Title: Environmental determinants of invasion hotspots and refugia at a river scale: implications for conservation of native biodiversity

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Abstract

Introductions of exotic invasive species are a global disturbance for natural habitats, native species and their related ecological services. The severity of invasions and impacts, however, can greatly vary from local to global scales. This variation can be observed in both invasion hotspots, exhibiting disproportionate invasion and impacts, or refugia, exhibiting lower than expected invasion and impacts. The latter are believed to be habitats where ecological, social or environmental conditions create deterrence of invaders. Dissolved ions and presence of wetlands have been suggested as environmental conditions that buffer the impacts of Ponto-Caspian invaders, notably the round goby (*Neogobius melanostomus*). In this study, we used a generalized additive model (GAM) to analyze the effects of local water conductivity and wetland presence on the density of the round goby in a large-scale study (> 1300 sites), spanning the major part of the non-tidal freshwater portion of the St. Lawrence River (Canada). Our results showed that, even in long-invaded regions, round goby density was null in sites with water conductivity under 100 µS/cm and increased toward a probable biological optimum of water conductivity ~300 µS/cm. Additionally, the presence of wetlands, even if they did not completely disrupt surpass the effect of conductivity, appeared to decrease the round goby densities along the conductivity continuum. Our study demonstrated that low water conductivity (<100 µS/cm), in interaction with the presence of wetlands can provide a refugium for native aquatic species, establishing a simple, yet robust, risk assessment tool for managers. Our results also highlighted the high value of wetland conservation and restoration as a promoter of biodiversity and an integrated management tool for conservation of native species.

Introduction

Biological invasions are devastating global anthropogenic disturbances that threaten biodiversity, and disrupt ecosystem functions and services (Pejchar and Mooney 2009, Simberloff et al. 2013, Lewis et al. 2016, Bacher et al. 2018, IPBES 2019). Distressingly, the number of non-native species introductions continues to increase around the world (Seebens et al. 2017, Seebens et al. 2018). The magnitude and frequency of invasions, however, can be highly variable (Dawson et al. 2017). At the global to the regional scale, some locations are experiencing a disproportionate invasion pressure while other neighbouring habitats seem to have been far less impacted (Latzka et al. 2016, Dawson et al. 2017, Dyer et al. 2017). This phenomenon is crystallized in the identification of invasion hotspots and refugia, exhibiting contrasting invasion prevalence (number and abundance of invasive species) (Dawson et al. 2017). Disproportionate levels of invasion across the landscape can often be explained by differences in propagule pressure or ecosystem characteristics that mediate invasion success (Catford et al. 2009, Lockwood et al. 2009). However, within invaded ecosystems, other factors that determine whether local sites become invasion hotspots or invasion refugia remain to be better described and understood. For example, invaded ecosystems with homogeneous habitats can become invasion hotspots when environmental conditions are suitable and invasive species become abundant, often resulting in extirpation of native species (Melbourne et al. 2007). By contrast, spatial environmental heterogeneity within invaded ecosystems can sometimes play an important role in promoting or suppressing invasive species density at local and regional scales (Melbourne et al. 2007, Vander Zanden et al. 2017). The identification and delineation of invasion hotspots and refugia are therefore an effective tool for planning invasive species management and conservation of native biodiversity (Byers et al. 2002).

Invasion refugia could arise within invaded regions or habitats where ecological, social or environmental conditions create a deterrence of invaders, either by preventing the propagule pressure or decreasing survival or performance of invaders (Melbourne et al. 2007, Anton et al. 2014, Vander Zanden et al. 2017). In an invasion refugia, even a small to moderate decrease of invasion pressure or invasive species density can allow coexistence of invasive and native species, hence promoting native species persistence (Yokomizo et al. 2009, Sofaer et al. 2018, Bradley et al. 2019, Strayer et al. 2019, DeRoy et al. 2020, Strayer 2020). This phenomenon appears to be in accordance with the environmental matching hypothesis, stating that the impacts of an invader decrease with environmental conditions that diverge from its physiological optimum (Ricciardi et al. 2013, Iacarella and Ricciardi 2015). Our study joins a growing body of literature exploring environmental factors that promote invasion refugia within invaded freshwater ecosystems (Grabowski et al. 2009, Kestrup and Ricciardi 2009, Priddis et al. 2009, Iacarella and Ricciardi 2015, Latzka et al. 2016, Astorg et al. 2020, Boddy et al. 2020, Boddy and McIntosh 2021). More specifically, we aimed to address environmental determinants of invasion hotspots and refugia of an invasive benthic fish, the round goby (*Neogobius melanostomus*), in a large and complex river system, the St Lawrence River, which drains the North American Great Lakes. Other previous studies on the role of environmental heterogeneity in establishment of invasion refugia in the St Lawrence River have been done at limited spatial scales or in laboratory experiments (Kestrup and Ricciardi 2009, Iacarella and Ricciardi 2015, Astorg et al. 2020), potentially limiting inferences at the whole ecosystem scale.

The round goby is an invasive benthic littoral fish that was first observed in in the St. Lawrence River in 1997 where it became increasingly abundant in many, but not all, habitats (Kipp et al. 2012, Morissette et al. 2018, Astorg et al. 2022). Its geographic range distribution in the St.

Lawrence River spans from Lake Ontario to the salt front of the St. Lawrence Estuary, ~30 km downstream of Québec City. When present, the round goby has strong ecological effects, notably by reducing the density of native benthic fishes such as darters (*Etheostoma spp.*) and sculpins (*Cottus spp.*) that use similar habitats (Jude et al. 1992, Poos et al. 2010). The round goby can also ravage the diversity and abundance of macroinvertebrate communities (Kipp et al. 2012, Astorg et al. 2022). However, certain types of habitats and environmental conditions can reduce round goby abundance. In the Great Lakes, oxygen concentration and riparian habitat quality were linked to invasion success of the round goby in some tributaries (Kornis et al. 2013, Krabbenhoft and Kashian 2022, McAllister et al. 2022). The concentration of dissolved ions (often measured by water conductivity or specific conductance, which is conductivity standardized at 25 °C) can also predict the presence and abundance of the exotic round goby in the Great Lakes (Baldwin et al. 2012) and in the St. Lawrence River (Astorg et al. 2020). Another laboratory experiment from a limited portion of the St. Lawrence River showed that the impact of conductivity on round goby performance was influenced by water calcium concentration, where low dissolved calcium ions (Ca^{2+}) resulted in low predation rates and, thus, reduced ecological impacts (Iacarella and Ricciardi 2015). Other studies have found evidence to support that wetlands, through their substrate properties and associated submerged aquatic vegetation, offer buffering effects from negative round goby impacts on native biodiversity at invaded sites (Cooper et al. 2007, Astorg et al. 2020). Those results, albeit highly pertinent for risk assessment and management of the round goby, were based on observations from a limited portion of the St. Lawrence River, impeding the potential for generalization of the results.

In this study, we synthesize two extensive fish surveys along the St. Lawrence River, the Fish Identification Nearshore Survey (FINS) and the *réseau de suivi ichtyologique* (RSI) respectively

operated by the River Institute and the *ministère des Forêts, de la Faune et des Parcs*. This provided us with the opportunity to test the phenomenon of invasion hotspots and refugia for the round goby on the largest scale of the entire non-tidal freshwater portion of the St. Lawrence River. The objective of our study was to explore the relative influence of local environmental conditions on the density of the round goby in the region covered by FINS and RSI. Specifically, we aimed to test two hypotheses: 1) round goby density increases positively with water conductivity in invaded waters and 2) the presence of wetlands in invaded waters reduces round goby density. We predict that invaded sites with high water conductivity and wetland absence act as invasion hotspots and invaded sites with lower water conductivity and wetland presence act as invasion refugia from the round goby. Our study provides information for delimiting round goby hotspots and refugia in the St. Lawrence River, helping to refine risk assessment of Ponto-Caspian invasion in this ecosystem and others under imminent threat of round goby, as well as promoting restoration and conservation of invasion refugium in the region.

Materials and Methods

Study area

We conducted our study over an area spanning approximately 400 km along the St. Lawrence River, extending from Kingston (Ontario, Canada) at the outflow of Lake Ontario to Batiscan (Québec, Canada) in the St. Lawrence River (Figure 1). The St. Lawrence River is a large fluvial ecosystem draining the Laurentian Great Lakes toward the Atlantic Ocean. Its narrow fluvial sections successively (upstream to downstream) drain three widenings of the St. Lawrence River, called the fluvial lakes (St. François, St. Louis and St. Pierre lakes). Where the St. Lawrence reaches the Archipelago of Montréal, the water from the Ottawa River, characterized by its low conductivity (~60 to 100 µS/cm) and brown coloration, joins the Great Lakes water mass, which

has a higher water conductivity (200 to 400 µS/cm) and green coloration. Downstream of Montréal, both water masses flow side by side, with very little lateral mixing (Vis et al. 1998, Frenette et al. 2003), until the St. Lawrence reaches its tidal portion downstream of Lake St. Pierre. Hence, the water masses keep their contrasted chemical properties for hundreds of kilometres, creating a large ecotone where brown waters (Ottawa River) are mostly restricted to the North shore and green waters (Great Lakes) to the South shore. The precise position of the mixing zone and the two water masses stay relatively stable, with seasonal variations depending on the magnitude of spring flood. Along the large-scale chemical gradients, various habitats can be observed, from highly vegetated wetlands to sandy and rocky bottom sections, creating an additional environmental variation of interest for fish and invertebrate communities.

Environmental and fish data

Fish community data were acquired using beach seine as part of both FINS and RSI annual fish surveys, in mid to late summer over 14 years, between July 2007 to September 2021. The FINS fishing was conducted using a 9.1 m long and 1.8 m deep purse seine, operated on three 20 m long hauls for every studied site, corresponding approximately to 182 m^2 of surveyed habitat per effort. The RSI used a 12.5 long by 4 m deep beach seine deployed on site and closed on itself by operators, corresponding to approximately 120 m^2 of surveyed habitat per site. Both nets were used in coastal, wadable (depth <1.5 m) habitats. Captured fish were identified to species and counted by capture sites. As the spatiotemporal effect of round goby presence on those littoral fish communities have already been assessed (Morissette et al. 2018), we limited the study to the analysis of goby density. Site-specific round goby counts were converted to density (goby/m^2) to allow comparisons between both FINS and RSI datasets.

Environmental data, conductivity (specific conductance) and wetland presence were either measured and observed on site during sampling (FINS) or extrapolated from geographical data available (RSI). During FINS surveys, conductivity was measured and recorded nearshore (maximum one-meter depth) at each sampling site using a calibrated water quality multi-parameter sonde (Professional plus model YSI ProDSS). Conductivity extrapolation was conducted using 1660 points dataset acquired between 2017 and 2021, spanning the entire study sites. Conductivity was interpolated using ordinary kriging analysis in the Spatial Analyst toolbox implemented in the software ArcMap 10.7.1 (ESRI). Validation was conducted by comparison of interpolated and measured values, producing a reliable agreement ($R^2_{adj} = 0.84$, Figure S1). Conductivity values on fish sampling sites were extracted using the sampling coordinates and the function *extract* coded within the package terra (Hijmans et al. 2022) implemented in R version 4.1.2 (R Core Team 2021). For both FINS and RSI surveys, the presence of wetlands on sites was extracted using a combination of an open-access high resolution cartography of Ontario (Ministry of Natural Resources and Forestry 2021) and Quebec wetlands (Canards Illimités Canada and ministère de l'Environnement et Lutte contre les changements climatiques 2021). To simplify the dataset, only “open water” class was considered as *non-wetlands* and all remaining classes (e.g., marsh, swamp, wet meadows) were considered as *wetlands*, creating a binary *habitat type* factor.

Statistical modelling

All statistical analyses were computed in R version 4.1.2 R (R Core Team 2021) and RStudio v2022.02.3+492 (RStudio Team 2020). Generalized additive models (GAMs) were used to assess the effect of conductivity and habitat type on round goby density using the *mgcv* R package v1.8-38 (Wood 2011). GAM is a useful framework to model linear and non-linear

relationships using smooth functions and can incorporate different family error distributions (Wood 2017). GAM allow for the estimation of the non-linear "partial effect" of a predictor variable, which represent the weighted sum of multiple basic functions of increasing wiggliness. Two models were built in relation to our hypotheses. Both models included round goby density (individual/m^2) as the response variable. The first model predictors were habitat type as a parametric effect, conductivity by habitat factor-smooth interaction, longitude and latitude smooth interaction and year as a random smooth while the second model included all listed predictors, but the conductivity smooth was considered without the interaction with habitat type and its parametric effect (Table S1). For both models, latitude and longitude smooth interaction was included to consider any spatial correlation to ensure that model residuals are more likely to be independent. Year was identified as a random predictor to generalize the effect over the years and to account for any effect of time since invasion (Astorg et al. 2022). The default thin plate spline was used for the conductivity smooth or for the smooth by factor interaction, the Duchon spline was applied to the latitude and longitude smooth interaction and a random smooth intercept was used for years. Since the response variable was continuous with left-skewed non-integer values including zeros, an identity log link function with a Tweedie error distribution was applied to both models. Model diagnostics and maximum basis functions (k) were verified using the *gam.check* function and autocorrelation was assessed using the *acf* function of the model residuals from the *stats* R package. No significant autocorrelation was detected in the GAMs and diagnostic plots suggested normality and homoscedasticity of the residuals (Figure S2). Model selection was done using the Akaike's Information Criterion (AIC) score (Wood et al. 2016). The best-fitted model showed the lowest AIC score (Table S1). Model visualization was

accomplished using the *mgcViz* package v0.1.9 (Fasiolo et al. 2020) and *ggplot2* package v3.3.5 (Wickham et al. 2016).

Results

The fish dataset comprised 1310 sampling sites, with an average density of 0.07 goby/m^2 (±0.17 SD), ranging from 0 to 1.78 goby/m^2. Conductivity was variable in the study area, ranging from 43.8 to 576 µS/cm, with an average value of 244.69 µS/cm (±70.27 µS/cm SD). The expected conductivity structure between the St. Lawrence North shore and South shore downstream of Montréal was observed (Figure 1). Conductivity in the upper St. Lawrence was more homogeneous, where variations were mainly influenced by small tributary outflows. Wetlands and non-wetlands were equally represented in the study area, with 662 wetland sites and 648 non-wetland sites in the dataset, with both habitats present in approximately equivalent amounts on both shores (Figure 1).

Our results indicate that both habitat type (wetland/non-wetland) and conductivity were important predictors of round goby density in the St. Lawrence River. The best-fitted GAM model showed the lowest AIC and included habitat type as a fixed effect, conductivity by habitat type factor-smooth interaction along with the latitude and longitude smooth interaction and year as a random smooth (Table S1). A statistical summary of the selected model is shown in Table 1. Both the parametric fixed effect and partial smooth effects were significant (p-value <0.05) and explained 55.8% of the null deviance with an R^2-adjusted value of 30.5%.

Habitat type showed a direct effect on the round goby density. Compared to non-wetland habitats, wetlands had an important negative effect and therefore hosted lower round goby densities (Figure 2). Water conductivity showed a non-linear partial effect on the round goby

density. However, the magnitude of the effect was different between habitat types and was dependent on the range of the observed values. Overall, below approximately 220 µS/cm, conductivity showed a negative effect on the round goby density (Figure 3). This negative effect was found to be amplified in wetlands (Figure 3B) compared to non-wetland habitats (Figure 3A). Above this threshold, water conductivity displayed a positive effect on the round goby density in both habitats. At higher levels of conductivity (> 380 µS/cm), a negative effect on round goby density was only observed in wetlands. However, the confidence interval is large and includes the null effect. Overall, the round goby seems to exhibit a maximum density around 295 µS/cm, a potential biological optimum. The best-fitted GAM model demonstrated a significant partial effect of latitude and longitude on the round goby density (Figure 4), showing a spatially-coherent weighted sum of models' predictors on the round goby densities. A considerable portion of the south shore of the St. Lawrence River displayed an important positive effect on the round goby density while some locations, notably the Ottawa River and Deux-Montagnes Lake (a widening of the Ottawa River) were locations with the most negative partial effects on round goby density.

Discussion

Our study aimed to analyze a previously unpublished and extensive dataset provided by two large-scale fish surveys conducted in the environmentally heterogeneous St. Lawrence River to examine the effects of two environmental conditions—water conductivity and presence of wetlands—on round goby presence and density. We used GAMs to determine thresholds for ecological optima along the water conductivity gradient and showed the large-scale effects of water conductivity on round goby density, as previously recognized in its invaded range (Baldwin et al. 2012, Astorg et al. 2020). Our results showed that round goby density was

positively influenced by increasing conductivity until reaching a probable biological optimum of ~300 µS/cm. Sites of water conductivity under 200 µS/cm had low density to complete absence of round goby (<100 µS/cm), even in regions hosting established populations for more than 10 years (Morissette et al. 2018), therefore representing possible invasion refugia. Additionally, even if the presence of wetlands did not completely disrupt the pattern of water conductivity effects on round goby density in invaded habitats, wetlands appeared to decrease round goby densities along the conductivity continuum, contributing to the invasion refugium effect. Our study is different from earlier research on the effect of wetlands and low water conductivity (or dissolved ions) on round goby density as the detected invasion refugium in these other studies were of either of limited size (Baldwin et al. 2012, Astorg et al. 2020) or laboratory-based (Iacarella and Ricciardi 2015). By contrast, our study addressed the influence of those two environmental factors along a over 400 km stretch of the St. Lawrence River, compiling more than 1300 capture sites on a 14-year-old-time series. Hence, our results provide an empirical criterion delineating round goby invasion hotspots and refugia. The sheer size of this study underlines the possibility of generalizing the phenomenon and emphasizes the importance of habitat diversity (i.e., wetland conservation and restoration) to buffer the effects of biological invasion.

The detection of a predicable response of round goby density in the St. Lawrence suggests that the risk of potential impact, that we consider density-dependent, could be identified by two simple metrics, water conductivity and wetlands presence (Table 2). Herein, we propose that non-wetland habitat with water conductivity under 100 µS/cm have a very low risk of goby impacts, evaluated as null in wetlands under this conductivity. This risk increases with increasing water conductivity until higher than 300 µS/cm, reaching the ecological optimum where impacts

267 are predicted to be maximal. Freshwater habitats over this threshold are known to host goby
268 populations with significant impacts (Baldwin et al. 2012, Kipp et al. 2012, Kornis et al. 2013).
269 However, In these round goby invasion hotspots, wetlands may still have buffering effects, albeit
270 limited in spatiotemporal scale, depending on submerged vegetation abundance, density and
271 phenology (Seilheimer and Chow-Fraser 2007, Janetski and Ruetz 2015). The simple risk grid
272 that our study provides (Table 2) can offer a fast and an easy to implement tool for managers and
273 could be disseminated on a large landscape with relatively accessible data. Management of
274 aquatic invasive species is often confronted with the challenge of rapidly identifying the present
275 or upcoming threat of a given species which can cause a vast array of impacts (Lodge et al.
276 2006). Identification of those impacts can largely vary in the invaded range and depart from what
277 has been identified in laboratory experiments and small-scale field studies. A broader
278 understanding of context-dependent potential density and their related impacts is needed to
279 implement an efficient management in heterogeneous landscapes and populate a more refined
280 impacts evaluation framework (Vander Zanden et al. 2017). Our finding that a local-scale
281 phenomenon, observed in 120 m^2 habitat patches, had a uniform response acrossat a large
282 environment scale underscores the value of observational studies in invasion biology and its
283 unique potential to offer generalizable risk assessment tools.

284 The negative effect of low water conductivity on round goby density is concordant with field
285 observations made by Astorg et al (2020) and Baldwin et al (2012), and our findings add to a
286 known effect of low conductivity on Ponto-Caspian invaders (Zhulidov et al. 2004, Kestrup and
287 Ricciardi 2009). Reduced Ponto-Caspian invader densities in waters with low concentrations of
288 dissolved ions are suggested to be linked with the evolutionary history of these euryhaline
289 species, which experienced repeated marine invasions—characterized by extreme variations of

290 salinity—favouring physiological processes requiring availability of high-dissolved ion
291 concentrations in ambient waters. Differences in round goby performance along freshwater
292 conductivity gradients may be linked to the concentration of calcium ions (Ca^{2+}), which
293 contribute to physiological processes and represent a likely common element between freshwater
294 and saltwater (Hunn 1985, Mayer et al. 1994, Baldwin et al. 2012, Iacarella and Ricciardi 2015).
295 Calcium represents a critical component of homeostasis in fish, by intervening on rates and
296 efficiency of gill-water exchanges. Accordingly, field observations suggest that the fish calcium
297 uptake from the environment seems to represent an evolutionarily conserved process, that does
298 not proportionally respond to large differences in environmental calcium, even after long-term
299 (multiple generations) residence along this environmental gradient (Sanderson et al. 2021).
300 Hence, the poor performance of round gobies—along with other Ponto-Caspian invaders—can
301 be a manifestation of the limited plasticity of those species under the unusual environmental
302 conditions imposed by low conductivity tributaries or water masses. This is an eloquent example
303 of environmental matching hypothesis and how the intolerance for low conductivity waters
304 translates in natural refugium to invasion (Ricciardi et al. 2013).

305 The mitigation of round goby presence and density in the St. Lawrence River by environmental
306 heterogeneity in water conductivity and local presence of wetlands are important for the
307 resilience of native fishes and macroinvertebrates populations in this culturally and socio-
308 economically important river system. Most ecological impacts of the round goby on littoral fish
309 community and macroinvertebrates appear to be density-dependant, and they are most severe at
310 local sites with environmental conditions favourable for the round goby establishment where the
311 fish has occurred since its introduction in the St. Lawrence River two decades ago (Morissette et
312 al. 2018, Astorg et al. 2022). In the face of this invasion, eradication and even population control

313 of the round goby is an unattainable goal with the present technology available to managers.
314 However, favouring coexistence of native species with round goby appears to be a more realistic
315 objective, both in the St. Lawrence River and in its different tributaries. Some tributaries of the
316 St. Lawrence Rivert have still not become completely colonized by the round goby, either
317 because of limiting environmental conditions or because of natural (e.g., waterfalls and rapids) or
318 anthropogenic (e.g., dams and weirs) fragmentation. Such habitats (e.g., St. Lawrence River
319 tributaries) host imperiled species predisposed to round goby impacts, notably the eastern sand
320 darter (*Ammocrypta pelludica*), the channel darter (*Percina copelandi*) and the pugnose shiner
321 (*Notropis anogenus*). Identification of the imminent risk is critical in ensuring conservation of
322 those species. We believe that our proposed risk analysis grid (Table 2) could assist management
323 agencies in either estimating the risk for round goby invasion and the identification of invasion
324 refugium meeting either the conductivity or wetlands criteria (or both).

325 Aside from its role buffering invasion impacts identified in our study, wetlands in freshwater
326 habitats are contributing to a vast array of ecological functions and services. For example,
327 wetlands have been shown to act as a buffer for wave-induced erosion (Silliman et al. 2019),
328 filtering runoffs inputs and contaminants (Díaz et al. 2012, Sileshi et al. 2020) and providing
329 spawning, nursery and feeding habitats for fishes, waterfowls, invertebrates and mammals
330 (Trebitz et al. 2009, Tanentzap et al. 2014). The sum of those ecosystem services underlines the
331 critical importance of wetlands in aquatic habitats. Sadly, wetlands have experienced drastic
332 declines, disappearing three times faster than forested areas (Convention on wetlands 2021).
333 Such declines, fuelled by anthropogenic modifications of freshwater habitats, pollution and
334 climate change (Johnson et al. 2010, Patenaude et al. 2015) can still be contained and even
335 reverted with the application of emergency plans of conservation (Tickner et al. 2020). Hence,

the preservation and restoration of wetlands does not onlydon't represent an aesthetic choice or an application for the sake of biodiversity preservation—which already represent valuable objectives—wetlands can also be viewed as a pragmatic tool in the integrated management of water quality and prevention of biological invasions (Trepel 2010, Patenaude et al. 2015, Astorg et al. 2020). Promotion of a diverse, yet complex mosaic of heterogeneous habitats could potentially decrease invasion impacts and offer refugium for native species, thus favouring coexistence and persistence (Melbourne et al. 2007, Priddis et al. 2009).

We recognize that factors for invasion success and ecological impacts of biological invasions are complex and subject to multiple—and potentially synergistic—biotic and abiotic influences (Catford et al. 2009, Ricciardi et al. 2020, Spear et al. 2021). Notably, over the large study region, the influence of climatic variations (i.e., water temperature, amount of precipitation, winter severity) could also contribute to the observed spatial effect. However, the contrasted densities of the round goby observed in close sampling sites (i.e., in the vicinity of Montréal and within Lake St. Pierre) suggest that climatic variations were probably of low importance in the observed patterns that we report here. Round goby invasion success could be influenced by other factors that we have not addressed by our study, such as the importance of propagule pressure, the feeding opportunities (i.e., abundance of dreissenid mussels or invertebrate), other environmental variables (i.e., sediment type and water flow) or ecological relationships (i.e., predation). However, overall, the striking effect of water conductivity on round goby density, and therefore ecological impact on native fish and macroinvertebrate communities, offers an interesting avenue to study mechanisms under invasion success and magnitude.

In conclusion, our study offers a unique opportunity to combine two ongoing and long-term systematic fish surveys along a highly structured and complex freshwater ecosystem. We

observed a consistent effect of water chemistry and wetland presence in decreasing the density of a notable Ponto-Caspian invader. Our results show that low water conductivity (<200 µS/cm), in interaction with the presence of wetlands, are linked to a lower round goby density, buffering the potential ecological impacts of this invader and providing a refugium for native aquatic species such as macroinvertebrates and fish. The combination of easily measurable environmental metrics can provide a simple, yet robust risk assessment tool for managers. Our results also highlight the high value of wetlands conservation and restoration as a promoter of biodiversity and an integrated management tool for conservation of native species, especially in invaded ecosystems subjected to anthropogenic disturbances.

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Committee either at MFFP, UQAM and the River Institute and authorized by licences for scientific fish collections from the Ontario Ministry of Natural Resources and Forestry and the ministère des Forêts, de la Faune, et des Parcs du Québec..

Authors contributions

All authors contributed to the ideation of the study, the manuscript writing and the revision. MW and CC contributed to the FINS survey and OM and AD contributed to the RSI survey. MW, CC and OM did the data curation and quality assessment and CC and OM realized the statistical analyses, the production of the figures and the tables.

Conflict of interest statement

The authors declare no financial or personal conflict of interest.

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Table 1. Statistical summary of the generalized additive model (GAM) selected including habitat type as a fixed effect, conductivity by habitat type factor-smooth interaction, longitude and latitude smooth interaction and year as a random smooth. Edf indicates the estimated degree of freedom and Ref.df represents the residual degree of freedom. Significant parametric (A) and partial effects (B) are indicated by p-value <0.05.

A. parametric coefficients	**Estimate**	**Standard Error**	**t-value**	**p-value**
(Intercept)	-3.8625	0.1487	-25.97	<0.0001
Wetlands	-0.4896	0.1479	-3.31	<0.005
B. smooth terms	**edf**	**Ref.df**	**F-value**	**p-value**
s(conductivity): non-wetlands	7.198	8.941	4.127	<0.0001
s(conductivity): wetlands	4.15	5.246	6.764	<0.0001
s(longitude, latitude)	55.791	79	17.365	<0.0001
s(year)	9.85	14	3.003	<0.0001
R2-adjusted	0.305			
Deviance explained	55.8 %			

613 **Table 2.** Binary risk of round goby density (and density-dependent impacts) evaluation grid
614 based on specific conductance (conductivity) and local presence of wetlands on a local to large-
615 scale study site.

	Water specific conductance (conductivity)			
Local habitat	<100 µS/cm	100 to 200 µS/cm	200 to 300 µS/cm	> 300 µS/cm
Non-wetlands	very low	low	medium	high
Wetlands	null	very low	medium*	high*

616 * General agreement to large-scale risk with possibility of local or seasonal buffering effects of
617 wetlands

618

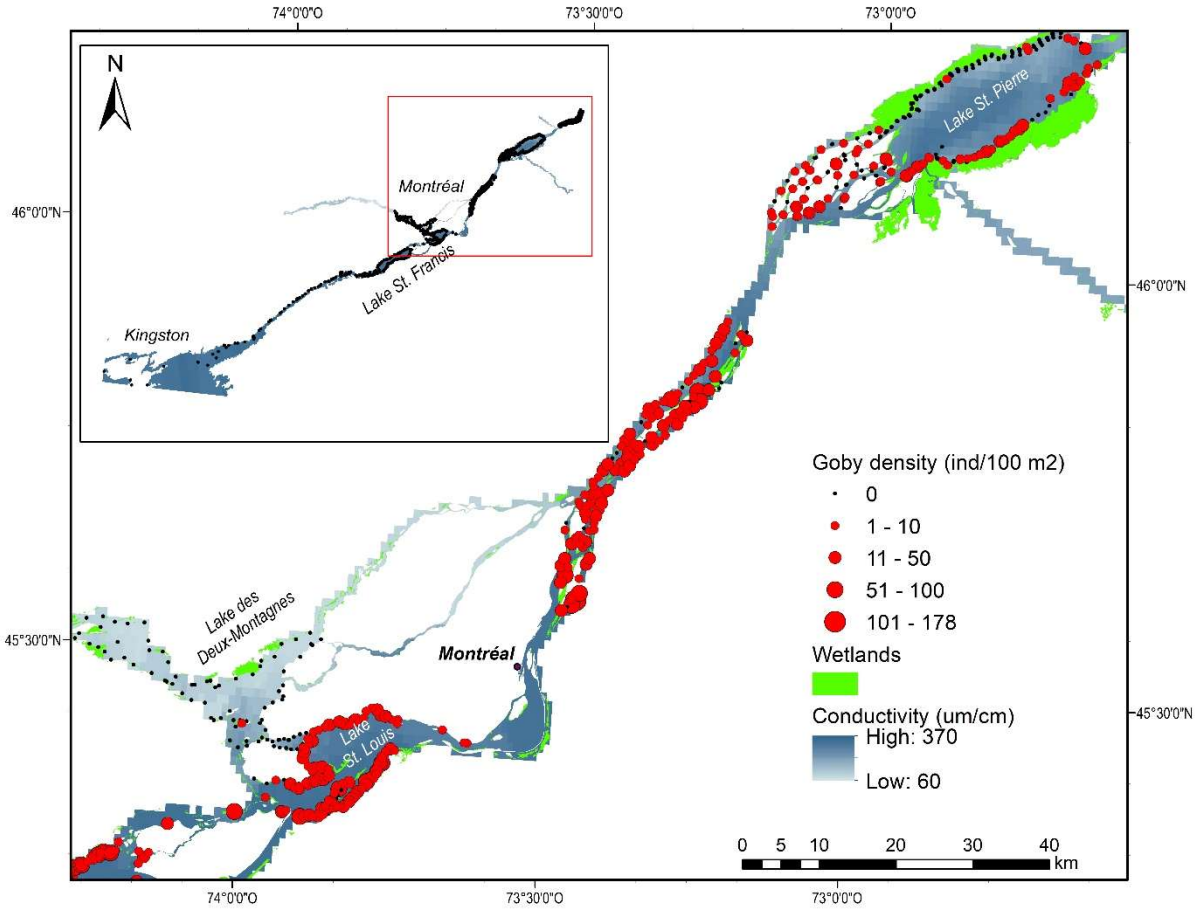
Figure 1. Round goby density (proportional red circles) in relationship to water conductivity gradient (blue color shade) and wetlands presence (green polygons) presented on a subset of the study for visualisation. The complete study area is presented in the smaller context map with fish sampling sites locations (black dots).

Figure 2. Generalized additive model (GAM) parametric effect of habitat type (non-wetland and wetland) on round goby density (individual/m^2). Non-wetland habitat represents the intercept in the GAM, rug plot shows observations of the predictor variable, and the dash lines indicate the 95% confidence intervals.

Figure 3. Generalized additive model (GAM) partial smooth effect of conductivity (µS/cm) on round goby density (individual/m^2) by habitat type: non-wetlands (A) and wetlands (B). Shaded area indicates the 95% confidence interval, rug plot shows observations of the predictor variable and dash lines represent the null effect.

Figure 4. Generalized additive model (GAM) of partial spatial smooth effect on round goby density (individual/m^2) along the geographic gradient of the St. Lawrence River study area. The range of colours represents the effect: yellow shows the most positive effect (higher density) and dark blue the most negative effect (lower density). Partial residuals are represented by dots.

637 **Figure 1.**



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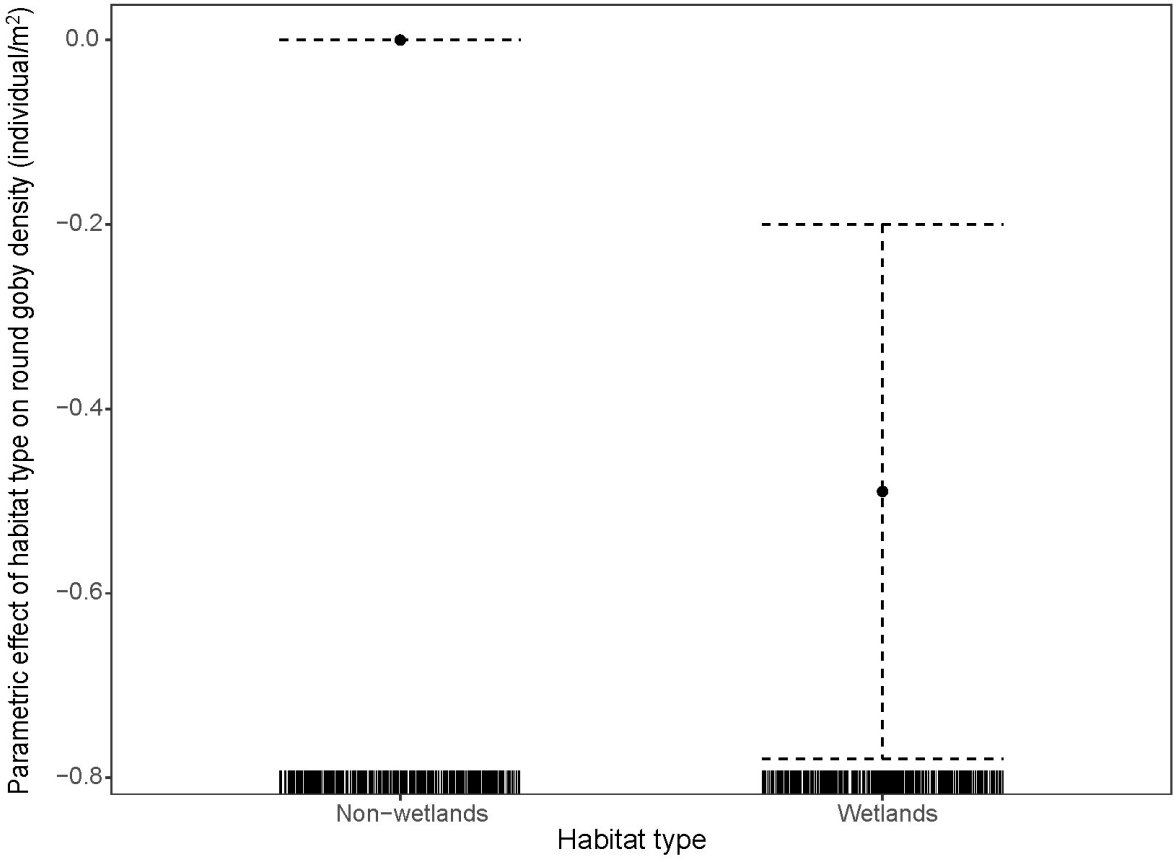
639 **Figure 2.**



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642 **Figure 3.**

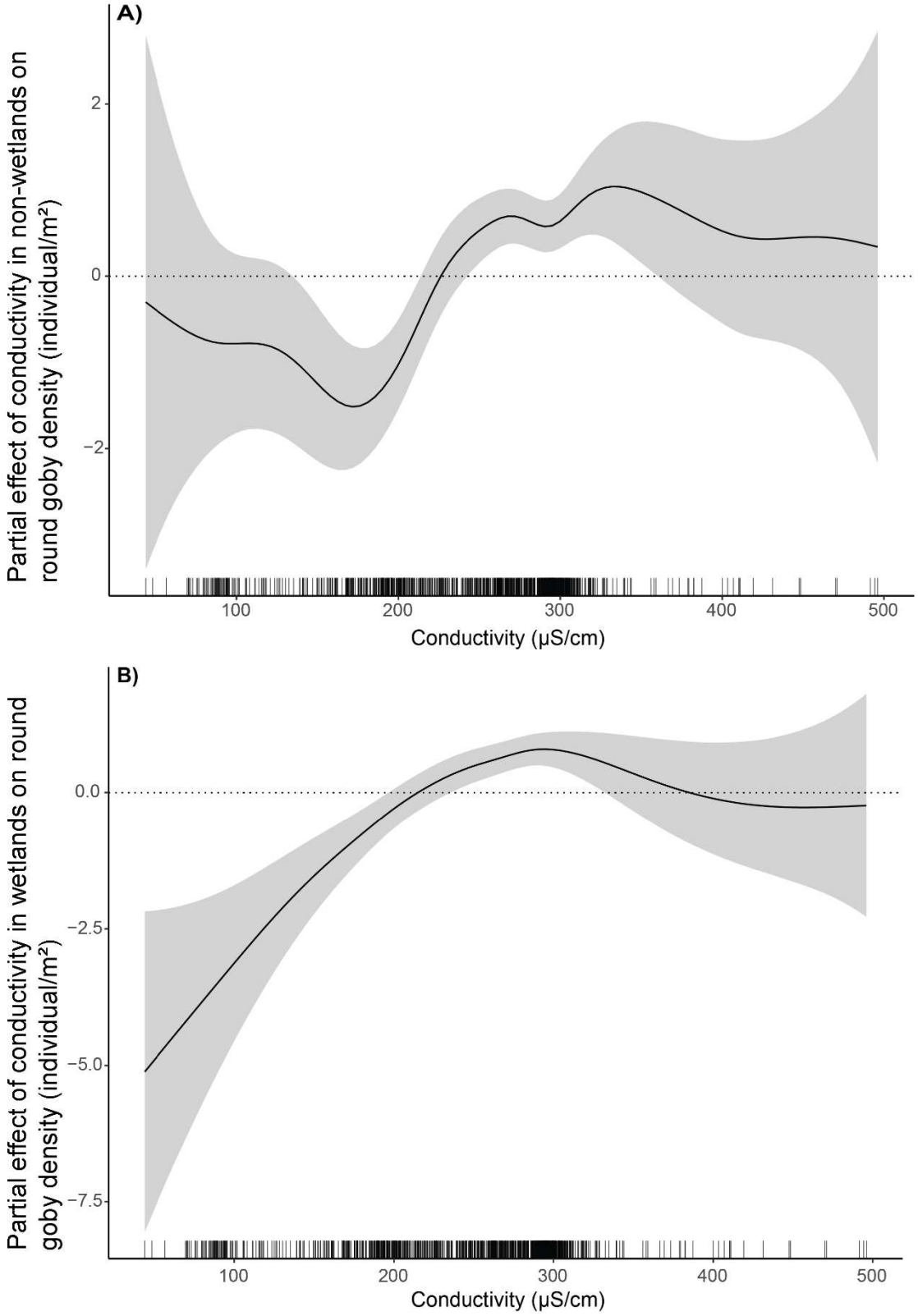

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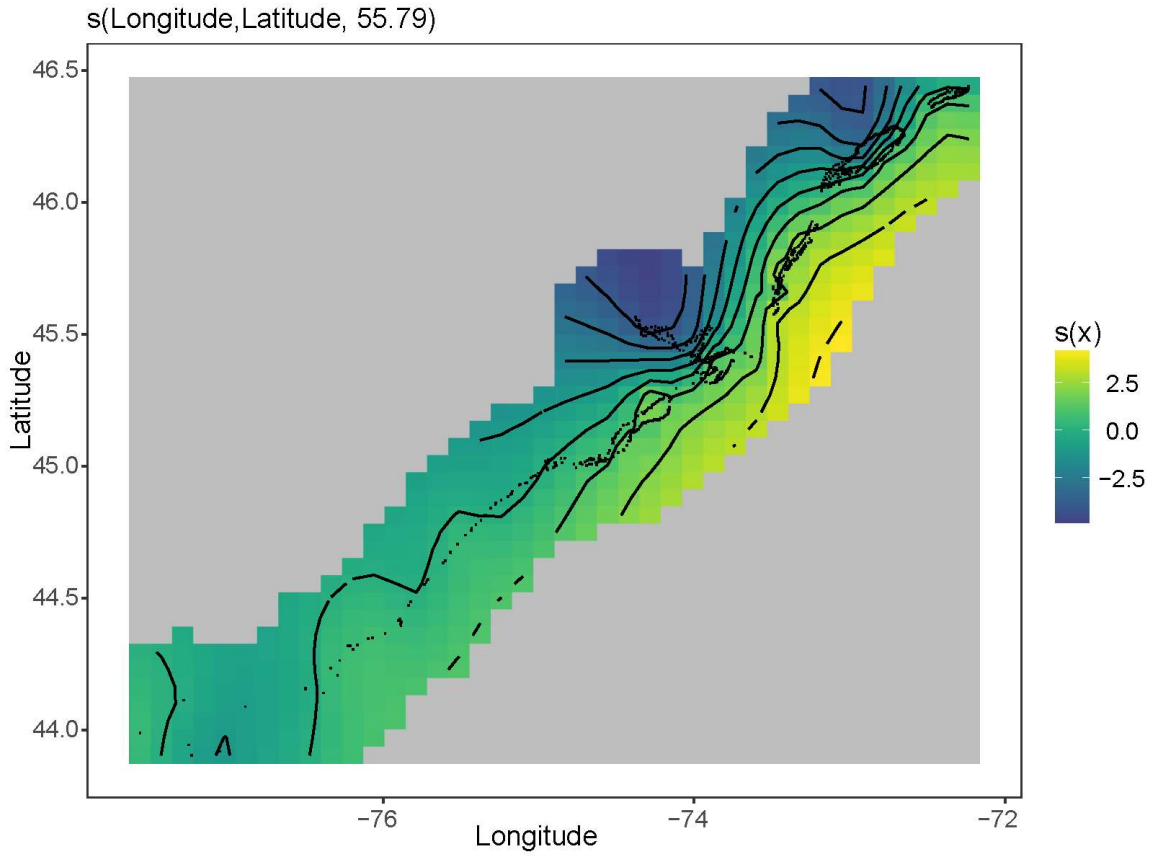
Figure 4.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