water temperature (C) and conductivity (µS.cm^{-2}) were measured using a Professional Plus Model YSI multi-parameter sonde (model 10102030; Yellow Springs Inc.). Dissolved organic carbon (DOC; mg.L^{-1}) and water calcium (Ca; mg.L^{-1}) were measured from water samples for a subset of the sites around Lake St. Louis where there are important gradients of DOC and water Ca. We also collected water samples to quantify total nitrogen (TN; mg.L^{-1}), and total phosphorus (TP: µg.L^{-1}). Detailed analytical methods for measured water chemistry variables are provided in ANNEX B. We provide a Principal Component Analysis (PCA) to visualize how study sites are distributed across the environmental gradients (ANNEX B; Fig. 6 and 7). PCA of the all sites had missing values; we imputed the missing data using an iterative PCA algorithm (Josse et Husson, 2012).

2.4 Data analyses

Diversity indices

Diversity indices were calculated using total abundances for the macroinvertebrate and fish community assemblages separately. We calculated taxon richness, Shannon diversity (Shannon, 1948) and Pielou’s evenness (Pielou, 1969). These diversity indices and total abundances were included as response variables in different generalized linear models that tested the influence of wetlands, conductivity and round goby abundance together in each model (see section below). Conductivity and water Ca correlated highly (Regression Calcium-Conductivity: R2 = 0.87, P value = 1.364e-06), and conductivity was selected for the generalized linear models as it had the most complete dataset across all sampling sites. Local Contribution to Beta Diversity (LCBD) was computed from a percentage difference dissimilarity matrix for each site for both macroinvertebrate and fish in order to distinguish sites that contributed the most to overall beta diversity. LCBD represents the degree of uniqueness of a site in terms of species composition (Legendre, 2014).

Generalized linear models

We investigated the effect of the broad-scale conductivity gradient and wetland on round goby abundance The effect of water conductivity, wetlands, and round goby abundance were tested on diversity indices (Shannon index, taxon richness and Pielou's evenness, and LCBD) as well as on the total abundance for each of macroinvertebrate and fish communities. The different variables included in generalized linear models required different probability distributions. Count data such as round goby abundance and total abundance of macroinvertebrates and fish were first assigned a Poisson distribution. The equi-dispersion hypothesis of Poisson models was tested using the AER package in R 3.6.3 (R Core Team 2020), and this indicated that all models in which a Poisson distribution was applied were over-dispersed. We therefore next applied a zero-inflated Poisson model to investigate the effect of the broad-scale conductivity gradient and wetland on round goby abundance because wetland sites inflated the number of sites with null round goby abundance (ANNEX B: Fig. 8). For each of macroinvertebrate and fish communities, we applied negative binomial distributions to models to the total abundance data. Zero-inflated models and negative binomial models all showed improvement over Poisson distribution models using Vuong test (Vuong, 1989). For Shannon index, taxon richness and Pielou's evenness, and LCBD that are positive continuous variables, we used Gamma distributions that best fitted the data. For all generalized linear models, we performed backward model selection, removing interaction and variables from a full model in a stepwise manner. We selected the most parsimonious model using model AIC values (Aho *et al.*, 2014). Following model selection, model residuals were investigated for non-linear patterns (residuals vs fitted values), distribution fit (qqplot), equal spread (scale location) and outliers (residuals vs leverage and sites outside 1.5 times the interquartile range above the upper quartile and below the lower quartile). Model diagnostics detected outliers in round goby abundances and in macroinvertebrate taxonomic abundances that influenced model outcomes; these sites were therefore removed from these models.

Effect size

To compare the relative importance of conductivity and wetlands on the abundance of invasive fish at each site, Cohen's D effect sizes (Cohen, 2013) were computed. The effect size of wetlands on round goby abundance were computed for the full dataset, for only high conductivity sites, and for only low conductivity to determine if the effect of wetland on round goby abundance was consistent throughout the conductivity gradient. We used the effsize package in R 3.6.3 (R Core Team 2020) to compute the different Cohen's D effect sizes.

Structural equation modelling

We wanted to determine if the effects of wetlands in invaded landscape (high-conductivity sites) were direct or mediated by reduced round goby abundance. We applied mediation analysis using structural equation models (SEMs) (Grace, 2006 ; Gunzler *et al.*, 2013) to test for indirect correlations between wetland presence and community diversity (Shannon index, taxon richness, Pielou's evenness, LCBD and Abundance) mediated by round goby abundance in high conductivity sites only. This was done for each of macroinvertebrates and fish communities diversity indices on which the effect of wetlands was potentially mediated by round goby abundance (Fig. 2.2). We therefore tested the total, direct and indirect effect of wetland on community composition and diversity indices (Fig. 2.2). The total effect c (Fig. 2.2a) tests the effect of wetland without an indirect or mediation path in the model structure (i.e., the unstandardized slope of the regression of wetland on community composition and diversity indices). The direct effect c0 (Fig. 2.2b) represents the effect of wetland on community composition and diversity indices after controlling for the proposed mediator variable, here round goby abundance. The effect of wetland on round goby abundance is represented by the path a (Fig. 2.2b), and the effect of round goby abundance on community composition and diversity indices, controlling for wetland, is represented by the path b (Fig. 2.2b). Finally, the indirect effect is the product of a*b = ab (Fig. 2.2b). The indirect effect (ab) is generally equivalent to c–c0 , the difference between the total effect and the direct effect, but it is easier to test the significance of ab because these coefficients are drawn from a single model, whereas c and c0 are from separate models (Rucker *et al.*, 2011). Each metric was analyzed in separate models for macroinvertebrates and fish. The SEM analysis was performed using the Lavaan package in R (R Core Team 2020).

Redundancy analysis

Redundancy analysis (RDA) is a canonical ordination procedure that examines relationships among response variables and predictor variables in multivariate space (ter Braak et Verdonschot, 1995). The resulting RDA diagrams summarize the major environmental variables structuring biological communities while showing the approximate species composition for the different samples (Blanchet *et al.*, 2014). We used RDA to evaluate environment-taxon relationships for macroinvertebrate and fish assemblages. We used forward selection to determine which environmental variables were related to response metrics. Forward selection (Blanchet *et al.*, 2008) of the explanatory variables was achieved using the ordistep{vegan} function in R 3.6.3 (R Core Team 2018) (a = 0.05). Prior to RDA, community data was Hellinger transformed to down-weight the influence of rare species (Legendre et Gallagher, 2001). RDAs were performed on the full broad-scale scale data set of sites in the Upper St. Lawrence River, as well as on St. Lawrence River and Ottawa River sites separately to test if different environmental variables structure the fish and macroinvertebrate communities with and without the broad-scale refuge. All statistical analyses were performed in R 3.6.3 (R Core Team 2020).

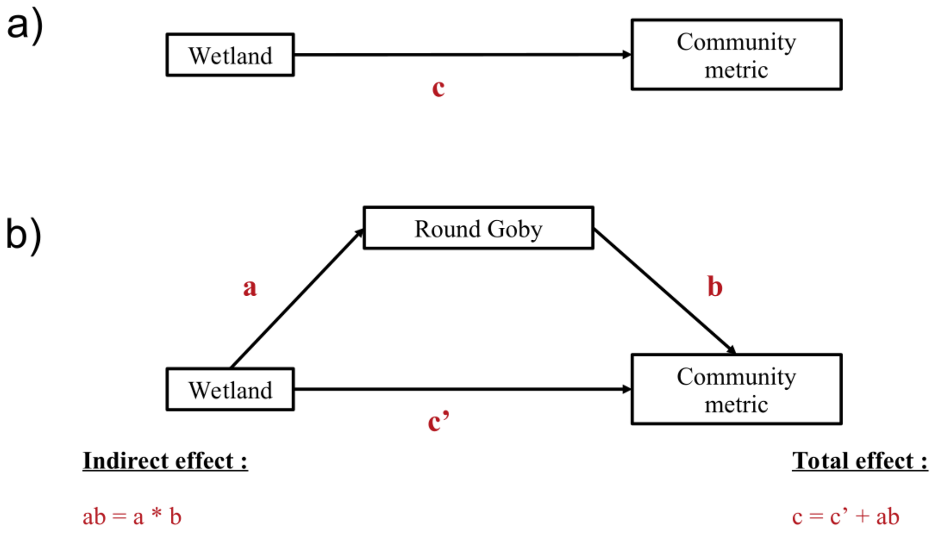

Figure 2.2. Structural equation models (SEMs) of hypotheses to test total, direct and indirect effects of wetlands on macroinvertebrate and fish community diversity and composition: a) Model without an indirect effect mediating wetland influence on community indices; path c represents the total effect of wetlands on community diversity and composition. The total effect includes the direct effect and all possible indirect effects of wetlands on community diversity and composition. b) Model with an indirect effect of wetlands on community indices via reduced round goby abundance; path a is the effect of wetland on the mediator variable (round goby abundance), path b is the effect of round goby abundance on community diversity and composition, and path c’ represents the direct effect of wetland on community diversity and composition; Path ab = a*b is the product of path a and path b and represents the indirect effect of wetlands on community diversity and composition via round goby abundance

2.5 Results

2.5.1 Broad-scale conductivity gradient and local wetland refuges reduce invader abundance

We detected broad-scale conductivity and local wetland refuges for macroinvertebrate and fish communities in the face of round goby invasion in the Upper St. Lawrence River. In accord with other studies in this system (Iacarella et Ricciardi, 2015 ; Kestrup et Ricciardi, 2009), we found a positive relationship between round goby abundance and conductivity at a broad spatial scale in the Upper St. Lawrence River (Table 2.1, Line 3, Fig. 2.3a, generalized linear model). Wetlands provided local refuges that limited round goby abundance: round goby abundances were lower inside wetlands compared to outside wetlands within invaded high conductivity waters (Table 2.1, Line 2, Fig. 2.3a, generalized linear model). The effect of wetlands in dampening round goby abundance was dependent on water conductivity, and only apparent in the high conductivity water and absent at low water conductivity sites (The wetland: conductivity interaction; Table 2.1, Line 4, generalized linear model; Fig. 2.3a). Conductivity and the presence of wetlands were therefore the two major environmental variables that structured round goby abundance across the Upper St. Lawrence River in our study. The effect size of conductivity on round goby abundance was approximately twice as large as the effect size of wetlands, but the effect size of wetland on round goby abundance was strongly negative in high conductivity water (Fig. 2.3b). The effect size of wetlands on round goby abundance was slightly negative with wide error bars in low conductivity water (Fig. 2.3b.).

Table 2.1. Generalized linear model results for the influence of the broad-scale conductivity gradient, wetlands, and round goby abundance as predictors of community diversity indices: Shannon diversity (Shannon), Pielou Evenness (Evenness), taxon or species richness (Richness), Local Contribution to Beta Diversity (LCBD), and total abundance of macroinvertebrate and fish communities (Abundance). The influence of conductivity and wetland on round goby abundance are reported. In each model, variables and interactions were selected using AIC values. Both macroinvertebrate and fish diversity indices were included in generalized linear models; these are referred to as Macro and Fish, respectively. Bold *P*-values are <0.05. Interaction between wetland and conductivity is referred to as Wet:Cond in the table. Significant findings are summarized in Fig. 2.3 for round goby abundance and Fig. 2.4 for macroinvertebrate and fish community diversity indices and composition.

Line	**Response variable**	**Predictor**	**Estimate (s.e.)**	**Df**	**T-value**	**P-value**
1	**Round goby**	Intercept	1.625 (0.452)	8	3.591	**0.0003**
2		Wetland	1.619 (0.479)	8	3.379	**0.0007**
3		Conductivity	0.005 (0.001)	8	3.199	**0.001**
4		Wet:Cond	-0.004 (0.001)	8	-2.37	**0.0177**
5	**Shannon Macro**	Intercept	0.932 (0.082)	25	11.317	**2.5e-11**
6		Conductivity	-0.0007 (0.0002)	25	-3.227	**0.003**
7	**Evenness Macro**	Intercept	1.99 (0.177)	25	11.241	**2.88e-11**
8		Conductivity	-0.0013 (0.0005)	25	-2.708	**0.012**
9	**Richness Macro**	Intercept	0.085 (0.006)	25	12.912	**1.47e-12**
10		Wetland	0.028 (0.009)	25	3.167	**0.004**
11	**Abundance Macro**	Intercept	7.287 (0.35)	23	20.809	**<2e-16**
12		Wetland	-0.567 (0.284)	23	-1.997	**0.045**
13		Conductivity	-0.002 (0.001)	23	-2.901	**0.003**
14	**Shannon Fish**	Intercept	0.77 (0.079)	25	9.629	**6.85e-10**
15		Wetland	-0.052 (0.095)	25	-0.551	0.586
16	**Evenness Fish**	Intercept	1.755 (0.183)	25	9.551	**8.04e-10**
17		Conductivity	-0.0007 (0.0005)	25	-1.33	0.196
18	**Richness Fish**	Intercept	6.0e-02 (2.089e-02)	23	2.874	**0.008**
19		Wetland	7.9e-02 (2.856e-02)	23	2.782	**0.011**

20		Conductivity	2.5e-04 (2.856e-02)	23	2.730	**0.011**
21		Wet:Cond	3.1e-04 (1.084e-04)	23	-2.873	**0.008**
22	**Abundance Fish**	Intercept	4.816 (0.289)	25	16.665	**4.75e-15**
23		Wetland	0.355 (0.354)	25	1.004	0.325
24	**LCBD Macro**	Intercept	21.722 (3.193)	25	6.803	**3.94e-07**
25		Wetland	9.013 (4.516)	25	1.996	0.057
26	**LCBD Fish**	Intercept	22.004 (1.423)	25	15.464	**2.63e-14**
27		Wetland	8.454 (1.991)	25	4.246	**0.0002**

2.5.2 Broad-scale conductivity gradient and local wetland refuges enhance community diversity

Conductivity and the presence of wetlands were two major environmental variables that structured the macroinvertebrate (Fig. 2.4a–d) and fish (Fig. 2.4e, f) diversity in the Upper St. Lawrence River (Table 2.1, generalized linear models). High conductivity water, where exotic round gobies are well established, had a higher Shannon diversity (Table 2.1, Line 6, Fig. 2.4a) and Pielou's Evenness (Table 2.1, Line 8), but lower total abundance of macroinvertebrate communities (Table 2.1, Line 13, Fig. 2.4c). For the native fishes, however, conductivity had positive effects on the fish community species richness (Table 2.1, Line 20). Across the conductivity gradient, sites within wetlands had, relative to sites outside wetlands, higher macroinvertebrate taxon richness (Table 2.1, Line 10, Fig. 2.4c), higher macroinvertebrate abundance (Table 2.1, Line 12, Fig. 2.4d) and lower fish species richness (Table 2.1, Line 26). Local Contribution to Beta Diversity (LCBD) of fish (Table 2.1, Line 27, Fig. 2.4f) was also higher inside wetlands. We found a significant interaction of wetland and conductivity on species richness of the native fish community: fish species richness was lower in wetlands within invaded high conductivity waters compared to in wetlands at low water conductivity sites (Table 2.1, wetland x conductivity Line 21, 4e).

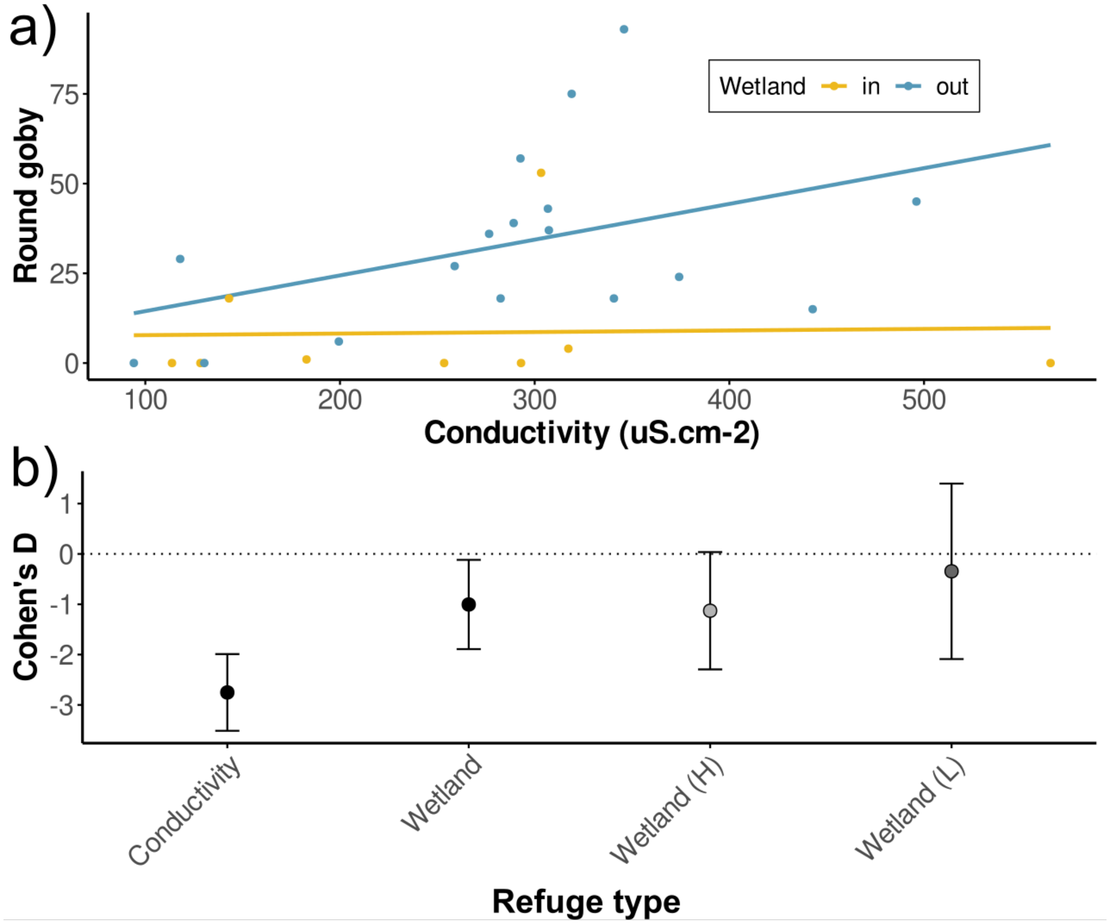

Figure 2.3. Identification of different refuge types in the Upper St. Lawrence River, and their relative influences in reducing round goby abundance. a) Linear positive relationship between broadscale water conductivity gradient and round goby abundance, (generalized linear model, Table 2.1, Line 2); b) Cohens' D effect size of conductivity and wetlands on round goby abundance: all sites, only high conductivity wetland sites (H), and only low conductivity wetland sites (L)

We found support for the positive effects of wetlands on taxon richness of macroinvertebrates (Table 2.2, Line 8), the negative effects of wetlands on fish species richness (Table 2.2, Line 38), and the positive effect of wetlands on LCBD of the fish community (Table 2.2, Line 78) at high water conductivity sites. Enhanced community diversity, richness, evenness, and LCBD of macroinvertebrate and fish communities were directly accounted by the habitat provisioning of wetlands; while wetlands provided refuges by limiting round goby abundance, positive community diversity effects were not explained by lessened round goby impact in wetlands (Table 2.2, SEMs, Fig. 2.2b).

2.5.3 Broad-scale conductivity gradient and local wetland refuges structure community composition

There were pronounced effects of conductivity and wetlands on macroinvertebrate and fish community composition (Fig. 2.5a, b, RDAs). The strong clustering of samples on the conductivity axis in both macroinvertebrate and fish communities confirmed that conductivity was the main driver of community differences between the low-conductivity and high conductivity shoreline habitats. To identify structuring variables of macroinvertebrate and fish communities at local scales within water types, only sites from either the Ottawa or St. Lawrence River were used in a subset of RDAs. Among low-conductivity sites, no variable was selected by the forward selection procedure. Thus, wetlands influenced macroinvertebrate and fish community composition only in the high conductivity invaded waters of the Upper St. Lawrence River (Fig. 2.5c, d, RDAs). Details on specific macroinvertebrate and fish community taxon differences across the conductivity and wetland refuges are provided in ANNEX B Figures 9–12.

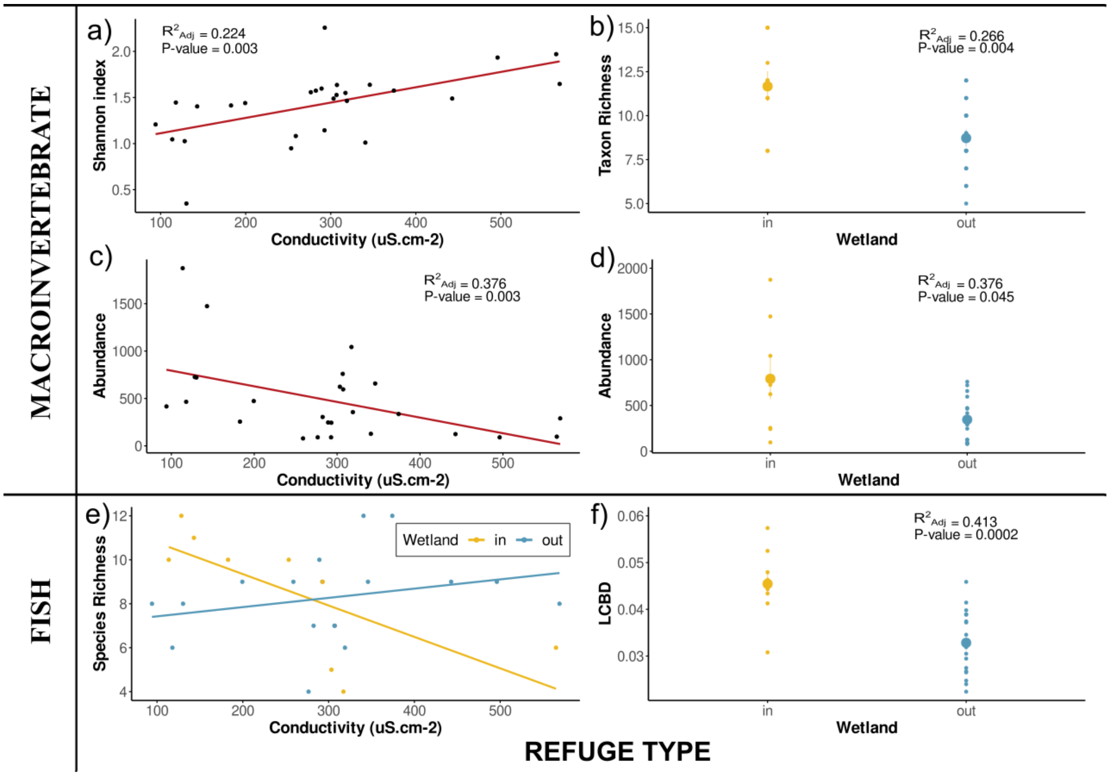

Figure 2.4. Broad-scale conductivity gradient and local wetland refuges enhance native community diversity. The left panels display linear relationships between the conductivity gradient across the Upper St. Lawrence River and macroinvertebrate community of the a) Shannon indices, c) abundance, and fish community e) species richness. The right panels displays relationships between inside and outside wetlands, macroinvertebrate community b) taxon richness, d) abundance, and fish community f) Local Contribution to Beta Diversity (LCBD). For the b), d) and f) mean and standard error are represented over raw data. Statistical results for generalized linear models associated with each of these panels are summarized in Table 2.1

2.6 Discussion

Our study supports the presence of different refuge types that constrain exotic round goby abundance and promote native freshwater biodiversity at the ecosystem scale in the Upper St. Lawrence River. The conductivity gradient had a twice as strong effect as wetlands in excluding round gobies from low conductivity habitats. Wetlands were effective in limiting round goby abundances in invaded waters. Wetlands, and not solely ecological interactions through reduced round goby abundances, increased the diversity of macroinvertebrate and to a lesser effect, fish, communities within invaded waters. Our findings suggest that environmental heterogeneity in producing different refuge types has an important yet under-appreciated role in combining to maintain native community diversity at a whole-ecosystem scale in face of exotic invasion.

2.6.1 Broad-scale conductivity gradient and local wetland refuges reduce invader abundance

Our results support the findings of other previous studies that found that low conductivity waters exclude round gobies (Baldwin *et al.*, 2012 ; Iacarella et Ricciardi, 2015), as well as other Ponto-Caspian exotics (Echinogammarus ischnus amphipods:, Kestrup et Ricciardi, 2009; dreissenid mussels: Neary et Leach, 1992; Jones et Ricciardi, 2005), and thus represent an important refuge in the Upper St. Lawrence River. However, we also detected previously underappreciated refuges from round goby invasion in wetlands along shoreline environments. The refuge effect from wetlands in reducing round goby abundance could be the result of substrate preferences of this benthic fish species. Round gobies preferentially colonize, and are found in greater densities, on rock and cobble substrates (Ray et Corkum, 2001 ; Young *et al.*, 2010). Soft-bottomed wetlands with high biological productivity appear to be less hospitable for this invasive fish in the Lower Great Lakes (Cooper *et al.*, 2007 ; Coulter *et al.*, 2015), although their role as a refuge for native aquatic species has not previously been fully explored. Local refuges provided by wetlands could be of particular importance because of their role in locally reducing invasive round goby abundance, especially in the invaded high conductivity waters of the Upper St. Lawrence River. Given that dispersal between communities is higher at smaller spatial scales than at larger spatial scales, local refuges from invasive species in patchy wetlands could potentially provide important demographic subsidies of individuals belonging to native species in surrounding areas (Melbourne *et al.*, 2007), enhancing native community resilience in more heavily invaded areas of ecosystems (Strayer *et al.*, 2006).

Table 2.2. Results of mediation analysis using structural equation models (SEMs) to test for total, direct and indirect (mediated by round goby abundance) effects of wetlands on community diversity and composition for macro (macroinvertebrates) and fish. The path c is the total effect of wetlands on community diversity and composition. The total effect includes the direct effect and all possible indirect effects of wetlands on community diversity and composition (Fig. 2.2a). Path a is the effect of wetland on the mediator variable (round goby abundance), path b is the effect of round goby abundance on community diversity and composition, and path c’ represents the direct effect of wetland on community diversity and composition; Path ab = a*b is the product of path a and path b and represents the indirect effect of wetlands on community diversity and composition via round goby abundance (Fig. 2.2b). The transformation used for each community is specified after each response variable in the table. Bold *P*-values are <0.05.

Line	Response variable	Path	Estimate	SE	Z	Ci lower	Ci upper	P-value
1	**Shannon macro**	**a**	36.100	13.547	2.665	5.928	59.312	**0.008**
2		**b**	0.001	0.002	0.636	-0.004	0.004	0.525
3		**c'**	-0.197	0.238	-0.828	-0.726	0.225	0.408
4		**ab**	0.045	0.071	0.644	-0.104	0.179	0.520
5		**c**	-0.152	0.231	-0.658	-0.609	0.319	0.511
6	**Richness macro**	**a**	36.100	13.547	2.665	5.928	59.312	**0.008**
7		**b**	0.027	0.015	1.771	0.006	0.064	0.076
8		**c'**	-3.909	1.250	-3.127	-5.903	-0.771	**0.002**
9		**ab**	0.981	0.546	1.795	0.108	2.314	0.073
10		**c**	-2.929	1.257	-2.330	-5.140	-0.137	0.020
11	**Evenness macro**	**a**	36.100	13.547	2.665	6.028	59.312	**0.008**
12		**b**	0.000	0.001	-0.276	-0.003	0.001	0.783
13		**c'**	0.023	0.095	0.244	-0.176	0.202	0.807
14		**ab**	-0.008	0.026	-0.308	-0.081	0.033	0.758
15		**c**	0.015	0.093	0.166	-0.159	0.213	0.869
16	**Abundance macro**	**a**	36.100	13.547	2.665	5.928	59.313	**0.008**
17		**b**	-0.482	1.211	-0.398	-3.502	0.916	0.690
18		**c'**	40.010	104.196	0.384	-289.596	197.290	0.701
19		**ab**	-17.410	42.727	-0.407	-133.529	40.346	0.684

20		**c**	22.600	96.282	0.235	-226.425	177.310	0.814
31	**LCBD macro**	**a**	36.100	13.547	2.665	5.928	59.312	**0.008**
32		**b**	0.000	0.000	-1.324	0.000	0.000	0.186
33		**c'**	-0.011	0.010	-1.129	-0.035	0.006	0.259
34		**ab**	-0.005	0.004	-1.299	-0.017	0.000	0.194
35		**c**	-0.016	0.009	-1.729	-0.038	0.000	0.084
36	**Shannon fish**	**a**	36.100	13.547	2.665	6.028	59.312	**0.008**
37		**b**	-0.004	0.003	-1.254	-0.014	0.000	0.210
38		**c'**	0.564	0.235	2.403	0.059	0.996	**0.016**
39		**ab**	-0.156	0.118	-1.322	-0.516	0.003	0.186
40		**c**	0.408	0.215	1.901	-0.018	0.861	0.057
41	**Richness fish**	**a**	36.100	13.547	2.665	6.028	59.312	**0.008**
42		**b**	-0.017	0.018	-0.976	-0.065	0.008	0.329
43		**c'**	2.252	1.400	1.609	-0.927	4.797	0.108
44		**ab**	-0.624	0.590	-1.057	-2.395	0.147	0.291
45		**c**	1.629	1.276	1.277	-0.969	4.162	0.202
46	**Evenness fish**	**a**	36.100	13.547	2.665	5.928	59.312	**0.008**
47		**b**	-0.002	0.001	-1.294	-0.005	0.000	0.196
48		**c'**	0.156	0.118	1.323	-0.092	0.376	0.186
49		**ab**	-0.057	0.040	-1.452	-0.166	-0.001	0.147
50		**c**	0.099	0.119	0.832	-0.129	0.337	0.405
51	**Abundance fish**	**a**	36.100	13.547	2.665	5.928	59.313	**0.008**
52		**b**	-0.482	1.211	-0.398	-3.502	0.916	0.690
53		**c'**	40.010	104.196	0.384	-289.596	197.290	0.701
54		**ab**	-17.410	42.727	-0.407	-133.529	40.346	0.684
55		**c**	22.600	96.282	0.235	-226.425	177.310	0.814
76	**LCBD fish**	**a**	36.100	13.454	2.683	7.358	59.336	**0.008**
77		**b**	0.000	0.000	-0.315	0.000	0.000	0.753
78		**c'**	-0.015	0.005	-2.654	-0.026	-0.006	**0.008**

79	**ab**	-0.001	0.003	-0.364	-0.007	0.004	0.716
80	**c**	-0.016	0.005	-3.232	-0.023	-0.003	**0.001**

2.6.2 Local wetland refuges enhance community diversity

Wetlands generally have different substrate, organic matter load, dissolved oxygen levels, nutrient concentrations and environmental complexity from other surrounding shorelines (Krieger, 1992 ; Wetzel, 1990), which can enhance the diversity of macroinvertebrate communities (Nelson *et al.*, 2000). These characteristics of wetlands likely contributed to the positive effects on community diversity that we observed in wetland macroinvertebrate communities in our study (Fig. 2.4). We did not detect indirect benefits of the wetlands on native macroinvertebrate and fish community biodiversity through reduced round goby abundances (Table 2.2, Fig. 2.2b). The SEMs and RDAs (Fig. 2.5) with only high-conductivity sites also indicated that wetland habitats enhanced macroinvertebrates taxon richness, fish community Shannon index and LCBD, as well as structured fish communities. Our study therefore confirms that wetland habitats can be of crucial importance for the preservation of aquatic biodiversity in invaded freshwater landscapes (Bowers et Szalay, 2004 ; Cooper *et al.*, 2007, 2009 ; Young *et al.*, 2010).

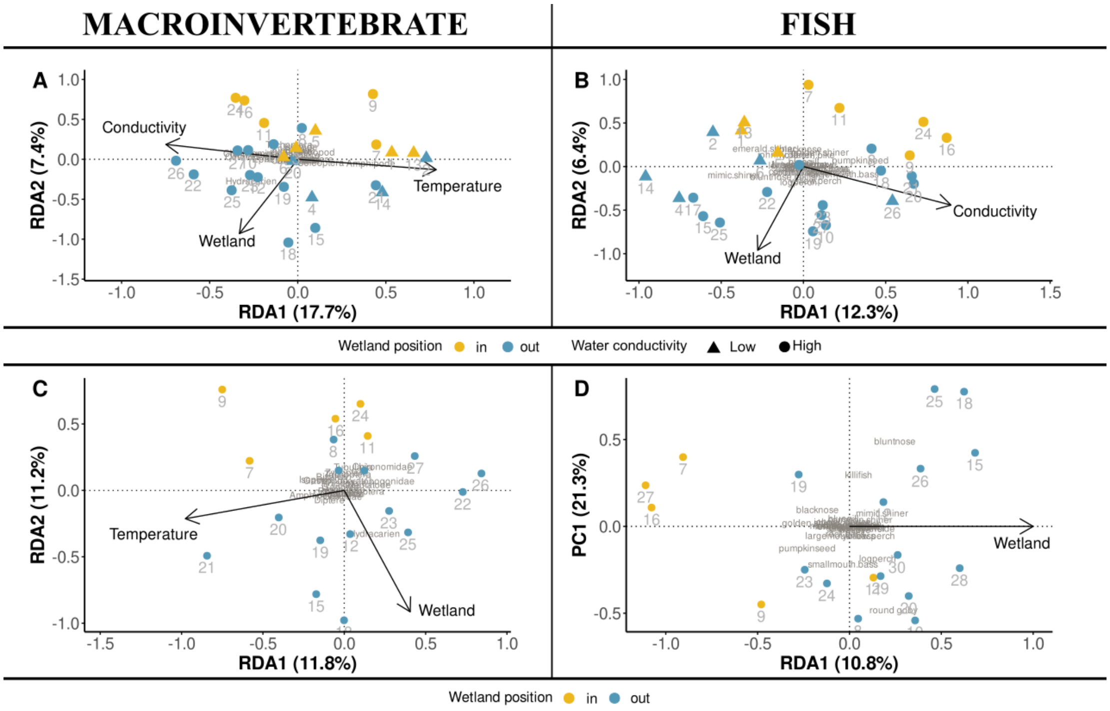

Figure 2.5. Broad-scale conductivity gradient and local wetland refuges structure communities: RDA biplots with the full dataset for a) macroinvertebrate and b) fish communities and RDA biplots with a reduced dataset of only St. Lawrence River sampling sites (high conductivity) for c) macroinvertebrate and d) fish communities. In all panels, arrows represent forward selected environmental variables; numbers represent sampling sites. The yellow symbols represent sampling sites within wetlands and blue symbols represent sampling sites outside wetlands. The triangles represent sampling sites in the low conductivity water and circles represent sampling sites in the high conductivity water.

Wetlands had a direct positive effect in increasing the diversity of macroinvertebrate communities, but less so in fish communities (Fig. 2.4). Wetlands in high conductivity water hosted lower fish species richness compared to wetlands in low conductivity water (Table 2.1, wetland x conductivity Line 21, 4e). Following their establishment in aquatic ecosystems over several decades, round gobies have become a key food source of piscivorous fish species in the Lower Great Lakes (Crane *et al.*, 2015) and in the St. Lawrence River (Morissette *et al.,* 2018). The lower abundance of round gobies inside wetlands may therefore be a limiting prey resource for piscivorous fish that is more plentiful at open-water shore sites in high conductivity waters. The difference in round goby abundance between wetland and open-water shore sites may therefore potentially cause certain fish species to favor open-water shore habitats over wetlands in invaded, high conductivity water. Further, different fish species utilize wetlands in various manners: some species are permanent resident of wetlands (e.g., *Ameiurus nebulosus* (brown bullhead), *Umbra limi* (central mudminnow) and *Lepisosteus osseus* (longnose gar)), while other fish species only spawn in wetlands and then leave them for open-water areas (e.g., *Esox lucius* (northern pike), *Cyprinus carpio* (common carp), and *Notropis hudsonius* (spottail shiner)) (Jude et Pappas, 1992). The dynamic nature of fish communities in wetlands may have limited our ability to properly estimate their alpha diversity at a given point in time. Although fish alpha diversity was reduced in high conductivity water wetlands, fish beta diversity was increased by wetlands. Therefore, high conductivity water wetlands in the Upper St. Lawrence River have relatively species-poor fish communities, yet also host to unique fish assemblages compared with open-water shore sites.

2.6.3 Different refuges dampen invasion and enhance diversity at the whole ecosystem scale

Wetlands presented refuges that both reduced local round goby abundance, and also directly increased both alpha and beta diversity of macroinvertebrate and beta diversity of fish within invaded, high conductivity waters. Interestingly, wetlands did not have strong effects on macroinvertebrate and fish community structure in the low conductivity water of the Ottawa River when community data from the high-conductivity water of St. Lawrence River and low-conductivity water from the Ottawa River were analyzed separately. The low-conductivity water is a refuge from invasion, therefore local wetlands seem to be less important for native species when nested within a spatially broader refuge. A caveat is that more wetlands and open-water shore sites were sampled in high conductivity water than in low conductivity water, which could have reduced our ability to detect wetland effects in low conductivity water. However, taken altogether, local refuge inside wetlands enabled diverse assemblages of macroinvertebrates and unique assemblages of fish, making these critical habitats for aquatic diversity, especially within invaded, high conductivity waters. The environmental heterogeneity provided by wetlands had a strong positive effect on macroinvertebrate community diversity, and also to a lesser extent for fish communities. Environmental heterogeneity has been shown to increase species diversity in many groups (Tews *et al.*, 2004), but it can also decrease species diversity in some cases (Sullivan et Sullivan, 2001). The effect of environmental heterogeneity can vary depending on how the studied animal guild perceives this heterogeneity and the spatial scale of the study (Tews *et al.*, 2004).

Most of research on environmental heterogeneity in invaded environments to date has been done in terrestrial ecosystems; our study joins a handful of papers that have addressed this topic in freshwater ecosystems (Iacarella et Ricciardi, 2015 ; Kestrup et Ricciardi, 2009 ; Latzka *et al.*, 2016). Refuges to invasion at local scales (Holway *et al.*, 2002 ; Krassoi *et al.*, 2008 ; Leprieur *et al.*, 2006 ; Menke et Holway, 2006) and at broad scales (Anton *et al.*, 2014 ; Kestrup et Ricciardi, 2009 ; Menke *et al.*, 2007) have been recognized as important driver of invasive abundance and native community diversity. Our results confirm the results of other studies that environmental heterogeneity can locally decrease invasion impact in invaded areas (Melbourne *et al.*, 2007 ; Ricciardi *et al.*, 2013 ; Vander Zanden *et al.*, 2017). Our findings uniquely highlight that environmental heterogeneity from different types of refuges can dampen invasion impact and enhance aquatic community diversity at the whole ecosystem scale. In our study, broad-scale environmental heterogeneity, such as the conductivity gradient across the Upper St. Lawrence River, can allow native species to be sheltered from invasive species and create diversity of communities by structuring composition of organisms. Local scale heterogeneity, such as the patchy wetlands within the invaded, high conductivity waters, have the potential to reduce invasive species abundance and increase local community diversity. Freshwater ecosystems are among the most invaded ecosystems in the world (Richardson et Pyšek, 2008), and our findings are reported from one of the most economically and culturally important invaded bodies of freshwater in North America, the St. Lawrence River (Carignan et Lorrain, 2000 ; Kavcic, 2016 ; Vincent et Dodson, 1999).

2.7 Caveats

Other previous research has investigated macroinvertebrate diversity patterns in the Upper St. Lawrence River, and this research found contrasting patterns to what we report in our study (Kipp *et al.*, 2012 ; Kipp et Ricciardi, 2012). These previous other studies focused on round goby impacts on macroinvertebrate communities in relation to invasion history, and in contrast with our results, found that round goby abundance was negatively correlated with macroinvertebrate diversity (Kipp et Ricciardi, 2012), especially for molluscs (Kipp *et al.,* 2012). These other studies used macroinvertebrate sampling methods that targeted sessile organisms such as molluscs, but these methods were not optimal for sampling the rapidly swimming invertebrates. Our field sampling methods targeted swimming macroinvertebrates, such as amphipods and insect larvae, and we found that macroinvertebrate community Shannon diversity was higher, not lower, in high conductivity water where round gobies are well-established and abundant. This finding can be explained because the evenness of the overall community assemblage is negatively affected by conductivity ($P = 0.012$, $R2 = 0.179$, ANNEX B Fig. 13); amphipod relative abundance was lower at heavily invaded sites with higher evenness ($P = 4.42e - 05$, $R2 = 0.482$, ANNEX B Fig. 14). Therefore, amphipods dominated in low conductivity refuges where macroinvertebrate community evenness and Shannon index were lower. The lack of detected effects of round goby abundance on macroinvertebrate diversity could be the result of not specifically sampling for gastropods in our study. In lentic habitats, round gobies favor molluscs and chironomids, but they have very high diet diversity and are capable of adapting to locally abundant food sources (Kornis *et al.,* 2012). Our study suggests that amphipods are likely an important food resource for round gobies at invaded, high conductivity sites in the Upper St. Lawrence River, which has been shown to be an important prey item of round gobies in other systems (Raby *et al.*, 2010 ; Tarkan *et al.*, 2019).

A long- term survey (1995 to 2017) of fish community diversity in the St. Lawrence River, with areas overlapping with our study (Morissette *et al.,* 2018), found no effects of the round goby on fish species diversity indices but rather specific local effects on certain fish species abundances such as the tessellated darter (Etheostoma olmstedi). We found that fish community Shannon diversity was reduced at high round goby abundance. Our study focused on lentic waters; Morissette et al. (2018) sampled both lentic and lotic habitats with different sampling gear over a wider geographic area. Round gobies prefer warmer water (optimum around 26 C) (Kornis *et al,.* 2012); they could therefore be more abundant and have stronger impacts in lentic waters. The results we show in this manuscript indicate that round goby continue to have negative effects on fish diversity in certain areas of the Upper St. Lawrence River. No other studies to our knowledge investigated patterns of fish diversity inside wetlands in the Upper St. Lawrence River, which we show here to host unique fish assemblages with high LCBD values (Fig. 2.4e, f). None of these other studies of fish and macroinvertebrates in the St. Lawrence River explored community patterns across different refuge types that amount to a net effect of constraining round goby invasion and enhancing aquatic biodiversity at the whole ecosystem scale.

2.8 Conclusions

We found that different refuge types dampened invasion impact and favored aquatic biodiversity at a whole-ecosystem scale in a complex, environmentally heterogeneous river system. Our findings suggest that conservation efforts will likely have greater effect if they focus on the maintenance of environmental heterogeneity outside of large protected areas, by protecting a wide variety of local patches of habitats that provide key refuges for the persistence of diverse native communities. The low conductivity of the Ottawa River water provided a strong refuge that excluded round goby presence, and so the relative importance of wetlands in structuring native communities was reduced in these waters. Local heterogeneity created by habitat patches could therefore be less important in maintaining native species diversity in face of exotic invasion when nested inside broader scale refuges. Within invaded habitats, other studies have shown that high levels of native diversity at small local spatial scales can reduce invasive species success because of biotic resistance (Byers et Noonburg, 2003 ; Davies *et al.*, 2005 ; Melbourne *et al.*, 2007). The maintenance of diverse communities across spatially environmentally heterogeneous habitats also has the added potential benefit of providing compensatory dynamics through a diversity of ecological responses that could further buffer impacts from exotic invasion and other environmental change (Gonzalez et Loreau, 2008). More empirical work is needed to understand the role of different refuges in combining to maintain native population and community diversity, and their importance in promoting ecological and evolutionary processes for native species coexistence with invasive species at whole ecosystem and landscape-level scales.

CHAPTER III

EFFECTS OF FRESHWATER SALINIZATION ON A PRISTINE PLANKTONIC FOOD WEB

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3.1 Abstract

Freshwater salinization is a widespread issue, but evidence of ecological effects on aquatic communities remains scarce. We experimentally exposed salt-naive plankton communities of a north-temperate, freshwater lake to a gradient of chloride (Cl^-) concentration (0.27-1400 mg Cl L^{-1}) with in-situ mesocosms. Following six weeks, we measured changes in the diversity, composition, and abundance of eukaryotic 18S rRNA gene. Total phytoplankton biomass remained unchanged, but we observed a shift in dominant phytoplankton groups with increasing salt concentration, from Cryptophyta and Chlorophyta at lower chloride concentrations (<185 mg Cl^- L^{-1}) to Ochrophyta at higher chloride concentrations (>185 mg Cl^- L^{-1}). Crustacean zooplankton and rotifers were sensitive to the salinity, and disappeared at low chloride concentrations (<40 mg Cl^- L^{-1}). While ciliates thrived at low chloride concentrations (<185 mg Cl^- L^{-1}), fungal groups dominated at intermediate chloride concentrations (185 mg Cl^- L^{-1} to 640 mg Cl^- L^{-1}), and only phytoplankton remained at the highest chloride concentrations (> 640 mg Cl^- L^{-1}).

Key Words: Salinization, freshwater, eukaryote community, chloride, plankton, water quality guidelines, 18S rRNA metabarcoding

3.2 Introduction

Salt pollution and accelerated weathering from human activities are drastically changing freshwater ion composition (Kaushal *et al.*, 2018). Such freshwater salinization syndrome (Kaushal *et al.*, 2018) is a widespread yet underappreciated environmental problem that profoundly affecting freshwater community composition, diversity, and stability (Hintz *et al.*, 2017 ; Hintz et Relyea, 2019 ; Mo *et al.*, 2021 ; Moffett *et al.*, 2021), which threatens freshwater ecosystems globally (Cañedo-Argüelles *et al.*, 2013 ; Castillo *et al.*, 2018 ; Herbert *et al.*, 2015 ; Hintz et Relyea, 2019). Plankton communities are the resource base that supports higher trophic levels, such as fisheries, and essential ecosystem functions such as primary productivity, decomposition, and nutrient and carbon cycling (Kalff, 2001). Recent studies have addressed the effects of anthropogenic salinization on zooplankton (Arnott *et al.*, 2020 ; Hintz *et al.*, 2017 ; Hintz et Relyea, 2019 ; Moffett *et al.*, 2021 ; Setubal *et al.*, 2020), but little research has addressed salinization effects on other planktonic groups, such as phytoplankton (Ballot *et al.*, 2009 ; Blinn *et al.*, 2004 ; Fay et Shi, 2012 ; Hintz *et al.*, 2017 ; Porter-Goff *et al.*, 2013), but little research has addressed salinization effects on other planktonic groups, such as phytoplankton (Ballot *et al.*, 2009 ; Blinn *et al.*, 2004 ; Fay et Shi, 2012 ; Hintz *et al.*, 2017 ; Porter-Goff *et al.*, 2013), fungi (Gonçalves *et al.*, 2019 ; Sauer *et al.*, 2016 ; Schäfer *et al.*, 2012 ; Silva *et al.*, 2021), and to our knowledge one other study has addressed ciliates and other unicellular eukaryotes (Mo *et al.*, 2021). We present one of the first study to address freshwater salinization impacts using a DNA metabarcoding framework that considers all of these groups together within the same community.

Planktonic food webs are composed of diverse organisms such as ciliates and flagellates, fungi, phytoplankton, and zooplankton (copepods, cladocerans, and rotifers) (Kalff, 2001). Zooplankton play a critical food resource for higher trophic levels, and regulate water clarity, energy and nutrients in freshwater ecosystems (Carpenter *et al.*, 1985 ; Pace et Orcutt, 1981). Cladocerans are usually relatively tolerant to salinization (Lind et Jeyasingh, 2018 ; Moffett *et al.*, 2021 ; Sarma *et al.*, 2006 ; Searle *et al.*, 2016). However, *Daphnia* in soft water lakes were sensitive to low chloride concentrations (between 5 and 40 mg $Cl^- L^{-1}$) (Arnott *et al.*, 2020). Copepods can also vary in their response to salinization; while certain calanoids decrease in abundance at 200 mg $Cl^- L^{-1}$ (Evans et Frick, 2001 ; Moffett *et al.*, 2021), cyclopoid species seem more resistant and can maintain high abundance over 500 mg $Cl^- L^{-1}$ (Moffett *et al.*, 2021 ; Van Meter et Swan, 2014). Rotifers possess a wide range of tolerances to salinization, with tolerant species showing signs of reduced abundance at or beyond 1.5 g $Cl^- L^{-1}$ NaCl (Sarma *et al.*, 2006 ; Van Meter et Swan, 2014). Overall, tolerance thresholds to chloride concentrations are greatly variable among zooplankton taxa and seem to be influenced by local conditions (Arnott *et al.*, 2020 ; Moffett *et al.*, 2021). For phytoplankton, responses to elevated chloride levels can increase phytoplankton biomass (Fay et Shi, 2012 ; Hintz *et al.*, 2017) and shift community composition (Ballot *et al.*, 2009 ; Mo *et al.*, 2021 ; Porter-Goff *et al.*, 2013). Freshwater salinization can reduce growth and abundance of diatoms (Porter-Goff *et al.*, 2013), which are nutritious food sources for higher trophic levels (Taipale *et al.*, 2013). However, overall, our understanding of the impact of elevated chloride concentration on phytoplankton is deficient (Hintz et Relyea, 2017).

Our study provides one if the first investigation to empirically address community changes in diversity and relative abundance from unicellular to zooplankton within a freshwater eukaryote community of a salt-naïve boreal lake in response to increasing salinity. Our objectives were to: 1) determine the sensitivity/tolerance of different plankton groups to freshwater salinization and 2) evaluate how planktonic eukaryote community sensitivity relates to salinity water quality guidelines for the protection of aquatic freshwater life in US, Canada and European Union (EU) drinking water guidelines. We predicted that the abundance and composition of most planktonic groups would be negatively affected by salinization in a salt-naïve freshwater ecosystem. Further, we predicted that phytoplankton biomass would increase as a result of the release of grazing pressure associated with a loss of sensitive zooplankton groups (Fay et Shi, 2012 ; Hintz *et al.*, 2017 ; Moffett *et al.*, 2021). Traditional ecological monitoring of communities is labor intensive, costly, and morphological identifications can be challenging. Molecular approaches, such as DNA metabarcoding can be very useful for monitoring freshwater biodiversity (Cristescu, 2014 ; Lim *et al.*, 2016). In this study we investigated the planktonic eukaryote community using DNA metabarcoding with the eukaryotic 18S rRNA gene as target sequence. This approach allowed us to detect major shifts in community composition of eukaryotic organisms in semi-natural experimental setting. Our study addresses the paucity of research on ecological effects of salinization on freshwater eukaryote communities, and our findings provide perspectives on the applicability of water quality guidelines for the protection of aquatic life in Canada and in the United States. (Environment Canada and Climate Change, 2011 ; US EPA, 1988), and drinking water guidelines of the European Union (EU).

3.3 Methods

We conducted an in-situ field experiment in which we employed a gradient design in sodium chloride (NaCl) treatment to increase chloride concentration ranging from 0.27 mg $Cl^- L^{-1}$ to 1400 mg $Cl^- L^{-1}$ in a salt-naïve, north-temperate lake with no prior history of salinity exposure. Our experimental design concentrations representative of long term (Canada: 120 mg $Cl^- L^{-1}$; USA: 230 mg $Cl^- L^{-1}$) and short term (Canada: 640 mg $Cl^- L^{-1}$; USA: 860 mg $Cl^- L^{-1}$) water quality guidelines for chloride concentrations in freshwater, for the protection of aquatic life in Canada and the United States (US EPA 1988; Environment Canada and Climate Change 2011). Drinking water guideline throughout most of the EU are 250 mg Cl^- L^{-1} (Schulz and Cañedo-Argüelles 2019), however in Europe salinity water quality standards for the protection of aquatic life of freshwater ecosystems are mostly absent (Schuler et al. 2019).

3.3.1 In-situ field experiment

The mesocosm experiment was implemented with water and biological communities from Lake Croche (45°59'17.34" N / 74° 0'20.75" O), which is located at the Station de biologie des Laurentides de l'Université de Montréal (Québec, Canada). Lake Croche is a salt-naïve oligo-mesotrophic lake situated in the Laurentian region of Québec, which lies within the Canadian Shield, and has a low ambient chloride concentration of 0.27 mg Cl^- L^{-1}. The experimental design involved 21 mesocosms, from which we focused DNA sampling on 9 mesocosms (Fig. 3.1). The experiment was conducted for 6 weeks (June 23 to August 3, 2018). Lake water used to fill the mesocosms was sampled and analyzed at the beginning of the experiment (hereafter referred as 'start'), and each mesocosm was sampled after 3 weeks and after 6 weeks from the start of the experiment (see Appendix for supplementary methods; ANNEX C). Initial chloride concentrations were measured along with conductivity from water samples collected from the mesocosms following the NaCl addition. Conductivity was subsequently utilized as a proxy of chloride concentration because of a strong relationship between chloride and conductivity in this experiment ($R^2 = 0.986$, $p = <2e-16$)(Fig. 3.2), and further analysis were performed using calculated chloride concentration from conductivity measures. Sodium cation might have been partly or jointly responsible for measured effects, but since we had no direct measures of sodium and most of the literature refers to chloride concentration, we present our results in units of chloride concentration.

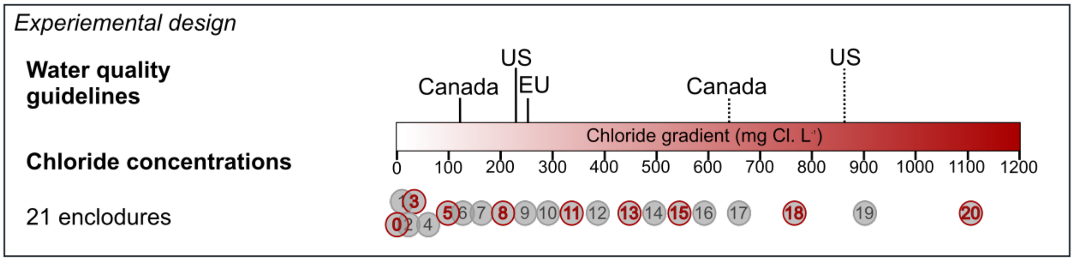

Figure 3.1. Experimental gradient design with chloride (Cl^-) concentrations of the 21 mesocosm enclosures (grey and red circles), 9 mesocosms enclosures sampled for 18S eukaryotic rRNA gene (red circle), and how mescocosm Cl^- concentrations relate to the short term application (dashed line) and long term (solid line) water quality guidelines recommended for Cl^- concentrations in freshwater environments by Canada and the United States (US EPA 1988; Environment Canada and Climate Change 2011) for the protection of aquatic life, and EU drinking water guidelines (Schuler *et al.,* 2019).

3.3.2 Molecular analyses

To detect changes in the diversity, relative abundance, and community composition of planktonic eukaryotes, we analyzed eukaryotic 18S rRNA gene (region V7) diversity from water samples collected from the mesocosms at the start of the experiment, and at each of weeks 3 and 6 of the experiment in 9 different mesocosms (Fig. 3.1, red circles). DNA field sampling methods and laboratory methods for filtration, DNA extraction, PCR amplification and sequencing are provided in ANNEX C. For bioinformatics of 18S metabarcoding, the DADA2 (Callahan *et al.*, 2016) workflow was used. Pseudo-pooling was used to infer Amplicon Sequence Variants (ASVs). ASVs refer to single DNA sequences recovered from a high-throughput marker gene analysis and are used to classify groups of species based on DNA sequences. We applied a variance stabilizing transformation method to the dataset of the different samples (McMurdie et Holmes, 2014). We investigated the potential positive relationship between Sequencing depth and ASV diversity in the different samples which was found to be negative (ANNEX C). We used R 4.0.3 (R Core Team 2020) phyloseq package (McMurdie et Holmes, 2013) rarefaction function to analyze rarefied data. Downstream analysis results of rarefied data are reported in ANNEX C Fig. A4-A6. Rarefaction did not have major impact on the results of the manuscript ANNEX C Fig. A4-A6. We therefore chose to report non-rarefied data in the main sections of the manuscript. Sequences are available at http://www.ncbi.nlm.nih.gov/bioproject/733220.

3.3.3 Data analyses

Multivariate regression tree

The Multivariate Regression Tree (MRT) technique splits the data into clusters of samples similar in their species composition based on environmental value thresholds. We included temperature, conductivity, DO, pH, and TP to construct the regression tree. Prior to MRT, community abundance data based on read counts was Hellinger transformed to down-weight the influence of rare species (Legendre et Gallagher, 2001). MRT analysis were performed in R 4.0.3 (R Core Team 2020).

Indicator species

To highlight indicator species in the different clusters generated by the MRT analysis, we used the indispecies package (De Cáceres et Legendre, 2009) in R 4.0.3 (R Core Team 2020). Indicator species are determined using species occurrences, species abundances and sites classification representing habitats type or disturbance states.

Diversity indices and generalized linear models

Community diversity indices were calculated using 18S metabarcoding read counts. We calculated taxon richness, Shannon diversity (Shannon 1948) and Pielou’s evenness (Pielou, 1966). These diversity indices were included as response variables in different generalized linear models that tested the influence of conductivity as a proxy of chloride concentration (ANNEX C).

Principal Coordinate analysis

To visualize differences in mesocosms ASV composition and abundance we performed Principal Coordinate Analysis (PCoA) on ASVs. We used Bray-Curtis dissimilarity distance on squared ASV community matrix. Each analysis produced a two-dimensional plot based on the first two PCoA scores. We used PERMANOVA using 9999 permutations to test the influence of salinity on the multivariate community data. All analysis were performed in R 4.0.3 (R Core Team 2020).

3.4 Results

3.4.1 Community shift with elevated chloride across trophic groups

Three plankton community clusters of ASVs were identified and splits were explained by conductivity corresponding to community splits at 185 and 640 mg $Cl^- L^{-1}$ (Fig. 3.2; MRT). The first cluster spanned low chloride concentrations between 0.27 and 185 mg $Cl^- L^{-1}$, the second cluster spanned intermediate chloride concentrations between 185 and 640 mg $Cl^- L^{-1}$ and the third cluster spanned high chloride concentrations greater than 640 mg $Cl^- L^{-1}$. The low chloride mesocosms (identified as 0 to 5 at week 3 and as mesocosm 8 at week 6) (Fig. 3.2) were comprised of diversified planktonic communities. These included phytoplankton (indicator phylums: Ochrophyta, Cryptophyta, Diatomea, Phragmoplastophyta) (details on indicator taxa ANNEX C Table A2), fungi (indicator phylums: Peronosporomycetes), as well as protozoans (indicator phylums: Ciliophora, MAST and Cercozoa) and multicellular eukaryotes, including zooplankton and rotifers, but with an increasing dominance of unicellular eukaryotes (mainly Ciliophora) as chloride increased within the group of low chloride mesocosms (Fig. 3.3). The intermediate chloride mesocosms (identified as 8 at week 3 to 13; Fig. 3.2) showed a sharp increase in fungal taxa (indicator phylums: Cryptomycota and Basidiomycota) in the planktonic community, but most zooplankton and

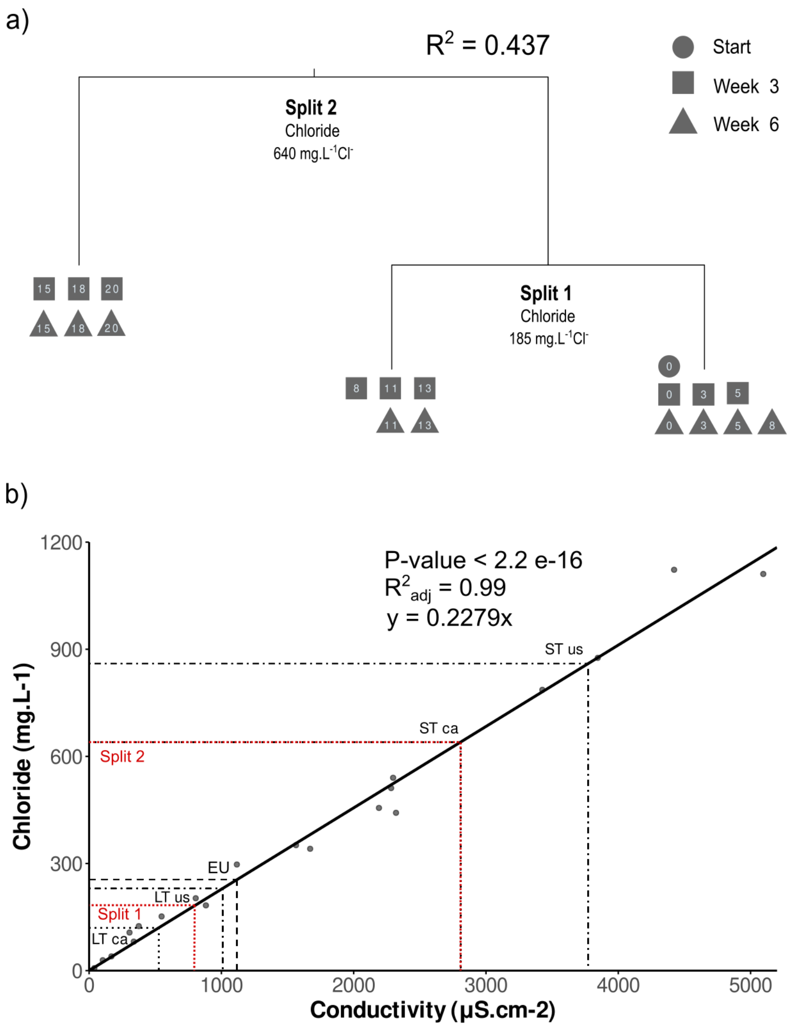

Figure 3.2. Multiple Regression Tree (MRT) of plankton community clustering in relation to chloride concentration and freshwater salinity water quality guidelines: a) MRT obtained from multiple regression analysis with environmental variables on the Hellinger-transformed ASV matrix. Each branch represents mesocosms with similar plankton communities, and splits are explained by chloride concentration. Enclosure shapes represent different sampling dates (circles refers to lake water at the start of the experiment, squares refer to week 3, and triangles refer to week 6) and numbers refer to the identity of mesocosms that correspond with different levels of the NaCl treatment (Fig 3.1). b) Linear regression between measured conductivity and chloride concentration in the larger set of mesocosms (21 mesocosms; Fig. 3.1). Black dashed lines are showing short term (ST) and long term (LT) water quality guidelines that are recommended for chloride concentrations in freshwater environments in Canada and the United States (US EPA 1988; Environment Canada and Climate Change 2011) for the protection of aquatic life. The EU dashed line represents drinking water guideline across much of the European Union (Schulz and Cañedo-Argüelles 2019). Red dashed lines indicate splits obtained with MRT analysis displayed above in panel a).

other unicellular eukaryotes were lost (Fig. 3.3). The high chloride mesocosms (identified as 15 to 20; Fig. 3.2) were characterized by the dominance of phytoplankton ASVs (indicator phylums: Ochrophyta and Diatomea), which represented almost the totality of the planktonic community at such water chloride (Fig. 3.3). Overall, chloride concentration had a significant effect on planktonic community composition (PERMANOVA p-value = 0.0001). The first planktonic community split as a response to increased chloride occurred at 185 mg Cl^{-} L^{-1} and is between the long-term freshwater chloride concentration recommended by Canada (120 mg Cl^{-} L^{-1}) and the United States (230 mg Cl^{-} L^{-1}) (Environment Canada and Climate Change, 2011 ; US EPA, 1988) (Fig. 3.2). The second planktonic community split occurred at 640 mg Cl^{-} L^{-1}, and represents the short-term freshwater chloride concentration recommended by Canada for the protection of aquatic life (Environment Canada and Climate Change 2011) (Fig. 3.2).

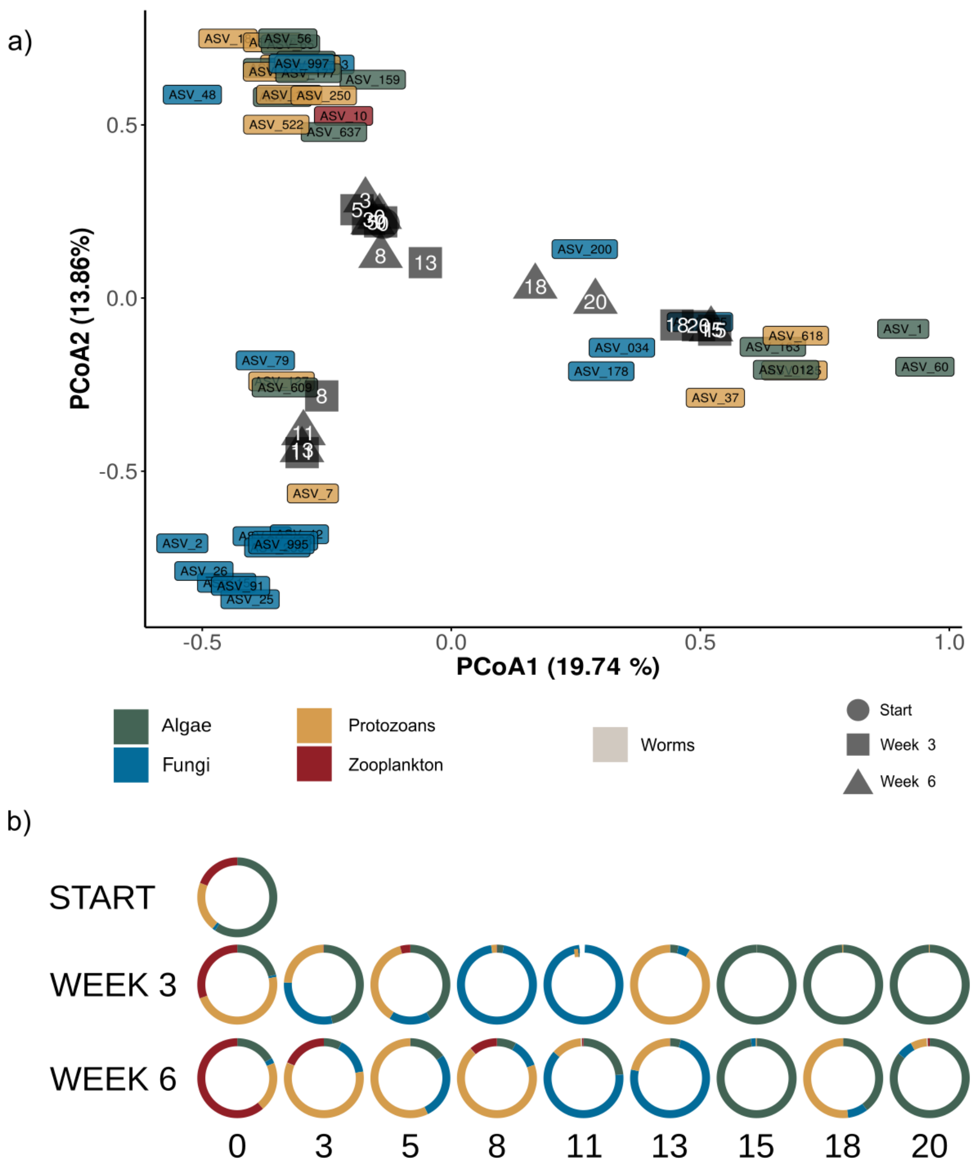

Figure 3.3. The response of the plankton community to elevated chloride concentration. a) Principal Coordinates Analysis (PCoA) with Bray Curtis dissimilarity matrix of squared ASV matrix. Labels are unique ASVs with colors showing their taxonomic group. Enclosure shapes represent different sampling dates (circles refers to lake water at the start of the experiment, squares refer to week 3, and triangles refer to week 6) and numbers are different levels of the NaCl treatment. Only significant ASVs from the indispecies analysis are displayed. b) Relative abundance of the different plankton groups. Each circle is an enclosure and the color within the circle are the proportions of ASVs from the different taxonomic groups displayed above. The different rows represent different sampling dates and numbers are different levels of the NaCl treatments in the experiment.

3.4.2 Phytoplankton community

The 18S gene showed that certain freshwater phytoplankton groups were sensitive to elevated NaCl concentrations (e.g., Cryptophyta, Dinoflagellata, Bacillariophyta, Charophyta, Protalveolata and Streptophyta), while others were more salt-resistant because they had large increases in relative abundance in medium and high conductivity mesocosms (e.g., Chlorophyta and Ochrophyta) (Fig. 3.3). Chlorophyta persisted at low and increased at intermediate water conductivity. High water conductivity due to high chloride concentrations, however, could only be withstood by Ochrophyta (of the Chrysophyceae class), and all other phytoplankton groups disappeared completely or were maintained at very low relative abundances. However, we also noted that Ochrophyta relative abundance increased in control mesocosms compared to the lake community over the duration of the experiment, and so may also partially reflect a positive response to mesocosm conditions. Overall, phytoplankton community diversity decreased with elevated chloride concentrations, especially in high conductivity mesocosms (ANNEX C Table A3, Fig. A2). However, chlorophyll *a*, an estimate of total phytoplankton biomass, had no detectable aggregate response to the salt addition across the experimental gradient. (ANNEX C Fig. A3, Table A4).

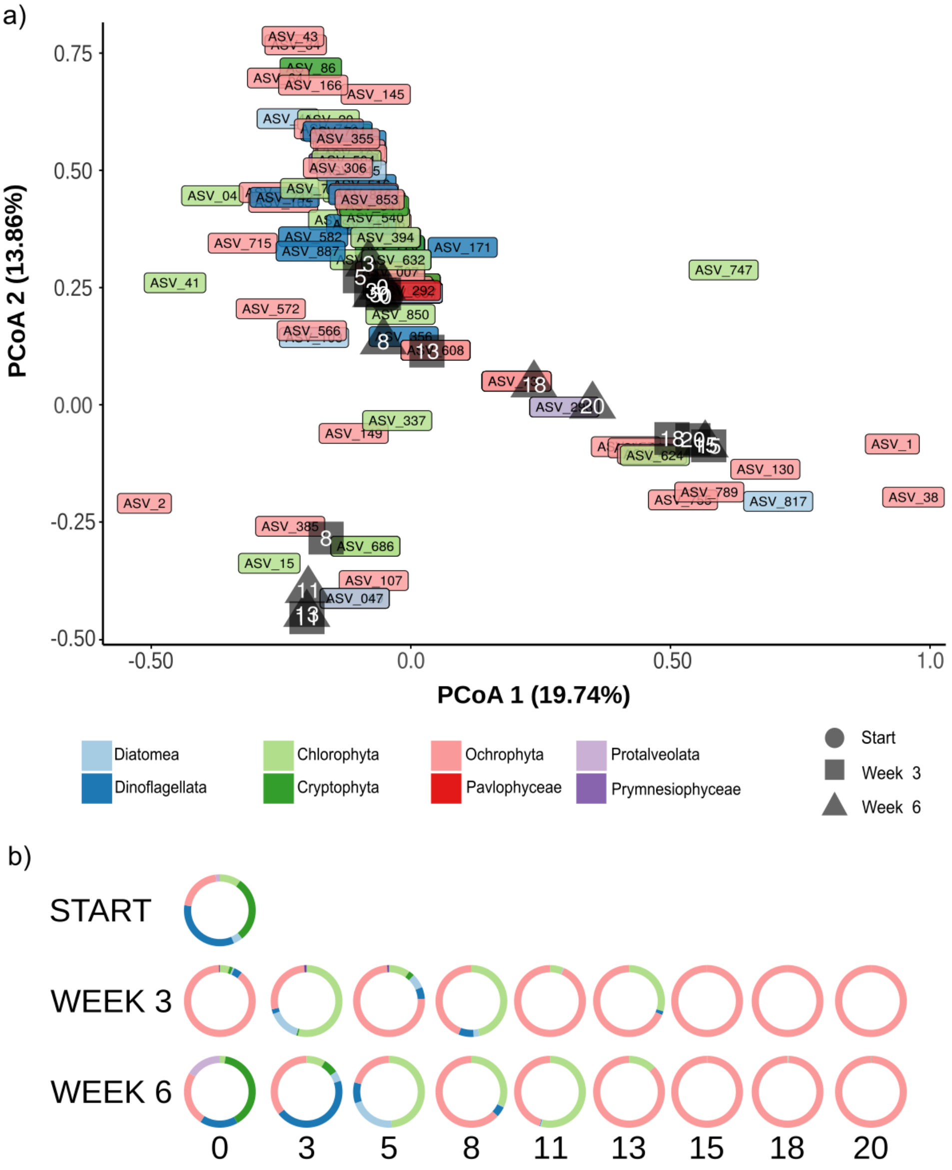

Figure 3.4. The response of the phytoplankton community to elevated chloride (Cl^-) concentration. a) PCoA with Bray Curtis dissimilarity matrix of squared phytoplankton ASV matrix. Labels are unique ASVs with colors showing the phytoplankton phylum. Enclosure shapes represent different sampling dates (circles refers to lake water at the start of the experiment, squares refer to week 3, and triangles refer to week 6) and numbers are different levels of the NaCl treatment. b) Relative abundance of the different phytoplankton phyla. Each circle is an enclosure and the color within the circle are the proportions of ASVs from the different phytoplankton phyla. The different rows represent different sampling dates and numbers are different levels of the NaCl treatment in the experiment.

3.5 Discussion

Our experiment supports that freshwater salinization may cause the simplification and potential collapse of aquatic eukaryote communities, especially in salt-naïve lakes with no prior exposure to salt. First, we found that major compositional shifts in the plankton community occurred at chloride concentrations that corresponded with long-term and short-term recommendations for water quality guidelines in Canada, EU and the United States (Fig. 3.2). Second, we observed that compositional shifts in the plankton community were associated with important shifts towards by fungal taxa at intermediate chloride concentrations (185 mg Cl^- L^{-1} to 640 mg Cl^- L^{-1}), and towards phytoplankton at elevated chloride concentrations (above 640 mg Cl^- L^{-1}) (Fig. 3.3). Third, we highlight that, with increasing chloride concentrations, the compositional shifts in the phytoplankton community were not associated with a strong decline in biomass (Fig. 3.4). Lastly, we found that the overall diversity of planktonic organisms was greatly reduced with elevated chloride concentration (Fig. A2 and Table A3). Our findings highlight the profound effects of freshwater salinization on all compartments of the planktonic eukaryote community, and that chloride concentrations recommended by water quality guidelines might not be sufficient to prevent major changes in salt-naïve aquatic eukaryote communities.

3.5.1 Simplified planktonic food web at elevated chloride concentrations

Increasing freshwater salinity was associated with decreased eukaryotic community diversity across trophic levels of the planktonic food web in a pristine freshwater lake (Fig. A2). As eukaryotic community diversity decreased with increasing salinity, we observed an increased dominance of fungal taxa at intermediate chloride concentrations and increased dominance by phytoplankton in mesocosms with the highest salinity (Fig. 3.3). The eukaryotic community was greatly simplified and held few ASVs in high chloride mesocosms compared to the hundreds of ASVs detected in low chloride mesocosms. In the intermediate and high chloride mesocosms, the food web was almost entirely reduced to phytoplankton or fungal species, and zooplankton were almost entirely lost. While other studies have found that certain zooplankton persist higher chloride levels up to 1300 mg.L^{-1} (Coldsnow *et al.*, 2017 ; Hintz *et al.*, 2017 ; Moffett *et al.*, 2021), this was not the case in our study where cladocerans, copepods, and rotifers were all sensitive to increasing freshwater salinity. The simplification of the planktonic food web detected in our experiment has the potential to modify ecosystem function and productivity in pristine freshwater lakes, if the responses that we measured in experimental mesocosms extend to the whole ecosystem scale in lakes (energy pathways: O'Gorman et al., 2019 ; Sherwood et al., 2011, productivity: Higgins et al., 2014 ; Liess et al., 2009, and food web stability: Binzer et al., 2016 ; Fussmann et al., 2014).

3.5.2 Phytoplankton

The phytoplankton community shifted towards Ochrophyta (Chrysophyceae) with the addition of chloride in mesocosms. This shift also occurred over time in the control mesocosms, suggesting that this response may also be a response to mesocosm conditions, but it was most strongly pronounced at high salinity. Moreover, there was no change in total phytoplankton biomass, indicated by chlorophyll a concentration, over the course of the experiment. This suggests that as certain phytoplankton groups were eliminated when their ecological tolerances were exceeded with increasing salinity, phytoplankton biomass was compensated by the increased abundance of salinity-tolerant taxa such as Ochrophyta. Only a handful of studies, including our study, have addressed community compositional shifts in phytoplankton as a response to elevated chloride concentrations (Ballot *et al.*, 2009 ; Mo *et al.*, 2021 ; Porter-Goff *et al.*, 2013). Studies that analyzed phytoplankton composition changes have found that benthic diatom were sensitive to relatively low chloride concentration (35 mg Cl^- L^{-1}) (Porter-Goff *et al.*, 2013), and very high chloride concentration (2000-

5000 mg Cl^- L^{-1}) favor cyanobacteria in eutrophic conditions with high nutrient loading (Ballot *et al.*, 2009). We also found that highly nutritious phytoplankton (cryptophytes and diatoms) were sensitive to increased chloride concentration, and were replaced by less nutritious groups (chlorophytes and chrysophytes) at relatively low chloride concentration ($<$185 mg Cl^- L^{-1}). However, we did not detect an increase of cyanobacteria in the phytoplankton community as a response to increased salinity, which could be explained by the absence of cyanobacteria in Lake Croche and the oligo-mestrophic conditions of the lake that are not suitable for cyanobacteria blooms (Davis *et al.*, 2009). Elevated chloride can result in an increase in the total biomass of phytoplankton under certain conditions (Ballot *et al.*, 2009 ; Hintz *et al.*, 2017 ; Moffett *et al.*, 2021), but this response is not consistent across studies (Hintz *et al.,* 2021 in prep). For our experiment, the oligo-mesotrophic nutrient status of the lake and nutrient additions to experimental mesocosms (ANNEX C) may explain the stability of phytoplankton biomass despite the reduction and near total loss of zooplankton grazers at elevated chloride concentrations.

Different phytoplankton groups have different nutritional value in terms of the essential fatty acids that they provide to higher consumers in pelagic food webs of lakes (Taipale *et al.*, 2013). The shift in phytoplankton community composition as a response to increasing salinity represented a change towards a lower quality resource base. Cryptophyta and Bacillariophyta (diatoms) are highly nutritious phytoplankton groups containing a high proportion of essential highly unsaturated fatty acids (Taipale *et al.*, 2013) that are critical for organismal reproduction at higher trophic levels such as zooplankton (Brett *et al.*, 2009 ; Trommer *et al.*, 2019). Chlorophyta, and Chrysophyceae provide an intermediate level of dietary quality for zooplankton (Taipale *et al.*, 2013). While the diverse phytoplankton assemblage at low chloride concentrations included highly nutritious groups of phytoplankton, such as diatoms and cryptophytes, the high salinity mesocosms contained less nutritious chrysophytes (Ochrophyta). Phytoplankton nutritional quality is important for somatic growth, reproduction, disease resistance, tissue development and pigmentation at higher trophic levels in aquatic food webs (Twining *et al.*, 2016). Moreover, the susceptibility of freshwater zooplankton to salinization can be highly dependent on the dietary quality of lipid supply available in the phytoplankton community (Isanta-Navarro *et al.*, 2021). Therefore, increasing freshwater salinization on landscapes may provide challenges to aquatic food webs not only through direct toxicity, but also through reduced nutritional provisioning to higher consumers such as zooplankton, fish, and other vertebrates.

3.6 Implications and conclusions

Short-term (640 mg Cl^- L^{-1} in Canada and 840 mg Cl^- L^{-1} in the United States), long-term (120 mg Cl^- L^{-1} in Canada and 230 mg Cl^- L^{-1} in the United States), and EU drinking water guidelines (250 mg Cl^- L^{-1}) recommended chloride concentrations (Environment Canada and Climate Change, 2011 ; US EPA, 1988) had profound effects on the planktonic eukaryote community of a salt-naïve lake ecosystem. Short-term salinity pulses in stream and rivers, and longer-term salinity exposure in lakes generally exceed three weeks of exposure (Kaushal *et al.*, 2018 ; Laceby *et al.*, 2019 ; Niedrist *et al.*, 2021). Therefore, the responses that we observed in the mesocosms over a short time scale the potential to occur in freshwater ecosystems. However, other complex and interacting factors occur in natural ecosystems that were excluded from our semi-natural mesocosm experiment, such as metacommunity dynamics through habitat connectivity and organismal dispersal, evolutionary responses, and the effects of multiple stressors interacting with the effects of salinity. Nonetheless, our experiment demonstrates that water quality guidelines for chloride concentrations in freshwater ecosystems provided by Canada, EU and the United States are not adequate to ensure the conservation of planktonic communities in salt-naïve freshwater ecosystems with low ambient chloride concentrations.

CONCLUSION

4.1 Key contributions

Freshwater biodiversity is under multiple threats driven by human activities, and their effects are complex, context dependent, and highly variable between taxa (Reid *et al.*, 2019). As a result, our understanding of the negative effects of anthropogenic stressors, and the mechanisms by which they impact freshwater biodiversity are still lacking. To explore such complexity and improve our understanding of anthropogenic impacts on biodiversity in freshwater ecosystems, this thesis focused on examining how both invasive species and salinization affect freshwater community diversity and inform ecosystem management through invasive impact mitigation and freshwater salinization water quality guidelines adequacy in pristine ecosystems. To do this, I explored how natural and experimental environmental gradients influenced biodiversity in the context of invasive species, and salinization of freshwater ecosystems to determine : i) what are the long term effects of invasive species along a gradient of historical presence, ii) how natural gradients in the form of environmental heterogeneity can mitigate invasive impacts on resident communities, and iii) what are the impact of salinization on pristine freshwater planktonic food webs, and how they relate to water quality guidelines. By studying invasive species in a temporal context, the influence of natural environmental heterogeneity on invasive species impacts, and salinization impacts in pristine freshwater ecosystems, I made several unique findings that significantly further our understanding of anthropogenic impacts on freshwater biodiversity. Furthermore, I highlight avenues for sustainable management of these valuable ecosystems.

4.1.1 Mitigation of exotic invasion impact in time and across spatial environmental heterogeneity

Few studies on invasive species have considered long term impacts of invasive species (Ricciardi *et al.*, 2013). Long term monitoring is complicated and requires continued funding which are challenging to maintain for long periods of time (Comín *et al.*, 2004). However, I show in the work presented here (Chapter 1) that using prior studies and considering the time invasive since invasion in the environment can uncover relationships between site-specific exotic species abundance, time since invasion, and impacts on food resources. I highlight that as time since invasion passes, the invasive abundance can stabilize and show signs of reduction in population growth rate. However, I found that biodiversity impacts of invasive species were most pronounced at latter stages of invasion. With time, invasive species can change local communities, and erode local prey communities through continued negative effects (Ricciardi *et al.*, 2013 ; Strayer *et al.*, 2006). Erosion of prey communities through time could lead to reduction in biodiversity by loss of sensitive species, and in turn limit invasive predator abundance because of more resistant local prey communities (Strayer *et al.*, 2006). Our results show the importance of continued monitoring of invasive species impact through time. Maintaining regular monitoring on a global scale could allow better understanding of mechanisms at play in invasive species dynamics, and the impacts they have on biodiversity. Furthermore, by strengthening our mechanistic understanding of invasive species dynamics and impacts through time, we will be able to make informed predictions and make adequate management decisions regarding one of the major threats to Earth biodiversity.

The management of invasive species is complex and mitigating their impacts on local biodiversity very challenging. Eradication of invasive species is logistically difficult, costly, and not always successful (Green et Grosholz, 2021). Furthermore, this type of intervention focuses on a single species despite the fact that species interact within communities, which can lead to negative effects on non-target species (Lampert *et al.*, 2014). Managing single species is limited because it does not account for trade-offs and natural interactions present in ecosystems (Lampert *et al.*, 2014). Attempting eradication of invasive species can come at important costs regarding local biodiversity (Green et Grosholz, 2021). Human intervention in natural systems is therefore better suited using less intensive management approach over longer time scales (Lampert *et al.*, 2014). The work highlighted in this thesis (Chapter 2), shows that environmental heterogeneity has the potential of reducing invasion success, and increasing community biodiversity at the whole ecosystem scale. I found that wetlands were particularly important environments that reduce invasion success, and simultaneously increase both alpha and beta diversity of resident prey which were most impacted by the prolonged presence of invasive predators. Furthermore, wetland are therefore among the most productive and valuable ecosystems that provide valuable services such as storm buffering, fishery production and biodiversity maintenance (Roebeling *et al.*, 2016). However, wetlands have been lost at exceptional rates in the past few decades (Keddy *et al.*, 2009). Conserving existing wetlands from urban and agricultural expansion, restoring impacted wetlands, and constructing artificial wetlands need to be a priority for management of freshwater ecosystems (Shutes, 2001). Invasive species abundance was also reduced by environmental heterogeneity at multiple spatial scales. Our results highlight the potential of environmental heterogeneity to mitigate invasive species at multiple scales in open systems where direct eradication is unlikely to succeed and would probably have important impacts on resident communities. I therefore advocate for the identification, protection and restoration of natural environmental heterogeneity we found has the potential to reduce invasive species abundance and mitigate their impacts on resident biodiversity at the whole ecosystem scale.

4.1.2 Ecological impact of freshwater salinization across planktonic trophic levels and implications for water quality guidelines

Salinization of freshwater has been rising in the past decade (Dugan *et al.*, 2017a ; Kaushal *et al.*, 2021), becoming a growing threat to biodiversity, and the ecosystem services biodiversity sustains in freshwater ecosystems (Castillo *et al.*, 2018 ; Suárez *et al.*, 2017). Virtually no studies had investigated the sensitivity/resistance of a whole planktonic food web in a pristine environment, from microbes to zooplankton. In freshwater planktonic food webs, it is important to study food webs across trophic levels because stressors can alter trophic structure (Amorim et Moura, 2021), and trophic cascades are frequent (Brett et Goldman, 1996 ; Ellis *et al.*, 2011). I found that salinization had dramatic impacts on the composition, and the biodiversity of planktonic food webs in pristine environments. Salinization at fairly low level (40 mg/L) devastated zooplankton species, and completely shifted phytoplankton composition towards less nutritious taxa. Such profound impacts on biodiversity can have serious negative implications on the stability, and productivity of freshwater ecosystems. Furthermore, the reduction of quality of primary producers, and the total loss of zooplankton which is key in transferring energy and biomass to higher trophic, would imply a total collapse of an entire ecosystem. Chapter 3 also provides important information regarding the capacity of both Canada and US water quality guidelines to protect pristine environments with low ambient salinity levels. We found that water quality guidelines are insufficient, and do not protect freshwater biodiversity. Moreover, salinization of pristine freshwater ecosystems at levels recommended by water quality guidelines would probably imply catastrophic consequences for ecosystem services these environments provide to human society. I therefore recommend that water quality guidelines should be adjusted and determined at more local scales. Guidelines should take into consideration ambient levels of salts, history of exposure to salts, and local community composition to efficiently protect pristine freshwater ecosystems. As it stands, water quality guidelines are not sufficiently protecting freshwater ecosystems from salinization, while salt levels are predicted to continue to rise. If no concrete actions are taken to protect freshwater ecosystems, salinization has the potential to have devastating impacts in the future.

4.2 Future directions

Developing a better understanding of the multitude and increasing threats freshwater ecosystems face is a major challenge for their continued conservation. This thesis provides some guidelines to take action toward a more informed management of both invasive species, and salinization. However, our work also raises new research questions and interesting avenues for future research. I highlighted the importance of continued monitoring of invasive species abundance, and resident community composition and diversity. Long term monitoring could benefit our understanding of invasive impacts, and uncover the mechanisms driving invasive species abundance and long-term impacts on freshwater ecosystems. Furthermore, I showed the importance of environmental heterogeneity for its potential of creating uninvaded refuges for resident communities and enhancing biodiversity. Investigating the connectivity between refuges, and the interactions of refuges with invaded habitats would further our understanding of positive effects of uninvaded refuges at a regional scale. Metabarcoding tools have greatly advanced in the past few decades, and are now showing promises for studying intraspecific dynamics (Adams *et al.*, 2019 ; Turon *et al.*, 2020). Such genetic tools could provide valuable information on community connectivity between environmental refuges, and they would assist with designing suitable protected areas to efficiently manage invasive species impacts. Conserving environmental heterogeneity in a wide variety of environmental dimensions, as well as at different spatial scales, could allow communities to buffer invasive species impacts through ecological or evolutionary processes that might counter negative invasive species impacts by providing increased inter- and intraspecific variation.

Salinization is a concerning threat to freshwater biodiversity, and I showed in this thesis that it can have catastrophic effects on whole food webs at concentrations deemed acceptable by Canadian and US authorities. Our conclusions are strengthening the growing literature on adverse effects of salinization, and adequacy of regulations in place. However, very few studies have investigated the long-term effects of salinization, and the potential reversibility of the negative effect found globally. Some studies have shown that increased tolerance was possible through evolutionary response in *Daphnia* (Coldsnow *et al.*, 2017). Understanding if evolutionary processes are capable of rescuing population and communities in natural settings would provide valuable information for efficient management of salinization in freshwater ecosystems. Furthermore, impacted habitats can receive demographic subsidies from other environments which could influence the impact of salinization on local ecosystems, and the probability of evolutionary responses. Connectivity between impacted and pristine habitats is important for both evolutionary and ecological processes that could potentially favor both the resistance and resilience of freshwater ecosystems to salinization. More knowledge is needed to fully understand the optimal conditions capable of facilitating ecological and evolutionary responses to freshwater salinization, and if such responses can mitigate the profound negative impacts increasing levels of salt in freshwater are having on biodiversity.

Ponto-Caspian invaders are causing major issue in the North American great lakes, and around 70% of invasive species discovered in this area since 1985 are of Ponto-Caspian origin (Ricciardi et MacIsaac, 2000). Ponto-Caspian invaders are also successful throughout parts of Europe (Ojaveer *et al.*, 2002), and having negative impacts on resident biodiversity globally. Several studies, including ours, showed that different Ponto-Caspian invaders are not adapted to low dissolved ion concentrations in the environment (Iacarella et Ricciardi, 2015 ; Kestrup et Ricciardi, 2010). Low conductivity refuges are therefore valuable for resident communities, and the conservation of biodiversity. However, because levels of salt in freshwater are rising globally, such low conductivity refuges might be in danger. Salinization of freshwater ecosystems, depending on which salt are increasing, could potentially increase the range of favorable habitats for Ponto-Caspian invader. Investigating which specific ions are responsible for the low success of different Ponto-Caspian invaders is important to understand the potential for salinization to increase their invasive range. More effort should be deployed toward assessing and understanding the potential risk applying important quantities of different salts represent for the invasive success of Ponto-Caspian invader in environments that are protected by low ion availability.

ANNEX A

Physico-chemical conditions

In the laboratory, Total Nitrogen (TN) was analyzed with a continuous flow analyzer (OI Analytical Flow Solution 3100 ©) using an alkaline persulfate digestion method, coupled with a cadmium reactor, following a standard protocol (Patton and Kryskalla, 2003). Total Phosphorus (TP) was measured spectrophotometrically on the same machine by the molybdenum blue method after persulfate digestion (Griesbach and Peters, 1991). TN and TP samples were analyzed at the GRIL- Université du Québec à Montréal (UQAM) analytical laboratory.

OBBN substrate characteristics (Jones et al., 2006)

Dominant substrate was described using 7 classes:

-Clay (hard pan)

-Silt (gritty, <0.06 mm particle diameter)

-Sand (grainy, 0.06-2 mm)

-Gravel (2-65 mm)

-Cobble (65-250 mm)

-Boulder (> 250 mm)

-Bed Rock

Citations

Cuthbert I.D. & del Giorgio P. (1992) Toward a standard method of measuring color in freshwater. Limnology and Oceanography, 37, 1319–1326.

Griesbach S.J. & Peters R.H. (1991) The effects of analytical variations on estimates of phosphorus concentration in surface waters. Lake Reservoir Management, 7, 97–106.

Jones, C., Craig, B., & Dmytrow, N. (2006). The Ontario Benthos Biomonitoring Network. In *In: Aguirre-Bravo, C.; Pellicane, Patrick J.; Burns, Denver P.; and Draggan, Sidney, Eds. 2006. Monitoring Science and Technology Symposium: Unifying Knowledge for Sustainability in the Western Hemisphere Proceedings RMRS-P-42CD. Fort Collins, CO: US Department of Agriculture, Forest Service, Rocky Mountain Research Station. p. 455-461* (Vol. 42).

Patton CJ, Kryskalla JR. Methods of analysis by the US Geological Survey National Water Quality Laboratory: Evaluation of alkaline persulfate digestion as an alternative to kjeldahl digestion for determination of total and dissolved nitrogen and phosphorus in water: US Department of the Interior, US Geological Survey; 2003.

Stomach content analysis

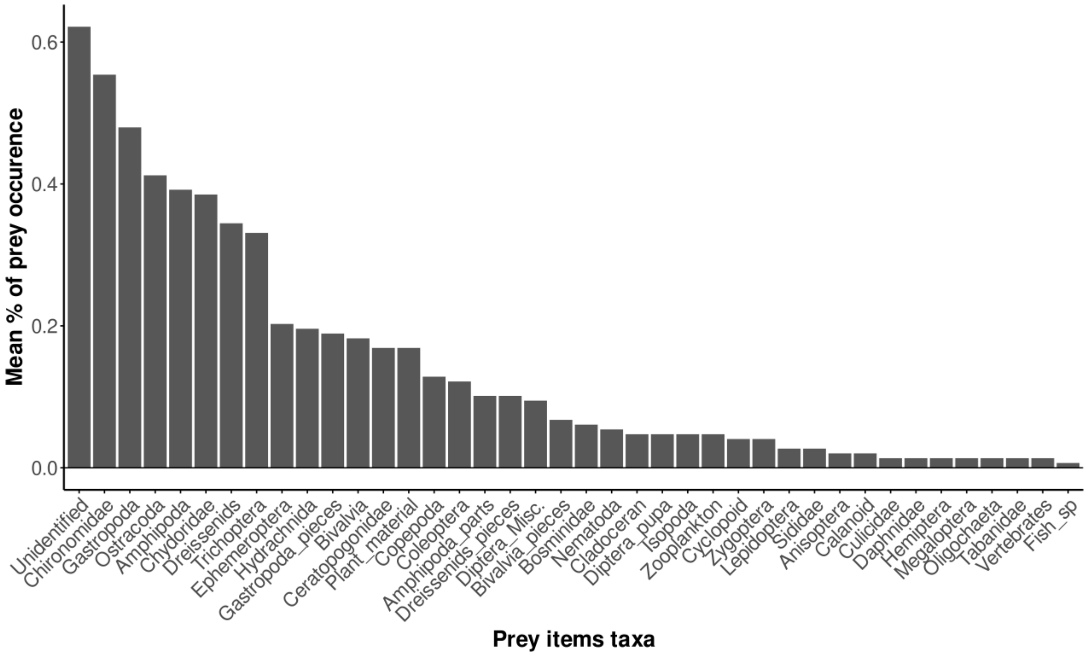

Figure 1: Round goby diet: Frequency of occurrence (%F) of prey item in round goby stomach content. On the x axis each taxon found in round goby stomachs content and each bar represent the frequency of occurrence (%F) of these prey in the different fish analyzed for this study.

Redundancy Analysis

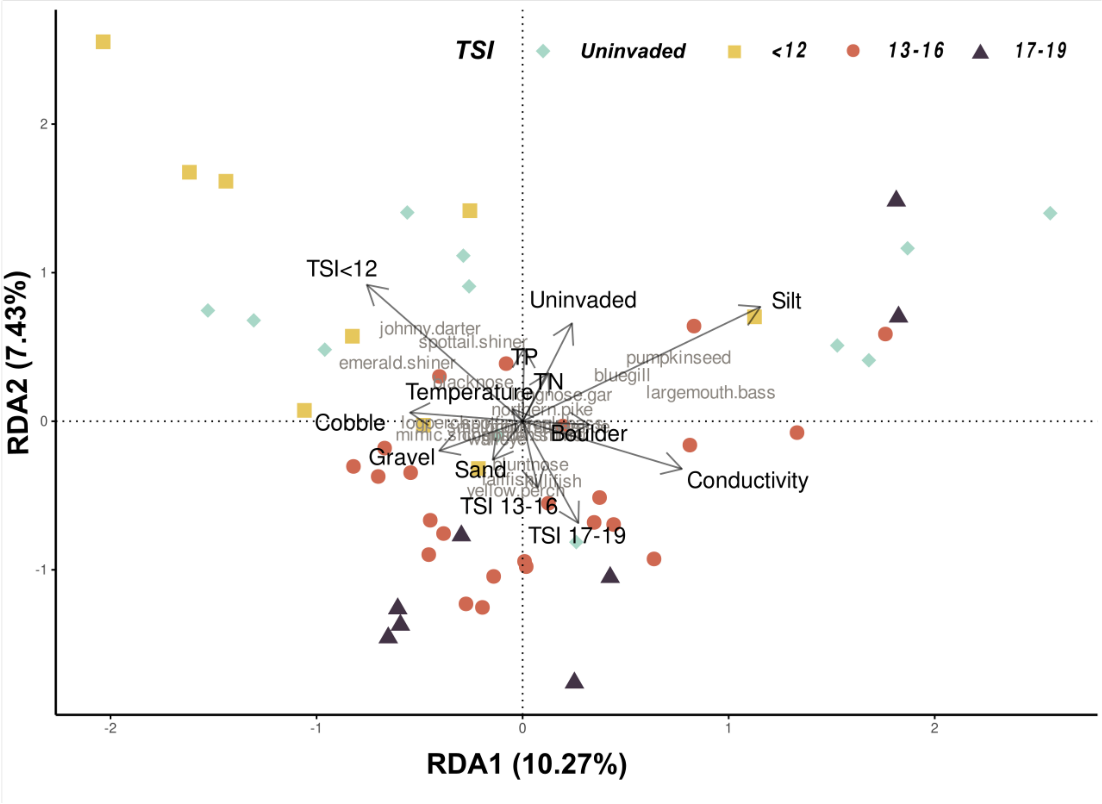

Figure 2. RDA biplots with the full dataset for macroinvertebrate communities. Arrows represent forward selected environmental variables. Light grey diamond symbols represent uninvaded sites, medium grey square symbols represent sites with TSI < 12, dark grey circle symbols represent sites with TSI between 13-16 years, and dark triangle symbols represent sites with TSI between 17-19 years.

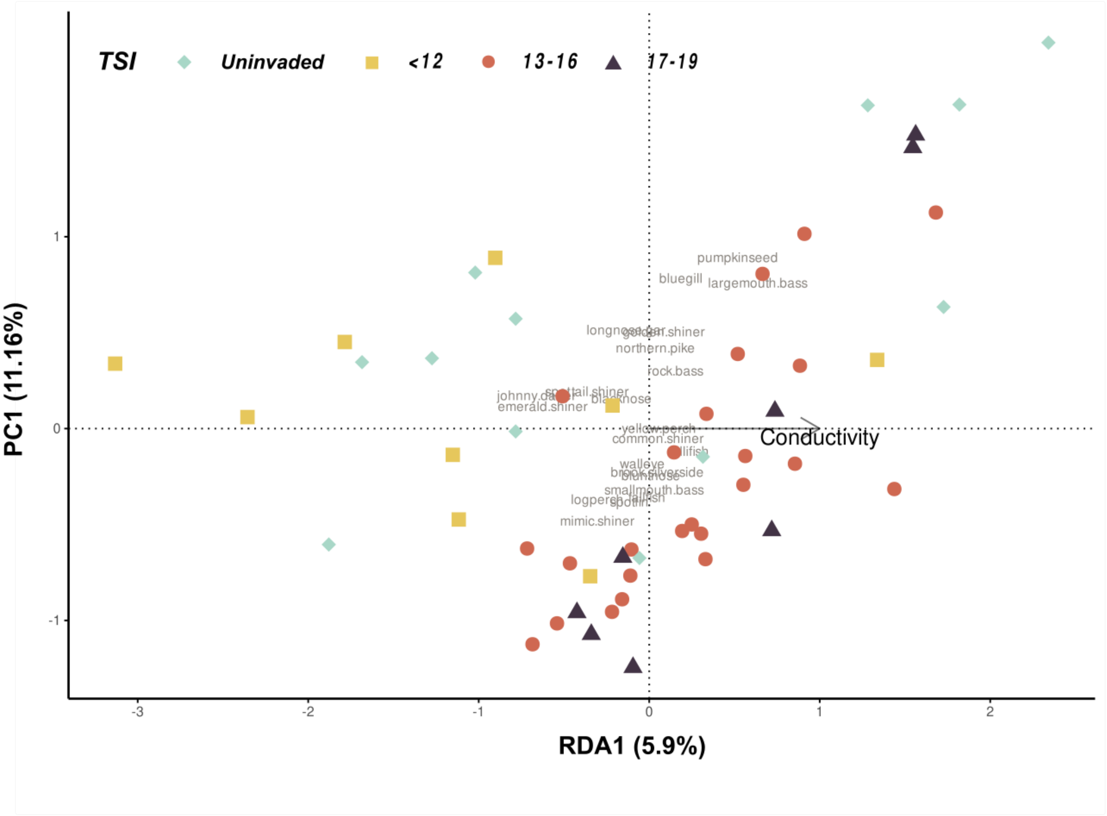

Figure 3. RDA biplots with the full dataset for fish communities. Arrows represent forward selected environmental variables. Light grey diamond symbols represent uninvaded sites, medium grey square symbols represent sites with TSI < 12, dark grey circle symbols represent sites with TSI between 13-16 years, and dark triangle symbols represent sites with TSI between 17-19 years.

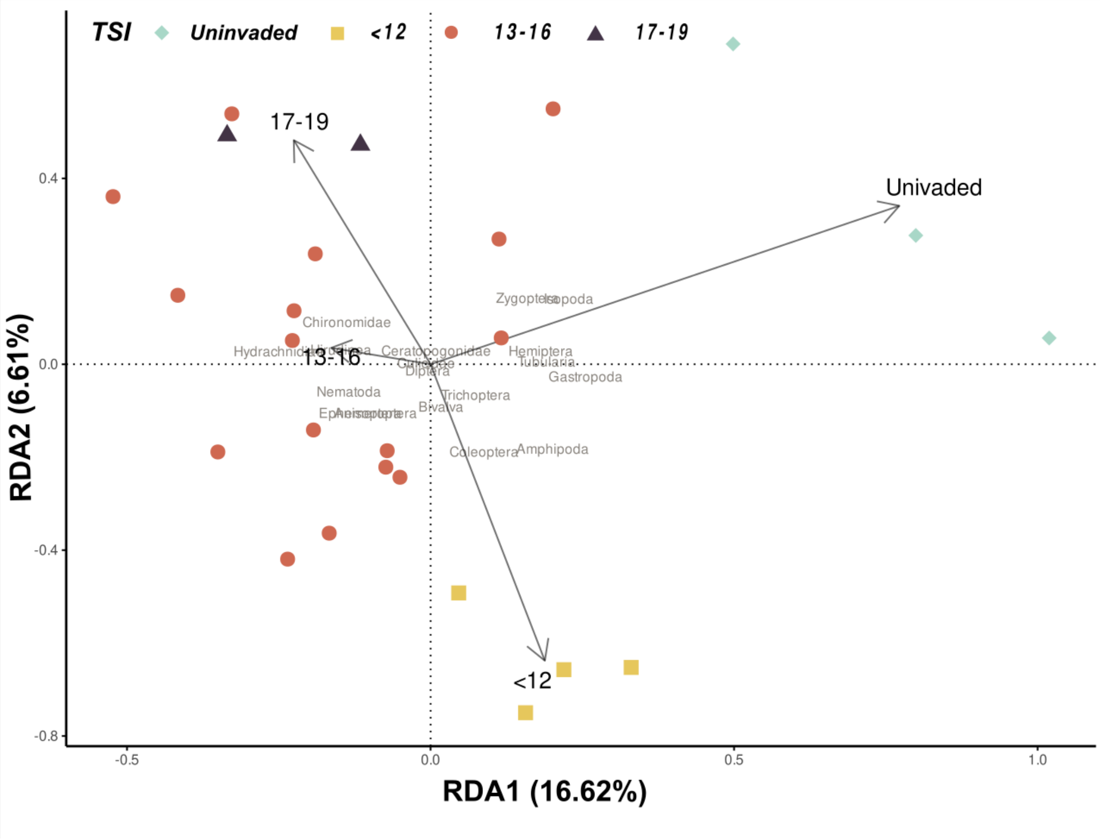

Figure 4. RDA biplots with the 27 sampling sites for which we collected dreissenid mussel density data, to infer the influence of forward-selected variables (TSI) on macroinvertebrate community composition. Arrows represent forward selected environmental variables. Light grey diamond symbols represent uninvaded sites, medium grey square symbols represent sites with TSI < 12, dark grey circle symbols represent sites with TSI between 13-16 years, and dark triangle symbols represent sites with TSI between 17-19 years.

Table 1. AIC scores of competing generalized linear models testing the effect of of independent variables TSI and invasion status on the dependent variable round goby abundance, and the effect of independent variables TSI, invasion status, and round goby abundance on dependent variables macroinvertebrate and fish community diversity indices (Shannon index, taxon richness and Pielou's evenness, and LCBD), as well as on the total abundance for each of these communities. Selected models are bolded.

Model	AIC
Goby ~ TSI	**378.96**
Goby ~ Invasion status	389.85
Macroinvertebrate Shannon Richness ~ TSI	70.41
Macroinvertebrate Shannon Richness ~ Invasion status	**67.59**
Macroinvertebrate Shannon Richness ~ Goby	67.41
Macroinvertebrate Taxon Richness ~ TSI	**262.00**
Macroinvertebrate Taxon Richness ~ Invasion status	268.30
Macroinvertebrate Taxon Richness ~ Goby	269.16
Macroinvertebrate Pielou's Evenness ~ TSI	-39.45
Macroinvertebrate Pielou's Evenness ~ Invasion status	-42.51
Macroinvertebrate Pielou's Evenness ~ Goby	**-42.76**
Macroinvertebrate Total Abundance ~ TSI	783.99
Macroinvertebrate Total Abundance ~ Invasion status	**784.20**
Macroinvertebrate Total Abundance ~ Goby	783.67

Macroinvertebrate LCBD ~ TSI	-355.20
Macroinvertebrate LCBD ~ Invasion status	-353.14
Macroinvertebrate LCBD ~ Goby	**-351.70**
Fish Shannon Richness ~ TSI	87.11
Fish Shannon Richness ~ Invasion status	**84.28**
Fish Shannon Richness ~ Goby	83.56
Fish Taxon Richness ~ TSI	276.70
Fish Taxon Richness ~ Invasion status	**272.95**
Fish Taxon Richness ~ Goby	272.60
Fish Pielou's Evenness ~ TSI	-14.61
Fish Pielou's Evenness ~ Invasion status	**-17.00**
Fish Pielou's Evenness ~ Goby	-18.51
Fish Total Abundance ~ TSI	668.63
Fish Total Abundance ~ Invasion status	**666.54**
Fish Total Abundance ~ Goby	667.69
Fish LCBD ~ TSI	**-450.71**
Fish LCBD ~ Invasion status	-448.68
Fish LCBD ~ Goby	-448.59

ANNEX B

Physico-chemical water conditions: laboratory analyses

We collected water samples to quantify dissolved organic carbon (DOC; mgL^{-1}), dissolved calcium (Ca; mgL^{-1}), as well as nutrients total nitrogen (TN; mgL^{-1}), total phosphorus (TP; µgL^{-1}). DOC, TN and TP samples were analyzed at the GRIL-Université du Québec à Montréal (UQAM) analytical laboratory. DOC concentrations of 0.45-µm filtered samples (surfactant-free membrane filters) were measured after acidification (phosphoric acid 5%) followed by sodium persulfate oxidation using a 1010 TOC analyzer (O.I. Analytical, College Station, TX, USA). The absorption at 440 nm (CDOM), used as measure of water colour, was measured on water samples with a 2 cm quartz cuve in a BiochromUltrospec® 2100 pro spectrofluorometer (Cuthbert and del Giorgio, 1992).Total Nitrogen (TN) was analyzed with a continuous flow analyzer (OI Analytical Flow Solution 3100 ©) using an alkaline persulfate digestion method, coupled with a cadmium reactor, following a standard protocol (Patton and Kryskalla, 2003). Total Phosphorus (TP) was measured spectrophotometrically on the same machine by the molybdenum blue method after persulfate digestion (Griesbach and Peters, 1991).Water calcium samples were analyzed with a Thermo ICAP-6300 Inductively Coupled Argon Plasma - Optical Emission Spectrometer (ICP-OES) following protocols described by

US EPA (1994) at the University of Alberta Biogeochemical Analytical Service Laboratory (U of A – BASL; Edmonton, Alberta, Canada).

Citations

Cuthbert I.D. & del Giorgio P. (1992) Toward a standard method of measuring color in freshwater. Limnology and Oceanography, 37, 1319–1326.

Griesbach S.J. & Peters R.H. (1991) The effects of analytical variations on estimates of phosphorus concentration in surface waters. Lake Reservoir Management, 7, 97–106.

Patton CJ, Kryskalla JR. Methods of analysis by the US Geological Survey National Water Quality Laboratory: Evaluation of alkaline persulfate digestion as an alternative to kjeldahl digestion for determination of total and dissolved nitrogen and phosphorus in water: US Department of the Interior, US Geological Survey; 2003.

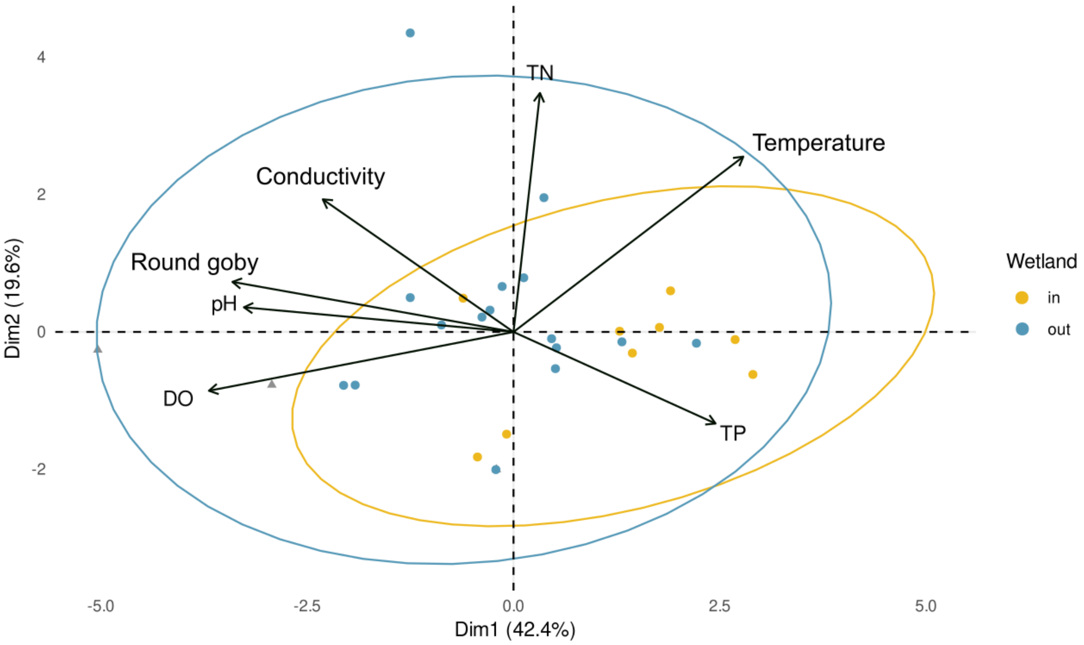

Figure 6. PCA biplot of environmental variables (vectors) sampled for all sites (symbols). Ellipses represent 95% confidence groups of sites that are in and out wetlands. Larger points are ellipses centroids.

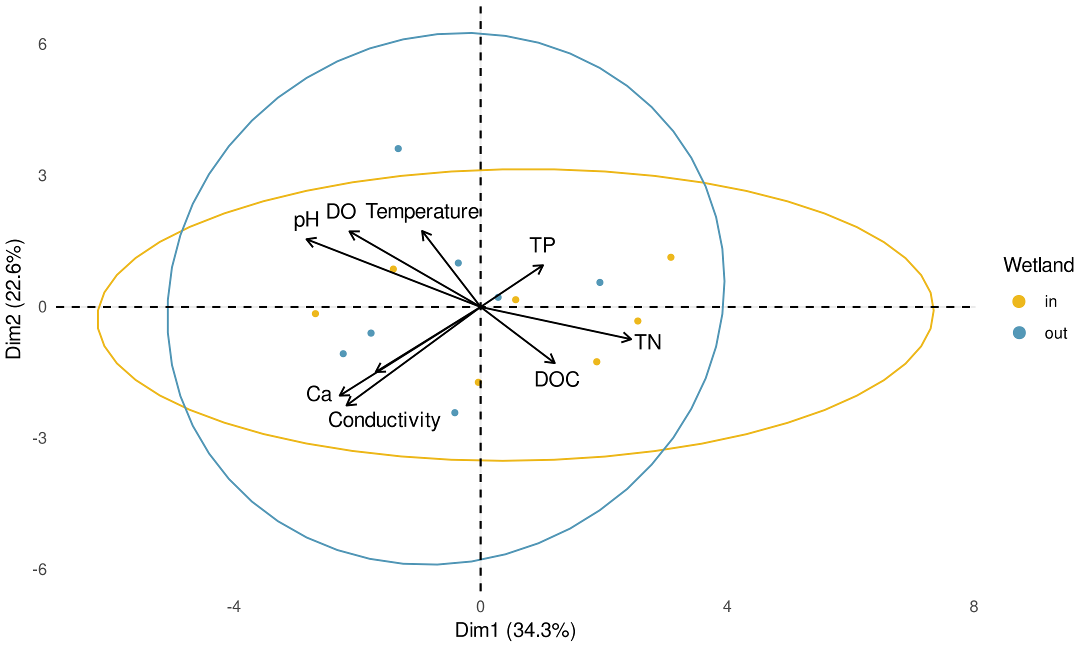

Figure 7. PCA biplot of environmental variables (vectors) sampled for sites (symbols) in Lake St. Louis. Ellipses represent 95% confidence groups of sites that are in and out wetlands. Larger points are ellipses centroids.

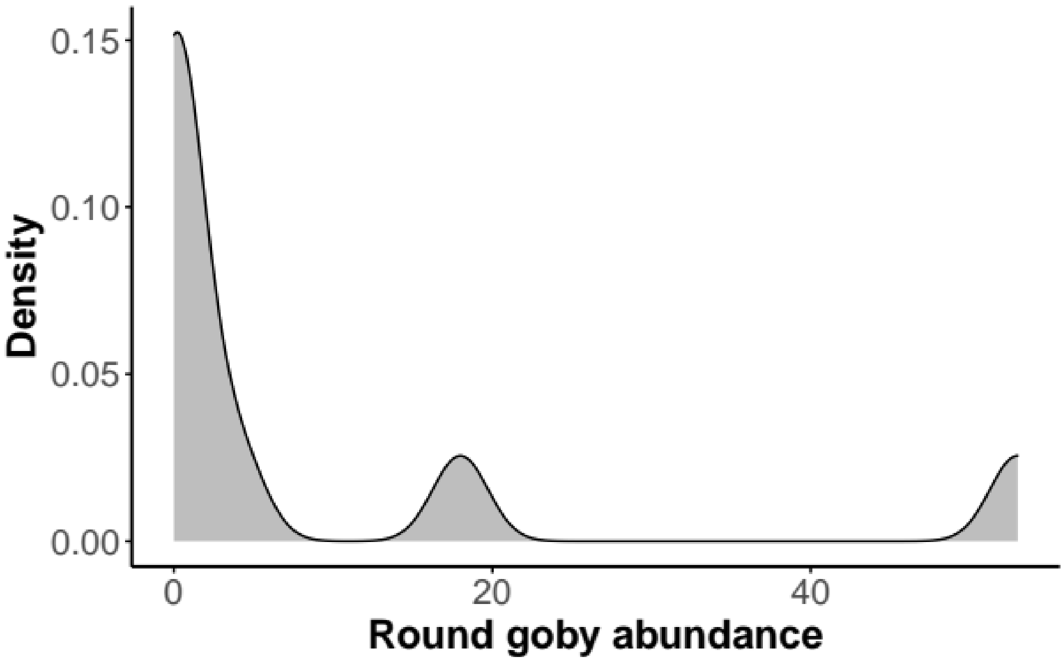

Figure 8. Kernel density of round goby abundance in wetland sites in the Upper St. Lawrence River.

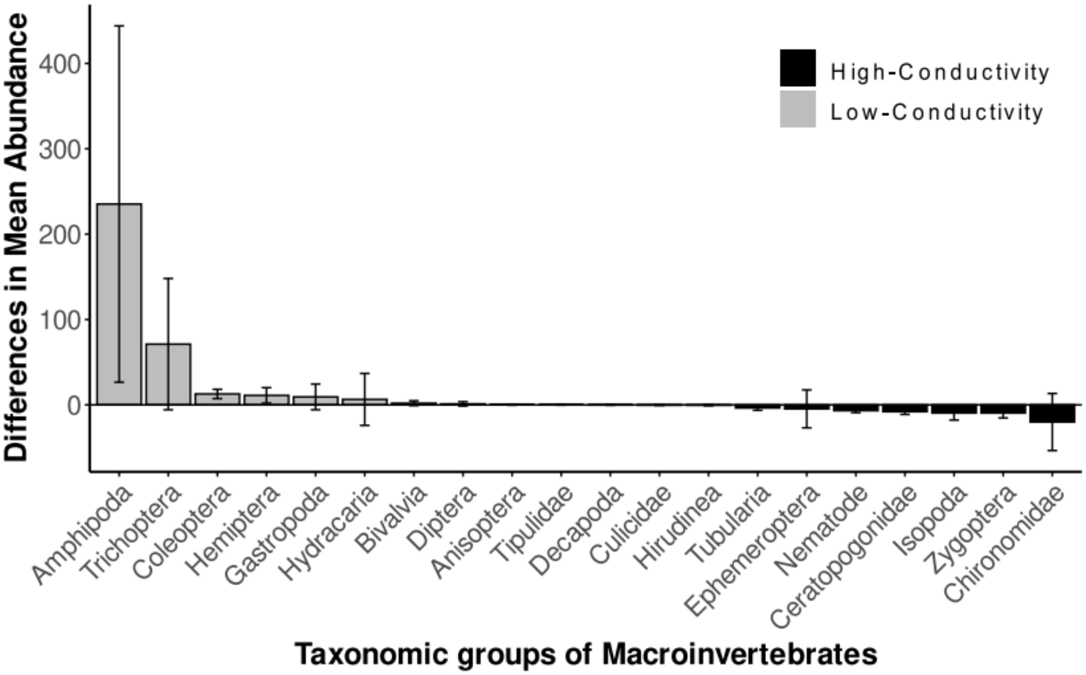

Figure 9. Differences between macroinvertebrate taxon mean abundance at low water conductivity sites and at high water conductivity sites. Positive values represent higher taxa abundance in low conductivity water and are represented by grey bars. Negative values represent higher taxa abundance in high conductivity water and are represented by black bars. Error bars represent standard error. Amphipoda and Trichoptera were more abundant in the low-conductivity water compared to high-conductivity shore sites.

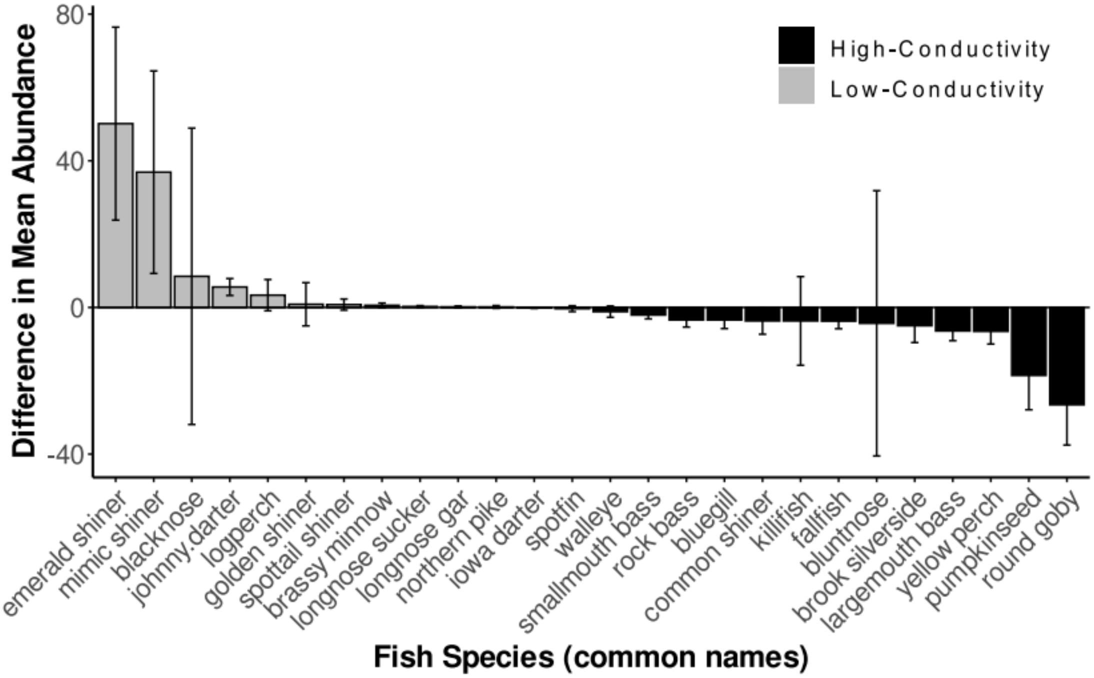

Figure 10. Differences between fish species mean abundance at low water conductivity sites and at high water conductivity sites. Positive values represent higher taxa abundance in low conductivity water and are represented by grey bars. Negative values represent higher taxa abundance in high conductivity water and are represented by black bars. Error bars represent standard error. Low conductivity shore ecosystems influenced by Ottawa River water had a higher abundance of *Notropis atherinoides* (emerald shiner) and *Notropis volucellus (*mimic shiner), as well as higher abundances of *Rhinichthys atratulus* (blacknose dace), *Etheostoma nigrum* (johnny darter) and *Percina caprodes* (common logperch). The high-conductivity ecosystems influenced by the St. Lawrence River water had higher abundances of *Perca flavescens* (yellow perch), *Lepomis macrochirus* (bluegill), *Micropterus salmoides* (largemouth bass), *Lepomis gibbosus* (pumpkinseed sunfish) and *Neogobius melanostomus (*round goby).

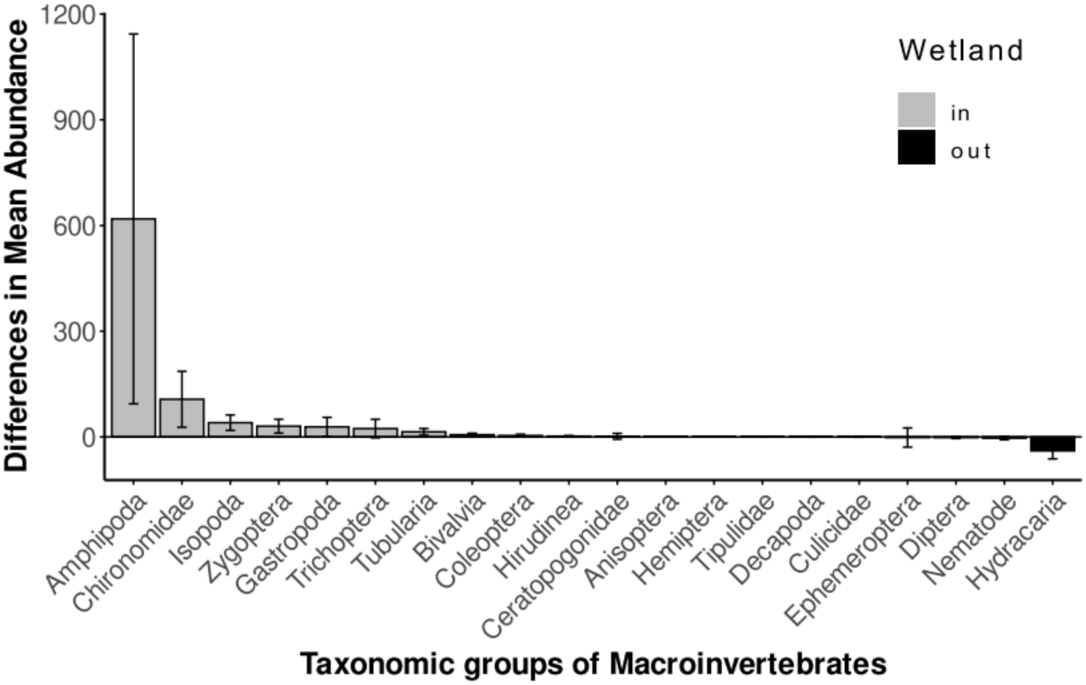

Figure 11. Differences between macroinvertebrate taxon mean abundance in wetlands and at open-water shore sites in high water conductivity. Positive values represent higher taxa abundance inside wetlands and are represented by grey bars. Negative values represent higher taxa abundance outside wetlands and are represented by black bars. Error bars represent standard error. Amphipoda, Trichoptera and Chironomidae were more abundant inside wetlands compared to outside wetlands in high water conductivity.

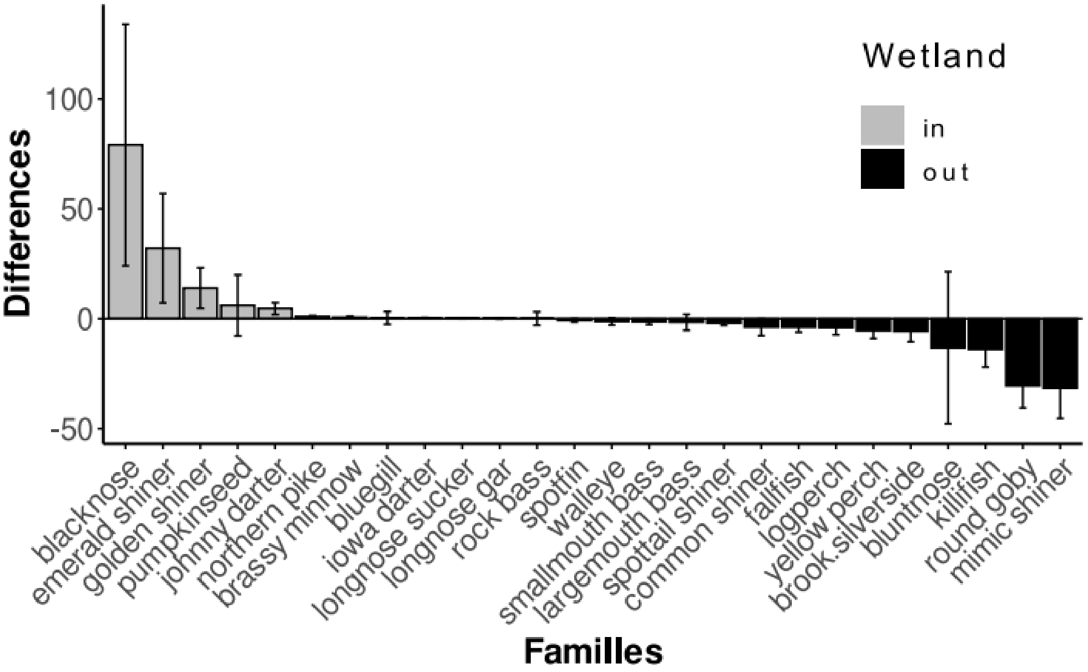

Figure 12. Differences between fish species mean abundance in wetlands and at open-water shore sites in high water conductivity. Positive values represent higher taxa abundance inside wetlands and are represented by grey bars. Negative values represent higher taxa abundance outside wetlands and are represented by black bars. Error bars represent standard error. *Rhinichthys atratulus* (blacknose dace), *Notropis atherinoides* (emerald shiner), *Lepomis gibbosus* (pumpkinseed sunfish), *Notemigonus crysoleucas* (golden shiner), *Lepomis macrochirus* (bluegill), *Etheostoma nigrum* (johnny darter) and *Esox lucius* (northern pike) were more abundant inside wetlands in high water conductivity. *Sander vitreus* (walleye), *Micropterus dolomieu* (smallmouth bass), *Percina caprodes* (common logperch), *Notropis hudsonius* (spottail shiner), *Notropis volucellus (*mimic shiner), *Luxilus cornutus (*common shiner), *Semotilus corporalis* (fallfish), *Labidesthes sicculus* (brook silverside), *Perca flavescens* (yellow perch), *Fundulus diaphanus* (banded killifish), *Pimephales notatus* (bluntnose minnow) and *Neogobius melanostomus (*round goby) had higher abundances outside of wetlands in high water conductivity.

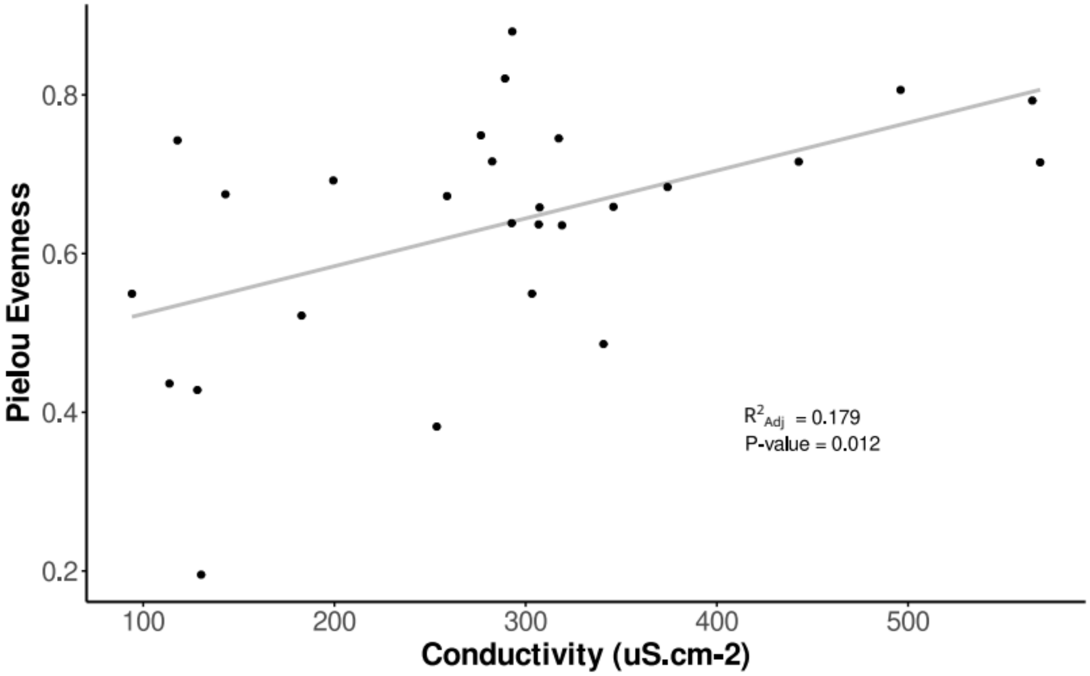

Figure 13. Linear regression between water conductivity and macroinvertebrate community Pielou Evenness.

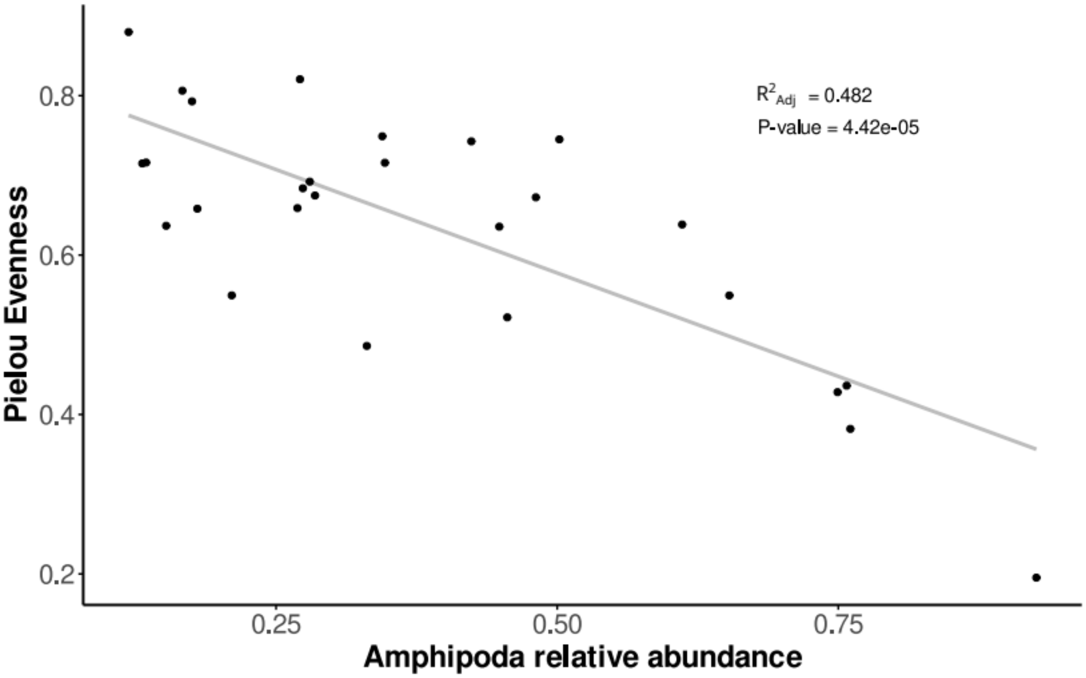

Figure 14. Linear regression between amphipod relative abundance and macroinvertebrate community Pielou Evenness

ANNEX C

Supplementary Methods

Mesocosm experiment

Mesocosms were constructed with transparent, polyethylene enclosures that were 1 m in diameter and 2.5 m in depth. The mesocosms were isolated from the lake because they were closed at the bottom, and the open surfaces of the mesocosms were covered with a coarse screen to exclude external aerial inputs from flying insects, jumping fish, etc. The mesocosms were suspended in Lake Croche at 2.5 m depth on anchored floating rafts. The temperatures and stratification in the mesocosms were representative of epilimnetic conditions within this lake. Each mesocosm enclosure was gently filled with epilimnetic water from Lake Croche by first passing the water through a double screen (100 µm over 54 µm Nitex mesh) to remove crustacean zooplankton and allow phytoplankton species to pass through into the mesocosms. Each mesocosm was filled to over 2000 L on June 11th 2018, and phytoplankton were allowed to equilibrate for 9 days before zooplankton stocking. On June 20th zooplankton were collected from Lake Croche for inoculation into the enclosures at similar densities to those found in the lake. To ensure similar densities from the lake in each of the mesocosms, we first sampled at zooplankton density in the source lake for the total volume of all mesocosms (for this experiment and an other one we needed 50 mesocosms x 2000L per mesocosm = 100000 L of lake water sampled), and then gathered these live zooplankton in an inoculation enclosure of known volume (2000L). We then homogenized this inoculation enclosure, and sampled water (40L) from the inoculation mesocosm by using ratios between lake water sampled volume and inoculation mesocosms volume to ensure that the zooplankton densities in each enclosure were similar, and approximately comparable with the density from the source lake. Live epilimnetic zooplankton were collected from Lake Croche and the inoculation enclosure using 54 μm Wisconsin nets and transferred into 20 L polyethylene container (2 containers had the equivalent of 2000 L mesocosms stocking) that were gently added to the mesocosms within half an hour of collecting zooplankton from the lake. Following zooplankton inoculation, the mesocosms were allowed 48 h to equilibrate before the first round of mesocosm sampling was done at the start of the experiment. NaCl was subsequently added to each enclosure on June 23nd following the first round of water and community sampling, and enclosures were well mixed to ensure homogeneity of water masses within each of the mesocosms.

Dissolved oxygen (DO; mg L^{-1}), pH, water temperature (^{o}C) and conductivity (μS cm^{-2}) were measured using a Professional Plus Model YSI multi-parameter sonde (model 10102030; Yellow Springs Inc.) every three weeks following the initial sampling at the start of the experiment (Table. A1). At these times, we also collected water samples to quantify total phosphorus (TP: μg L^{-1}) and phytoplankton biomass (chlorophyll *a*; Chl*a*). To avoid zooplankton decline due nutrient limitation on phytoplankton, we added phosphorus in the form of 0.0193 g of dissolved KH_2PO_4 in each mesocosm on two occasions (July 6th and July 20th) to replace nutrients loss as a result of phytoplankton and periphyton growth, and sedimentation (Downing et al. 2008). Before any water sampling, the mesocosm enclosures were carefully mixed to homogenize them and mix any water masses created by the addition of the salt.

Physico-chemical conditions

For the field collection of water samples for total phosphorus (TP), chlorophyll *a* (Chl*a*), and chloride ions, the collection tubes and bottles were rinsed with enclosures water three time prior to the final sample collection. Each rinse consisted of filling a fraction of the tube or bottle with water and vigorously shaking the tube. Water samples were then returned to the laboratory in coolers and stored at 4 °C prior to analyses. In the laboratory, TP was measured spectrophotometrically on a continuous flow analyzer (OI Analytical Flow Solution 3100 ©) by the molybdenum blue method after persulfate digestion (Griesbach and Peters, 1991). Chl*a* was sampled with 1L brown bottles and quantified by passing water samples through glass fibre filters (Whatman GF/F). Chl*a* was subsequently extracted in hot ethanol and measured spectrophotometrically on a BiochromUltrospec 2100 pro with a 10-cm quartz cuvette (Winterman & de Mots, 1965; Sartory & Grobelaar, 1984). The TP and Chl *a* samples were analyzed at the GRIL- Université du Québec à Montréal (UQAM) analytical laboratory. Chloride concentration was measured by ion chromatography (Pfaaf 1993) using Dionex DX-600 Ion Chromatography at University of Alberta Biogeochemical Analytical Service Laboratory.

Environmental DNA sampling

Lake water for 18S metabarcoding was sampled using sterilized (using an autoclave) 1.14L glass bottles (VWR® CAT NO. 10754-820). Each bottle was rinsed 3 times using lake or mesocosm water before being filled with lake or mesocosm water. After sampling water bottles were directly stored in cooler before storage in the laboratory at 4°C in dark condition. Water samples were used for filtration within 72 hours after field sampling. All DNA samples manipulation were done in fume hood sterilized using 70% alcohol and using sterile nitril gloves. Filter boxes were only manipulated in sterile conditions under the fume hood. All instrument involved in filter manipulations were sterilized by rinsing with 70% alcohol and passing through a Bunsen burner flame before use. Filtration system was sterilized using the autoclave before every use.

Molecular analysis

Water collected for 18S metabarcoding analyses (1000 L) was filtered through 0.2 µm polyethylsulfone filters (Sartorius™ - Type 15407- 47 mm) in the laboratory at the Université du Québec à Montréal. The filters were then stored in -80 °C prior to DNA extractions. DNA extractions were conducted with the Qiagen™ DNeasy PowerWater® kit and protocols (Qiagen, 2017). The V7 region of 18S rRNA were amplified using QuantStudio™ 3D by ThermoFisher Scientific PCR machine. A one-step PCR was performed using the UCP HiFidelity PCR Kit from Qiagen (ready-to-use 2x concentrated master mix). Primers were at 0.25 µM final concentration and we added between 2-4 µl of DNA template. The PCR program is summarized in Table A5. We put 5 µl on agarose gel before PCR clean-up, normalization and pooling. The Eukaryotic 18S rRNA gene was sequenced using the 960Fc

(3’-YRYRGGCTTAATTTGACTCAACRCG-5’)-NSR1438 (5’-GGGCATCACAG ACCTGTTAT-3’) primer pair (Capo et al. 2016), with an Illumina Miseq analyzer of the CERMO platform at Université du Québec à Montréal (UQAM).

Quality trimming/filtering, error models, dereplication, inferring ASVs and chimera identification were performed using the {dada2} package R 4.0.3 (R Core Team 2020). Primers were removed from all reads. After inspecting reads quality, both forward and reverse reads were trimmed to 200 nucleotides. Paired reads were then merged and chimera reads were removed. Taxonomic assignments were performed using SILVA SSU v138 Ref database (Quast et al. 2013) with the {DECHIPER} package R 4.0.3 (R Core Team 2020) with default 60 % threshold, using both DNA strands, bootstraps were set such that 99% of k-mers are sampled in each sequences, the minimum fraction of bootstraps required to descend the tree during the initial descent phase of the algorithm was 0.98, and the fold-difference in sequence lengths between sequences in the samples and reference database allowed was set to 0 to consider all sequences regardless of length. Biologically significant ASVs detected in downstream analysis were compared to publicly available sequences databases (http://www.ncbi.nlm.nih.gov/ BLAST) to identify closest matching sequences. After extraction, DNA concentrations were sufficiently high that we felt contaminant sequences would have minor influence on the result and therefor decided to not sequence blank samples. ASVs refer to single DNA sequences recovered from a high-throughput marker gene analysis and are used to classify groups of species based on DNA sequences. Similarly to OTUs, ASVs are utilized to classify groups of species based on DNA. However, ASVs sequences can distinguish sequences variation by a single nucleotide change which is not the case for OTUs that are generated by clustering sequences based on a shared similarity threshold. ASVs are also referred as exact sequence variant and provide more precise measurement of sequence variation than OTUs. ASVs are therefore comparable between studies but OTUs are not and can vary between researchers, experiments, and databases.

Generalized Linear Models

The effect of chloride concentration was tested on diversity indices (Shannon index, taxon richness and Pielou's evenness). The different variables included in generalized linear models are positive continuous variables, we used Gaussian distributions that best fitted the data for Shannon index and evenness, and we used a negative binomial distribution for taxon richness. Model residuals were investigated for non-linear patterns (residuals vs fitted values), distribution fit (qqplot), equal spread (scale location) and outliers (residuals vs leverage and sites outside 1.5 times the interquartile range above the upper quartile and bellow the lower quartile). All statistical analysis were performed in R 4.0.3 (R Core Team 2020).

Supplementary Results

Diversity indices

Community diversity indices (Shannon diversity, taxon richness and Pielou evenness) displayed a strong negative relationship with chloride concentration (Table A3, Fig. A2). Phytoplankton diversity was especially negatively affected by increased chloride concentration, with sharp decreases in both richness and evenness at the most elevated chloride concentrations. All other planktonic taxonomic groups (fungi, zooplankton, protozoans and worms), however, showed decreased richness but relatively stable evenness.

Citations

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Supplementary Figures

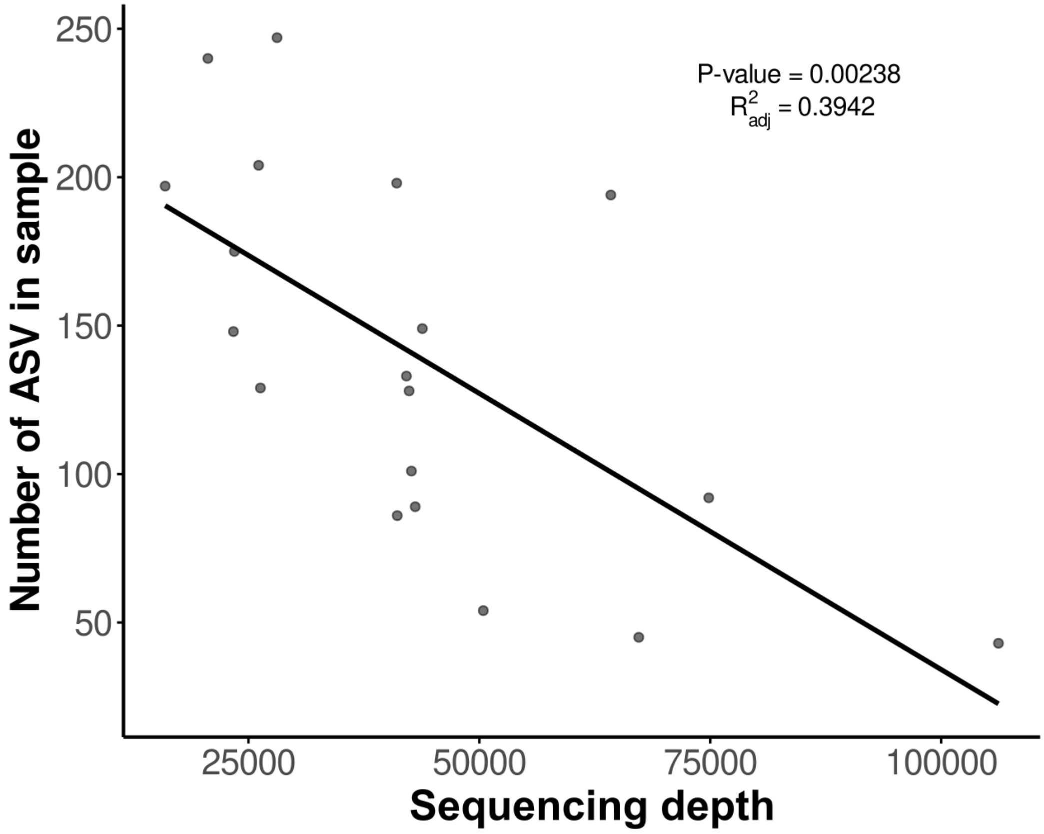

Figure A1. Relationship between ASV diversity and sequencing depth (number of sequences) in each sample.

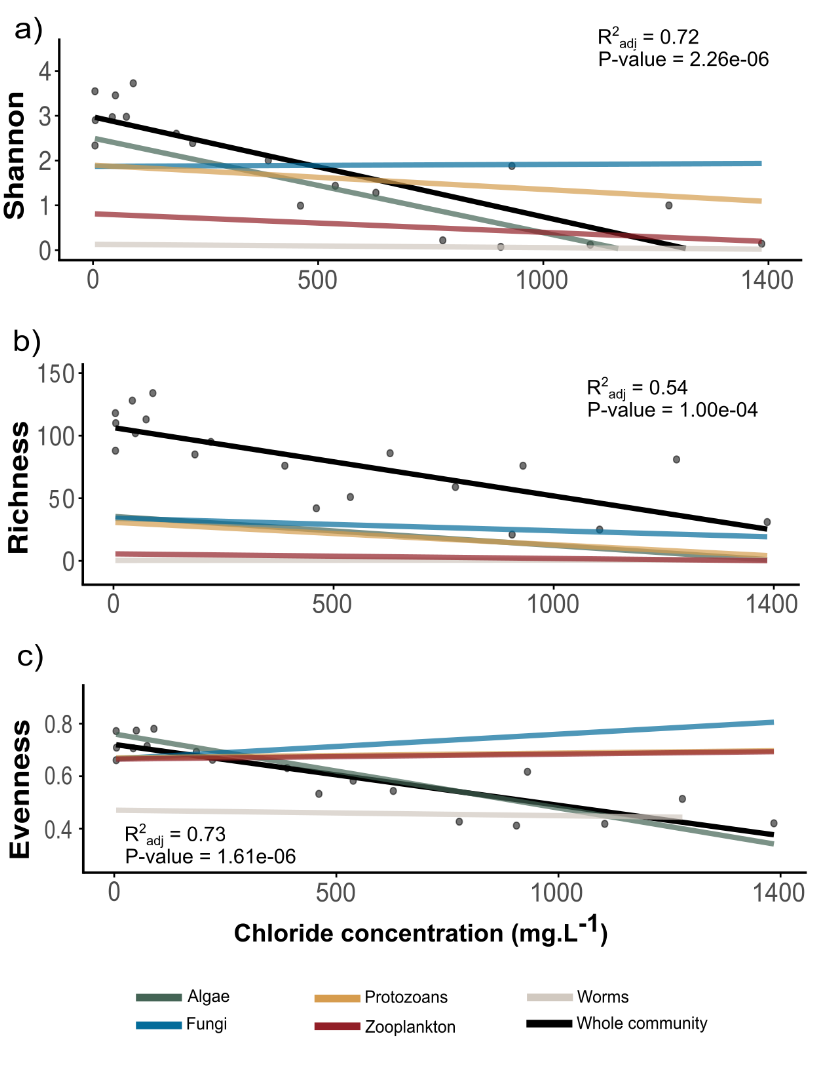

Figure A2: Influence of elevated chloride concentration on the planktonic community diversity. **a)** Linear regression of Shannon diversity and chloride concentration. **b)** Linear regression of ASV richness and chloride concentration. c) Linear regression of Pielou evenness and chloride concentration (mg Cl$^-$ L^{-1}). The black lines are regressions using the complete ASV dataset, colors are regressions using subset of ASV from different taxonomic groups detailed at the bottom of the figure.

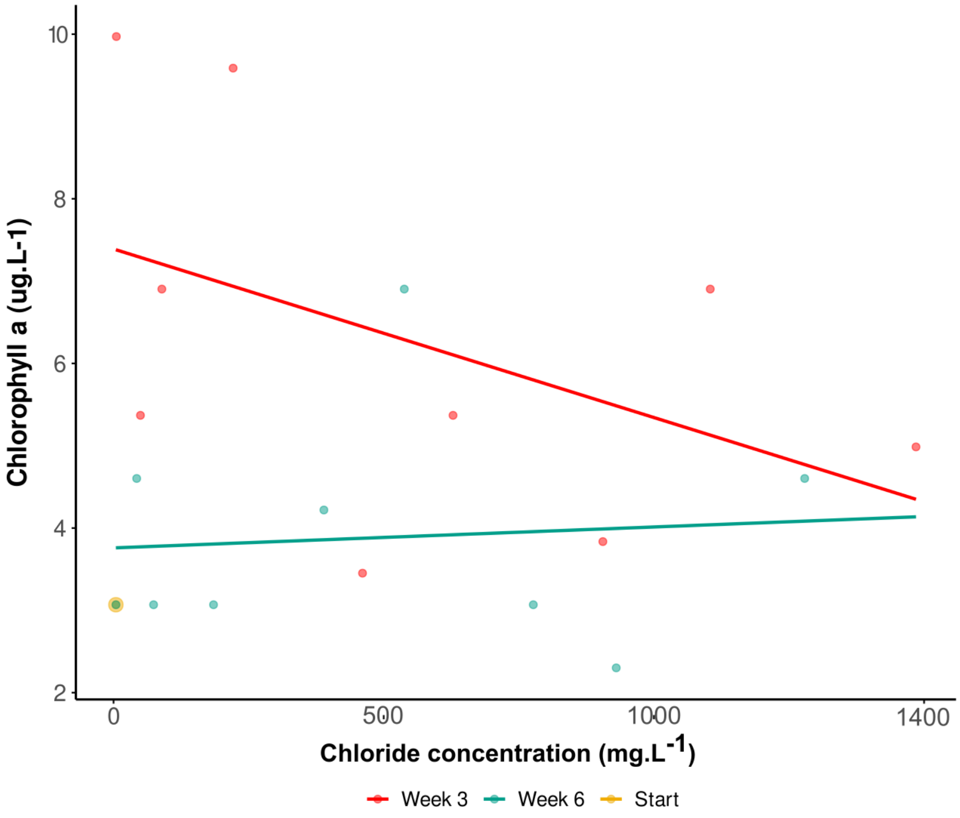

Figure A3. Relationship between chloride concentration (mg Cl^- L^{-1}) and phytoplankton biomass, as measured by chlorophyll a, in lake water (yellow points), week 3 mesocosms water (red points) and week 6 mesocosms water (green points).

Supplementary Tables

Table A1. Summary of environmental variables measured in the mesocosms across the gradient of salinity treatment on each sampling date.

Date	NaCl Treatment	Temperature (°C)	Conductivity (µS cm^{-2})	Chloride concentration (mg L^{-1})	pH	Dissolved Oxygen (%)	Total Phosphorous (µg L^{-1})
23-06	0	21.3	17.4	3.97	6.26	99	3.574
13-07	0	24.2	20.7	4.72	7.28	96.3	2.945
13-07	3	24.2	199.1	45.37	7.26	96.6	5.31
13-07	5	24.2	357.5	81.47	7.17	96.2	7.23
13-07	8	24.3	885	201.69	6.98	97.3	4.033
13-07	11	24.5	1843	420.02	6.7	96.8	7.36
13-07	13	24.3	2513	572.71	6.77	94.4	8.38
13-07	15	24.2	3622	825.45	7.64	97.7	12.99
13-07	18	24.2	4417	1006.63	7.32	99.5	5.95
13-07	20	24.2	5940	1353.73	7.07	94.2	7.93
03-08	0	24.6	17.9	4.08	6.87	116.9	4.34
03-08	3	24.6	171.3	39.04	7.1	115.3	4.085
03-08	5	24.6	296.3	67.53	7.06	118.7	4.851
03-08	8	24.5	740	168.65	6.64	114.8	4.532
03-08	11	24.6	1557	354.84	7.75	119.8	4.723
03-08	13	24.5	2152	490.44	6.98	115.3	3.766
03-08	15	24.6	3107	708.09	6.82	116.9	5.68
03-08	18	24.6	3721	848.02	7.13	119	3.319
03-08	20	24.5	5116	1165.94	6.95	117.6	4.085

Table A2. Summary of the indicator species analysis using three salt levels determined by the MRT analysis

ASV	Phylum	Class	Order	Family	Genus	Salt level
ASV 10	Ciliophora	Intramacronucleata	Spirotrichea	Hypotrichia	Halteria	low
ASV 12	Ciliophora	Intramacronucleata	Spirotrichea	Hypotrichia	Halteria	low
ASV 15	Rotifera	Monogononta	NA	NA	NA	low
ASV 46	Ochrophyta	Chrysophyceae	NA	NA	NA	low
ASV 56	Ciliophora	Intramacronucleata	Conthreep	Prostomatea	Cryptocaryon	low
ASV 58	Cryptophyta	Cryptophyceae	Cryptomonadales	NA	Cryptomonas	low
ASV 64	Ochrophyta	Chrysophyceae	NA	NA	NA	low
ASV 66	Diatomea	Mediophyceae	NA	NA	NA	low
ASV 86	Ochrophyta	Chrysophyceae	NA	NA	NA	low
ASV 90	Phragmoplastophyta	NA	NA	NA	NA	low

ASV 107	Phragmoplastophyta	NA	NA	NA	NA	low
ASV 133	Ciliophora	Intramacronucleata	Conthreep	NA	NA	low
ASV 145	Ciliophora	Intramacronucleata	Conthreep	Prostomatea	Cryptocaryon	low
ASV 148	MAST	MAST-12C	NA	NA	NA	low
ASV 163	Ochrophyta	Chrysophyceae	NA	NA	NA	low
ASV 188	Ochrophyta	Chrysophyceae	Synurales	NA	Mallomonas	low
ASV 265	MAST	MAST-12C	NA	NA	NA	low
ASV 338	Peronosporomycetes	NA	NA	NA	Aphanomyces	low
ASV 478	Ochrophyta	Chrysophyceae	NA	NA	NA	low
ASV 622	Cercozoa	NA	NA	NA	NA	low
ASV 2	Cryptomycota	NA	NA	NA	NA	medium
ASV 8	Ciliophora	Intramacronucleata	Conthreep	Colpodea	Cyrtolophosis	medium
ASV 16	Cryptomycota	NA	NA	NA	NA	medium
ASV 24	Cryptomycota	NA	NA	NA	NA	medium
ASV 26	Cryptomycota	NA	NA	NA	NA	medium
ASV	Cryptomycot	NA	NA	NA	NA	medium

31	a					
ASV 83	Basidiomycota	Tremellomycetes	Filobasidiales	Filobasidiaceae	Naganishia	medium
ASV 85	Cryptomycota	NA	NA	NA	NA	medium
ASV 92	Cryptomycota	NA	NA	NA	NA	medium
ASV 100	Cryptomycota	NA	NA	NA	NA	medium
ASV 128	Cercozoa	Glissomonadida	NA	NA	Viridiraptor	medium
ASV 263	Cryptomycota	NA	NA	NA	NA	medium
ASV 336	Cryptomycota	NA	NA	NA	NA	medium
ASV 453	Ochrophyta	Chrysophyceae	Chromulinales	NA	Chrysamoeba	medium
ASV 1	Ochrophyta	Chrysophyceae	NA	NA	NA	high
ASV 45	Ochrophyta	Chrysophyceae	NA	NA	NA	high
ASV 78	Cercozoa	Incertae Sedis_6	NA	NA	Gymnophrys	high
ASV 146	Cercozoa	Incertae Sedis_6	NA	NA	Gymnophrys	high
ASV 147	Ochrophyta	Chrysophyceae	NA	NA	NA	high
ASV 180	Basidiomycota	Agaricomycetes	Polyporales	NA	NA	high
ASV 255	Basidiomycota	Agaricomycetes	Corticiales	Corticiaceae	Hyphodontia	high

ASV 366	Basidiomycota	NA	NA	NA	NA	high
ASV 410	Cercozoa	NA	NA	NA	NA	high
ASV 512	Diatomea	Bacillariophyceae	NA	NA	Pinnularia	high
ASV 579	Basidiomycota	Agaricomycetes	Agaricales	NA	NA	high

Table A3. Influence of Chloride concentration on plankton community diversity as revealed by the 18S rRNA gene. Generalized linear model results for the influence of Chloride concentration (mg Cl^- L^{-1})as predictors of community diversity indices: Shannon diversity (Shannon), taxon richness (Richness), Pielou Evenness (Evenness). Bold *P*-values are <0.05. Findings are summarized in Appendix Fig. A2.

	Shannon			
Coefficient	***Estimates***	***Standard error***	***t-value***	***P-Value***
Intercept	2.974	0.214	13.888	**1.04e-10**
Chloride	-0.002	0.0003	-6.969	**2.26e-06**
Observations	19			
R^2 adj	0.725			
	Richness			
Intercept	106.397	7.644	13.919	**1.01e-10**
Chloride	-0.059	0.013	-4.774	**0.000176**
Observations	19			
R^2 adj	0.849			
	Evenness			
Intercept	6.413e-01	4.325e-02	14.826	**3.72e-11**
Chloride	-5.076e-04	7.094e-05	-7.155	**1.61e-06**
Observations	19			
R^2 adj	0.736			

Table A4. The influence of chloride concentration on chlorophyll a concentration. Generalized linear model results for the influence of chloride concentration (mg $Cl^- L^{-1}$) and sampling week as predictors of chlorophyll a concentration. Bold *P*-values are <0.05. Findings are summarized in Appendix Fig. A3.

	Model			
Coefficient	***Estimates***	***Standard error***	***t-value***	***P-Value***
Intercept	6.853	0.826	8.293	**5.51e-07**
Chloride	-0.001	0.001	-1.105	0.287
Sampling week	-2.473	0.895	-2.762	**0.015**
Observations	18			
R2 Nagelkerke	0.272			

Table A5. Summary of the PCR program used to amplify the 18S rRNA gene segment from water filtered from mescosms.

Temperature	**Time (hour:min)**	**Cycles**
98	0:30	1
98	0:30	1
55	0:30	33
72	1:00	1
72	10:00	1
8	Hold	1

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