Movers and shakers: exploring the complex dynamics of aquatic biological invasions

By

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ABSTRACT

Human-mediated introductions of non-native species have provoked innumerable biological invasions, which can have a suite of adverse effects on the communities into which they are introduced. Despite extensive research, there remains a need in invasion ecology for simple methods of predicting how an introduced species will spread and become established. While I predicted that spread can be modelled simply using the characteristics of the invading population, establishment should be explained by the characteristics of the receiving ecosystem. Using the brown trout (*Salmo trutta*) invasion on the Island of Newfoundland as a case study, I fit a reaction-diffusion model to brown trout population data to predict expected spread and test these predictions against extensive occurrence data. I use statistical models to test the influence of a suite of environmental variables on the establishment of brown trout within the invasion range. I find that observed spread in Newfoundland is slow compared to invasions elsewhere and that two landscape environmental variables show evidence of explaining establishment patterns, but their influence is likely moderated by other factors. My study contextualises the mechanisms contributing to slow aquatic invasions, revealing that studies need to integrate a variety of methods to elucidate the processes governing biological invasions.

DEDICATION

This dedication has four parts: first, to my parents for their unwavering love and support for all of my ideas and far-away adventures, b) to my partner Branden (and our cat Cheesecake) who kept me grounded in reality and without whom Newfoundland would have been even more of an island, iii) to Covid-19, for making grad school harder than it should have been and teaching me that I could do what I thought I couldn’t, and finally to myself, this one’s for you.

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the other ranked models, LL is the log-likelihood ratio, and Nagelkerke's R^2 is an adjusted measure of the variation in the data explained by the model parameters. All models in the north dataset ranked below the intercept, meaning they are *pretending variables* and do not explain any of the variation (Leroux 2019), as did all of the abiotic and biotic models in the South dataset. However, two single parameter landscape models explain variation in the South, as well as the top ranked model which is a combination of the same two parameters.

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calculated the Odds Ratio (OR, exponent of the model coefficient). Represented by the black points, the Odds Ratio is the odds of brown trout being present at a river under each environmental regime. The line at OR = 1 represents the threshold for the direction of the relationship of brown trout presence with each variable, with OR < 1 corresponding to a negative relationship, and OR > 1 a positive relationship with trout presence.

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Figure 2.6.1 Methodological overview of chapter 2. Using contemporary occurrence data (Porter et al. 1974) and historic distribution data (Maitland 1887, Hustins 2007, Westley and Fleming 2011) from past research in Newfoundland, we were able to estimate the actual rate of spread of brown trout in Newfoundland. We used this to test the ability of a Reaction-Diffusion model, parameterized using independent values from the literature, to predict the spread. We then analysed the environmental variables that explain establishment dynamics using local abiotic, biotic (Porter et al. 1974) and landscape-level environmental data (Westley and Fleming 2011).

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CHAPTER 1: Introduction and Thesis Overview

1.1 Species range shifts during periods of large-scale change

With the most recent glacial retreat, Atlantic salmon (*Salmo salar*) colonized North American rivers from their glacial refuges in the North Atlantic and became a naturalized part of the landscape (Jonsson and Jonsson 2011). This large-scale establishment was dictated by salmon's long-distance dispersal ability, and their colonization of the landscape was possible because of the recession of the Wisconsinan Ice Sheet, revealing a plethora of pristine freshwater environments which salmon depend upon (Daniels and Peteet 1998). Atlantic salmon's recolonization of North American rivers is an example of an extensive range shift, in which the limits of a species' geographic range contracts or expands. The spatial limits of a species typically shift as a response to changing abiotic and biotic conditions (Gaston 2009), and are influenced by the evolution of traits that facilitate or limit expansion (Tomiolo and Ward 2018). There exist a variety of methods to define species ranges, which vary in time, dimension, spatial extent, and in the ecological processes that may underlie them (Yalcin and Leroux 2017). Range shifts are a natural ecological response, yet their frequency and magnitude are growing due to climate change (Gaston and Gaston 2003), generally causing species shifts to occur poleward, towards higher altitudes or greater depths (Chen et al. 2011). Besides shifting, species may respond by adapting to their changing local conditions to track warming (Berg et al. 2010), or else either go locally extinct and contract their range (Franco et al. 2006). The mechanisms influencing range shifts often parallel those that describe biological invasions (Sorte et al. 2010, Morriën et al. 2010), though the role of humans in the introductions of non-native species can hardly be considered 'natural' as they involve the transplantation of individuals to a novel area unreachable by the species' own dispersal mechanism (Chapman and Carlton 1991).

1.2 The elements of a successful invasion

Elton (1958) is recognized as the founder of invasion ecology, having observed that the different continents support very distinct animal and plant communities, that globalization and connectivity through human activity are slowly blurring these groupings, and that this phenomenon is detrimental to biodiversity. Biological invasions are an ecological consequence of human development, and have occurred on all continents save for Antarctica, in the same general pattern (Jeschke 2014). Individuals (ex. embryos, juveniles or breeding adults) are introduced to an area outside their natural range limits. If the environmental conditions satisfy their ecological requirements, they may establish a successfully reproducing population and individuals may spread outward to increase the size of the geographic invasion range (Williamson 2006). Invasive species ranges are often heavily fragmented and subject to many environmental, demographic, and anthropogenic challenges. Many within the field define a non-native species as ‘invasive’ only once they have been introduced, established, commenced geographic spread *and* had a negative impact on the receiving ecosystem (Alpert et al. 2000, Davis and Thompson 2001). However, studies have recently demonstrated that a species does not have to have been established or spread to have an ecological impact (Richardson et al. 2000, Blackburn et al. 2011), and that species that are capable of more rapid establishment and spread are not more likely to have negative impacts (Ricciardi and Cohen 2007). Thus, for the sake of clarity I use the term “non-native” or ‘introduced’ to describe a species that has be taken from its native range and transplanted into a novel ecosystem, and I use ‘invasive’ to describe a non-native species that has rapidly established and commenced spread after being introduced, irrespective of the impact it may cause (Richardson et al. 2000, Jeschke and Strayer 2005, Simberloff 2011).

While studies most often focus on successful invasions, it is important to note that only a minority of introductions (likely 10 percent) actually become established and only 10 percent of them may spread (Williamson and Fitter 1996, Williamson 2006). A successful biological introduction is often driven by a high propagule pressure, which is a measure of the introduction effort or the total number of individuals released (Kolar and Lodge 2000, Lockwood et al. 2005). A higher number of propagules may increase genetic diversity and ensure a higher likelihood of overcoming environmental and demographic stochasticity (Lockwood et al. 2005, Catford et al. 2009). This has been exploited by humans, who use repeated large-scale introductions to ensure the successful establishment of desirable species (Ewel et al. 1999). Introduced species are often edible (e.g., the feral pig, *Sus scrof,* in Hawaii), aesthetic (e.g. *Acacia spp*. trees and shrubs worldwide), may be used for erosion control (e.g. kudzu, *Pueraria lobata*, in the United States), provide a resource for sport (e.g. brown trout, *Salmo trutta*, in New Zealand), or else are accidentally introduced through global trade and importation (e.g. zebra mussels, *Dreissena polymorpha*, to the Great Lakes).

The characteristics of the ecosystem into which a non-native species is introduced influences the success of an invasion (Alpert et al. 2000, Hui et al. 2016). There are several possible mechanisms that make an ecosystem invasible, though determining their influence is complicated by the fact that the theories are not mutually exclusive. The Biotic Resistance Hypothesis posits that the success or failure of an introduced species is based on the native environment’s ability to limit their establishment (Elton 1958, Simberloff 1986). For example, areas with low species, functional or trophic diversity, such as islands or disturbed habitats are the most easily invaded (Elton 1958, Simberloff 1995). Limiting Similarity is a related hypothesis that dictates that invasion is more likely when there is low overlap between the non-native and native species’ ecological requirements, signalling the presence of an available niche (MacArthur and Levins 1967). These mechanisms are complimented by the Theory of Island Biogeography, which suggests that the arrival of a colonizing species to an island at equilibrium will be less likely to result in establishment than one not at equilibrium (MacArthur and Wilson 1967). Simberloff and Wilson (1969) used an experiment to demonstrate that right after species removal from small islands, colonization rate was high due to the presence of available habitat, and then extinction rate of established species increased as the island approached species saturation. Furthermore, the theory of Invasional Meltdown asserts that the presence of non-native species in an area will facilitate the introduction and invasion of other non-native species, by increasing the probability of establishment and ecological impact (Simberloff and Von Holle 1999). Such facilitation most often arises from shared evolutionary history and the occurrence of positive interactions in the species’ native range. For example, the intermountain region of the American West was dominated by tussock grasslands prior to European settlement, and the grasslands had not been exposed to large, hooved, grazers such as buffalo (*Bison bison*) (Mack 1986). With European expansion in the west came the introduction of livestock and the accidental importation of non-native plant seeds. The intense trampling and grazing of the former created bare areas that were easily established by the latter. The diversity of possible environmental mechanisms that can determine the success of a biological introduction signifies the need for empirical and experimental studies of biological invasion.

The invasibility of an ecosystem is also relative to the invasiveness of the non-native species, i.e. the characteristics that make it a strong invader (Leung and Mandrak 2007), which vary according to the environment into which they are introduced (Alpert et al. 2000). However, species are often most successful when introduced into habitats that closely resemble their native range (Moyle and Marchetti 2006). More generally, introduced species that have a broad native range and strong dispersal mechanisms are most likely to succeed (Wilson et al. 2009). Such species often have high fecundity, short generation times and are strong competitors (Crawley et al. 1986). As mentioned above, the taxonomic or functional distinctiveness of the non-native species from native species may play a role in its successful introduction (Bennett 2019), as there may be stronger competition between two species that are more phylogenetically related than two that are distinct (Burns and Strauss 2011). Furthermore, distinctiveness of the invader from native species is a predictor of the magnitude of impact of the invasion (Ricciardi and Atkinson 2004).

1.3 Ecological impacts of biological invasions

Until recently, it was assumed that the majority of non-native species introductions did not have a significant impact on the receiving ecosystem (Williamson 1996). However, impacts may be difficult to detect, be indirect, or else there may be a 'lag' in time before the ecological impact can be fully quantified (Simberloff 2011). Alternatively, a minority of non-native species can have a positive ecological impact. Invasive species can benefit humans, especially rural populations, by providing them with a novel food source, firewood, or pest management (Shackleton et al. 2007, Desbiez et al. 2011). Non-native species can also provide pollination services, increase habitat complexity or become a trophic subsidy for the native ecosystem (Rodriguez 2006). It is unclear how rare positive impacts of biological invasions are, as there exists a certain level of bias against invasive species within invasion ecology (Guerin et al. 2018). However, there is undeniable evidence that non-native species can have a series of negative ecological impacts on recipient communities (Cucherousset and Olden 2011; Ricciardi *et al.* 2017) and that these negative impacts are often irreversible (Paolucci et al. 2013).

Biological invasions are a major driver of biodiversity loss, and their impacts may only be intensified by future climate change and anthropogenic perturbation (Young and Larson 2011). Introduced species can cause a change in the behaviour of local species by imposing a novel selection pressure (Townsend 1996), and can affect the latter's genetic and phenotypic composition through hybridization (Cucherousset and Olden 2011). Invasion may result in the creation of new trophic links that affect native abundance, demography and may cause trophic cascade (David et al. 2017). For example, the introduction of the poisonous cane toad (*Rhinella marina*) in Australia indirectly increased the abundance of several small lizard species by inducing mortality in their common predator (Feit et al. 2020). Indeed, introduced animals may directly affect natives through predation and indirectly through competition for resources, resulting in extinction or displacement of native species. As well, invasive plants can alter nutrient cycling, fire regime and local hydrology, which can have drastic effects on both native plants and animals (David et al. 2017). With the introduction of exotic species comes the transportation of parasites and associated diseases. For example, the grey squirrel (*Sciurus carolinensis*), largely replaced the native red squirrel *S. vulgaris* upon its introduction to the United Kingdom through its infection of the latter with *Parapoxvirus* (Tompkins et al. 2003). Additionally, invasive keystone species can have a disproportional impact on the native ecosystem relative to their abundance (Anderson et al. 2006). The introduction of the North American beaver (*Castor canadensis*) to Chile has caused ecosystem-level changes, such as a change in forest composition, increase in flooding and alteration of carbon storage due to beaver impacts on riparian forests (Papier et al. 2019). Thus, a successful invader can have a suite of possible effects on the native ecosystem, however, due to the complexity of biological interactions that exist within a community, identifying an impact becomes as challenging as mitigating it.

1.4 Aquatic biological invasions and the brown trout

Aquatic habitats are changing at an unprecedented rate due to changes in climate and anthropogenic activities (Kolar and Lodge 2000). Biological invasions in fresh water are a major cause of biodiversity loss and the global homogenization of fauna (Moyle and Garcia-Berthou 2011). As non-native species, fish are among the most commonly introduced animals (Gozlan 2008) and as natives, they represent one of most vulnerable groups to the negative impacts of invasion (IUCN 2020), such as hybridization, disease transmission, predation, competition, habitat degradation, and local extinction of native species (Gozlan et al. 2010, Cucherousset and Olden 2011). Salmonids are some of the most successful invasive fishes (Buoro et al. 2016) due to their existence along a migration continuum (Boel et al. 2014): while some individuals inhabit only fresh water, called residency, others are anadromous, spawning in fresh water yet migrating to marine ecosystems. This variety of life-history strategies is exhibited by individuals within the same species, and within the same populations (Jonsson and Jonsson 2011). This allows salmonids to feed and grow in freshwater and marine environments and facilitates the colonization of new watersheds using marine pathways (Labonne et al. 2013).

Brown trout (*Salmo trutta*) is one of the most globally pervasive aquatic invaders and is listed on the IUCN top 100 global invader's list (Lowe et al. 2000). Brown trout has an extensive natural range, encompassing most of Europe and parts of North Africa, the Middle East to the Ural Mountains (Jonsson and Jonsson 2011). Due to the popularity of this species for sport fishing, humans have introduced brown trout to most of the areas where it can successfully persist, typically temperate (or mountainous) areas with fresh water cool enough for incubation

(Buoro et al. 2016). As a relatively long lived species with high fecundity, brown trout has the potential for high population growth, allowing it to quickly establish populations in areas it has been introduced (McDowall 2010). Brown trout's large body size (Jonsson and Jonsson 2011) combined with its generalist feeding strategy (Frost 1940) make it a strong competitor. The polytypic nature of brown trout contributes to its adaptability to a variety of conditions, and has allowed it to successfully invade diverse geographical areas (Elliot 1994). Successful introductions of salmonids tend to import individuals from resident populations (Thorpe 1987, Nolan 1993) though once established many individuals revert to anadromy, which is hypothesized to arise from high population densities or low food availability (Olsson et al. 2006). Anadromous individuals then migrate to the ocean, where failed homing or straying likely drives their establishment of new rivers. In some systems, freshwater connectivity allows spread within watersheds (Hein et al. 2011, Sharma et al. 2021), but due to the smaller size of island watersheds, marine dispersal drives spread in Newfoundland. However, freshwater dispersal is unlikely to drive natural spread between watersheds (though it occurs when there is transplantation by humans) as individuals cannot overcome watershed barriers (i.e. mountains) unless they use the ocean as a corridor (Launey et al. 2010). Brown trout invasion has disrupted food webs and caused behavioural shifts of aquatic invertebrates in New Zealand rivers (Townsend 1996), has largely displaced native galaxiids in the southern hemisphere (Fletcher 1979, McDowall 2006), rainbow trout in the Appalachians (Gatz et al. 1987), and bull trout in Montana (Al-Chokhachy et al. 2016) and introduced the parasite *Myxobolus cerebralis* to native trout populations in the United States (de la Hoz Franco and Budy 2004). Despite the extensive research on biological invasions and invasive brown trout studies conducted in the past few decades, predictions of the spread of invaders and their ecological impacts remain uncertain and imprecise, especially for species with complex life-histories.

Brown trout have been introduced to 9 of the 10 Canadian provinces (MacCrimmon and Marshall 1968). From the mid 1880s to 1906, over 400,000 brown trout embryos were imported to the Island of Newfoundland from Scottish (Loch Leven), English and German resident populations and introduced to 15 watersheds on the Avalon Peninsula and one on the Bonavista Peninsula (Hustins 2007). They have successfully established populations in many of the watersheds on the Avalon and are considered a prized angling fish. A recent study in Newfoundland revealed that natural colonization of brown trout follows a stepping stone pattern from St. John’s westward (O’Toole et al. *in press*). O’Toole et al. (*in press*) found lower levels of genetic diversity in populations furthest from St. John’s (where there was most intense stocking) and that natural colonization was likely the result of individuals reverting to anadromy and straying to new rivers. As well, these authors found two distinct pathways of natural colonization, corresponding to the north and south coasts of the Avalon Peninsula. These two independent invasion pathways are likely highly influenced by the differential stocking history (higher propagule pressure in the north and different genetic origin) and stark differences in oceanographic conditions between the two coasts. The divergence of these invasion pathways and the differential coastal environmental conditions encountered by the invaders could significantly impact the continued establishment and spread dynamics of this invasion. Thus, though brown trout in Newfoundland have been studied, further exploration of spread and establishment dynamics using different types of models may elucidate the mechanisms that are determining the success and speed of this invasion along the two invasion pathways, which is a first step towards understanding their ecological impacts.

1.5 Modelling biological invasions

Mathematical models are abstractions of natural systems and are used extensively in ecology to understand complex biological phenomena and in invasion ecology, to make predictions about current and future biological introductions (Marco et al. 2002, Edelstein-Keshet 2005). Models provide a framework for interpreting theoretical and empirical results, and for generating predictions (Otto and Rosales 2020). Model results are interpreted within a scientific narrative, the former functioning to challenge or support the latter. Strong biological models are simple (i.e., as few parameters as possible), and clearly define what biological phenomena is represented by each parameter (Mollison et al. 1986). The strength of the interpretation of results relies on an understanding of the underlying assumptions of the model as well as the ability of the model to represent a complex biological system in a simple way. There exists a general trade-off in mathematical modelling between creating a parsimonious model that can still allow one to draw relevant conclusions.

A foundational model in ecology was Fisher's equation (1937), which was ground breaking in that it gave empirical support to Mendelian genetics and modelled the spread of advantageous alleles (Otto and Rosales 2020). This equation formed the basis of the classic reaction-diffusion equation by Kolmogorov, Petrovsky and Piskunov (1937), which represents the temporal and spatial change in concentration of chemical substances, but can be adapted to geology, physics, and biology. Work by Skellam (1951) and Kierstead and Slobodkin (1953) directly applied the reaction-diffusion model to ecology, where local population density is a function of the population growth (reaction) and the random dispersal of individuals through space (diffusion) (Cosner 2008). This model uses simple parameters that clearly represent quantifiable ecological processes. If it is assumed that there is a threshold density needed for a population to be detectable in an area, then the model predicts that this threshold will move as a front (Andow et al. 1990). This equation can thus be used to make predictions of the rate of spread of the invasion front of a species, which is assumed to be asymptotic (Fisher 1937, Kolmogorov et al. 1937). The study of spread is central to invasion ecology because it is a metric for assessing and comparing the speed of an invasion and can be used to identify areas that are at risk of being invaded in the future (Goldstein et al. 2019). Though recent work in invasion ecology has successfully created more complex models (Neubert and Caswell 2000, Hadeler and Lewis 2002, White et al. 2017, Trewin et al. 2021), the classic reaction-diffusion model remains a simple and relevant tool to make predictions of spread.

Mathematical models, when used correctly, excel at testing how various processes interact and can provide a framework for making quantitative predictions about biological phenomena (Otto and Day 2011). However, they are limited by the biological questions being asked and the assumptions needed to make an abstraction of the system. Statistical models, which are fit to a set of data, allow us to make inferences about a wider population based on probability theory. So, while mathematical models can represent the rate of spread of an invasion based on a few simple parameters (Ōkubo and Levin 2001), they are less adept at analysing the effect of several predictors on a binary response variable. In ecology, occurrence patterns of species are most often analysed using the logistic regression model (Warton and Hui 2011), which is a type of generalized linear model that uses a binomial probability density function. The strength of such a statistical model is that it directly models probability of the response variable based on the variance explained by each of the predictor variables (Salas-Eljatib et al. 2018). Though the use of any mathematical model in ecology requires abstractions and assumptions to be made, studies that combine empirical and statistical models, data and methods of inference progress towards a more robust ecological theory.

1.6 Thesis overview

The aim of this thesis is to untangle the mechanisms that influence the stages of biological invasion by using brown trout in Newfoundland as a case study. We integrate a variety of analytical methods to explore simple ways of predicting spread and explaining establishment of non-native species. Chapter 1 gives an overview of invasion ecology literature, the important mechanisms that influence spread and establishment, as well as the methods we used to analyse them.

In Chapter 2, we first test whether a reaction-diffusion model parameterized with demographic and dispersal population-level data can make a spread prediction comparable to the observed spread. Then, we run a series of statistical models to examine what influences the ability of trout to establish by analysing environmental predictor variables at the local and landscape scale. Our results demonstrate that spread of brown trout is slow on the Island of Newfoundland and that the observed spread is on the lower end of the values predicted by the reaction-diffusion model. As well, there is weak evidence that two landscape level environmental variables influence the establishment patterns of brown trout, and that their importance may be influenced by the coastal direction of the invasion and the introduction history. Slow spread in Newfoundland is likely the result of limitations imposed by the environment that affect the growth and dispersal of brown trout. The reaction-diffusion’s wide range of predictions may stem from the estimation of parameters from different brown trout populations or because the data did not fit the assumptions of the model.

In Chapter 3, I provide an overview of the study and the major results of our analyses. I reflect on the limitations of our study and the wider implications for the field of invasion ecology and our ability to mitigate future invasions. Our study reveals the importance of considering the local environment's influence on spread rate and suggests that the environmental factors that explain trout establishment are complex and may be highly variable between biological invasions.

1.7 Co-Authorship Statement

I wrote Chapter 1 and 3, thus I use 'I' to refer to the author. Chapter 2 of this thesis is co-authored with Shawn J. Leroux and Craig Purchase, thus I use 'we' to refer to the authors. S. J. Leroux and C. Purchase were awarded the funding, developed the project idea, and provided guidance on research design, sampling methodologies, and assisted with analyses, results and interpretation and writing. I developed the project methodologies, conducted the sampling, analysed the data, parameterized the model, interpreted the results and wrote the final documents. Chapter 2 will be submitted to the *Biological Invasions* and will be formatted for that journal.

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CHAPTER 2. Exploring predictions of spread and establishment dynamics of brown trout on the Island of Newfoundland

2.1 Introduction

Biological invasions

Understanding the mechanisms governing the distribution of species in space and time is essential to ecology (Darwin 1859, Hutchinson 1959, Paine 1966, Simberloff and Wilson 1969) and has never been more important than during periods of large-scale change, characteristic of the Anthropocene (Zalasiewicz et al. 2010). Notably, the introductions and subsequent invasions of non-native species are becoming increasingly frequent due to human activities (Maxwell et al. 2017, Kueffer 2017), and though widely studied, our understanding of their dynamics is rudimentary (Kumschick et al. 2015).

Successful biological invasions all share three main components: introduction of the non-native species to a new ecosystem, the establishment of breeding populations, and their geographic spread to new areas beyond the introduction point (Jeschke and Strayer 2005). Humans modify the success of all three of these invasion components. Specifically, introduction has historically been limited to species capable of long-distance dispersal, however human-mediated introductions have increased exponentially over the last century following a rise in global connectivity, international trade and climatic change (Hulme 2009, IUCN 2017, Kueffer 2017). Likewise, propagule pressure or the total number of introduced individuals, drives introductions and directly influences the probability a population can establish (Lockwood et al. 2005). Establishment of populations is facilitated by landscape modifications and disturbance (D’Antonio 1993, Fausch 2008) and is a function of local environmental conditions (Richardson et al. 2000). Finally, spread is driven by the propagule pressure from established populations and the ability of the invader to disperse to new areas. Again, this is facilitated by human-assisted dispersal (Burney 2005) and is strongly influenced by landscape structure (With 2002). Thus, a successful introduction, establishment and spread is not only a function of the invasiveness of the species but also of the receiving ecosystem's ability to exclude it, called the 'invasibility' (Marco et al. 2002, Hui et al. 2016). Though a biological invasion can be broken into these three components, it is often difficult to disentangle the mechanisms that may be influencing one or more of them (Catford et al. 2009). Understanding the relationship between ecosystem and invader characteristics is essential to the mitigation of current biological invasions and the prevention of future introduction events (Fletcher et al. 2016, Lenzner et al. 2020). Here, we integrate modelling and empirical data to study the rate of spread and the mechanisms of establishment of a pervasive invader that has been introduced all over the world, leading to a significant number of successful invasions with considerable impacts.

Making predictions of spread

Studying mechanisms of the spread component of biological invasions poses a particular challenge as the frameworks used by studies remain inconsistent and the resulting predictions can be conflicting (Suarez et al. 2001, Hulme 2015). We follow Johnson and colleagues (2006) by defining spread as an increase in geographic extent according to a species-specific dispersal mechanism, dependent on the characteristics of the environment that make it suitable. Thus, spread is a function of the characteristics of the non-native species as well as their response to the local environment. However, in reality the influence of the former on the spread is more widely supported. Namely, dispersal ability of the non-native species consistently drives the spread of biological invasions (Ramula et al. 2008, Adams et al. 2015), along with their demographic rates such as fecundity and longevity (Bazzaz 1986, Marco et al. 2002). While environments are rarely homogenous, the inclusion of environmental heterogeneity is not always required to make accurate predictions when modelling long-distance dispersal (Marco et al. 2011). Indeed, while the majority of individuals in a population may exhibit shorter distance dispersal, it is widely accepted that the minority who travel longer distances can account for the majority of the spread rate (Degerman et al. 2012). Thus, a central tenet in invasion ecology is the search for simple mathematical models that can make precise predictions about spread of non-native species (Andow et al. 1990, Lewis et al. 2016), such as those where the environment remains largely implicit.

Common approaches to modelling the rate of spread of an invasion include the use of partial differential equations (Fisher 1937, Kolmogorov et al. 1937) or integrodifferential equations (Kot et al. 1996, Neubert and Caswell 2000), and may incorporate dispersal kernels (Hengeveld 1989), metapopulation models (Hanski et al. 1995) or spatially explicit simulations (Renton et al. 2011). Reaction-diffusion models use a few simple parameters to predict the rate of spread of an invasion, propagating as an invasion front, while assuming a homogenous environment in continuous time (Shigesada and Kawasaki 1997, Ōkubo and Levin 2001). The reaction-diffusion model is a simple spatially explicit model that is easily adaptable to many different systems, as it predicts spread using demographic and dispersal parameters specific to the non-native population (Andow et al. 1990, Kot et al. 1996, Ōkubo and Levin 2001). This type of model is more commonly applied to terrestrial systems (such as White et al. 2012; Andow et al. 1990 but see Suksamran and Lenbury 2019, Upadhyay et al. 2019), as terrestrial species generally face fewer barriers (i.e. mountains and rivers) than do freshwater species (i.e. any non-aquatic habitat). However, we surmise that the framework also has the potential to make relevant predictions about rate of spread of an invader in an aquatic environment.

Explaining patterns of establishment

The characteristics of the environment into which the non-native species is introduced are not unimportant. Once spread occurs during a successful invasion, populations may become naturally established in new areas and the process of spread and establishment is repeated. Establishment (or naturalization) is thus the ability of the species to overcome environmental barriers to colonize, grow and successfully reproduce in a new area (Richardson et al. 2000), making it (like spread) a function of both the intrinsic characteristics of the non-native species and those of the native ecosystem (Alpert et al. 2000, Hui et al. 2016). Where spread is the ability of the species to reach a new area, establishment is the successful founding of a self-sustaining population. However, while we predict that spread can be modelled simply using the characteristics of the invading population (i.e., intrinsic growth and dispersal), establishment dynamics should be explained by the characteristics of the receiving ecosystem (Alpert et al. 2000) as the invader's realised niche reflects the suitability of local environmental conditions (Korsu et al. 2007, Hui et al. 2016). Thus, the non-native species may establish populations in areas that have a suite of environmental conditions that allow it to grow and reproduce.

Environmental factors can influence the ability of invaders to establish populations (Havel et al. 2002), these factors are often scale-dependent (Levine 2000). For example, variables such as temperature, precipitation and soil or water chemistry vary along spatial gradients, and the abiotic tolerance of a species determines in which areas along this gradient they are able to persist (Havel et al. 2002, Mott 2010). As well, biotic factors such as the presence of native competitors dictates the availability of resources, the niche space and the potential for biotic interactions between native and non-native species (Korsu et al. 2007). Such abiotic and biotic variables at the local scale will likely determine a non-native species' ability to establish and persist in a particular vacant patch (Harig and Fausch 2002). More broadly, landscape scale variables such as ecosystem productivity, environmental heterogeneity, connectivity, and topography can influence the genetic structure of invasive populations (Launey et al. 2010) and their ability to disperse, contributing to broader scale patterns of establishment (Muthukrishnan et al. 2018). The distance to the nearest established patch, sometimes used as a proxy for the intensity of propagule pressure (Havel et al. 2002), may influence the probability of establishment (Rouget and Richardson 2003). This array of local and landscape scale environmental variables that can influence the establishment of aquatic invasive populations illustrates the need to not only ask where an invader is spreading but also why they are able to establish there.

Exploring spread and establishment dynamics using a case study

We studied brown trout, *Salmo trutta,* as this species has been introduced globally in a variety of climates, where its life history variability affords high potential for large-scale geographic spread but makes predicting the invasion and the accompanying ecological impacts complex (see review in Buoro et al. 2016). We integrate several datasets, mathematical modelling and statistical analyses to 1) make predictions about the rate of spread of an aquatic invasion using a simple reaction-diffusion model parameterized by values from independent literature, 2) compare them to the actual rate of spread estimated using the introduction history and several measures of marine migration distance, 3) identify the environmental variables that best explain the patterns in establishment of populations within the invasion and 4) determine whether the influence of these variables differ along the two pathways of the invasion.

We hypothesize that parameterizing a simple model with data for demographic and diffusion parameters from the literature can make accurate predictions of the rate of spread of brown trout in Newfoundland, while assuming a homogenous environment (Figure 2.1 panel a.). We predict then that i) the predicted rate of spread obtained from the classic reaction-diffusion model will be comparable to the actual spread rate observed (Andow et al. 1990, Shigesada and Kawasaki 1997) using coastal distance (Labonne et al. 2013). Next, by first considering the ecological requirements of brown trout, we hypothesize that where natural establishment is possible, patterns in establishment can be explained using local abiotic, biotic and landscape-scale environmental variables (Figure 2.1 panels b and c). We thus predict that ii) of the local abiotic environmental variables, water conductivity (Enge and Kroglund 2011), turbidity (Birtwell et al. 2008) and calcium (Hartman et al. 2016) will be positively correlated whereas pH (Matena 2017) will be negatively related to the presence of brown trout, iii) a local biotic variable, the presence of native Atlantic salmon, will negatively correlate with brown trout establishment (Bietz et al. 1981, Korsu et al. 2007), and iv) landscape-level variables such as relief (Mostafavi et al. 2014), watershed size (Harig and Fausch 2002) and estuary area (Warner et al. 2015) will positively correlate with brown trout presence, whereas distance to original introduction point and distance to nearest introduction (Havel et al. 2002) will be negatively associated with trout presence. Finally, as the north and south coasts of Newfoundland have different introduction histories, and more dramatic marine environmental differences than implied by latitude, we hypothesize that the brown trout invasion has split into two pathways, with differential establishment dynamics (Figure 2.2). We then predict that v) different environmental variables will be responsible for explaining establishment patterns between the north and south coasts (O’Toole et al. *in press*).

2.2 Methods

Study System

The introduction history of salmonids on the Island of Newfoundland is well-documented (Westley and Fleming 2011), and as a case study, brown trout in Newfoundland present the opportunity to predict salmonid invasions that are relevant to invasive species research. Glacial gouging led to the creation of hundreds of lakes and streams on the Avalon, Bonavista and Burin peninsulas (Protected Areas Association of Newfoundland and Labrador 2008), making this area both an ideal landscape for freshwater studies, and a potentially hospitable place for an aquatic invader. Native to Eurasia, brown trout were introduced to the Island of Newfoundland from 1883 to 1906. A total of 16 watersheds on the Avalon Peninsula of eastern Newfoundland were stocked with trout from Scotland (of the Loch Leven strain), England or Germany (Frost 1940, Hustins 2007). Since then, brown trout have spread westward. By 2010, brown trout were located in at least 67 watersheds in eastern Newfoundland including those that drain into Trinity Bay and Placentia Bay (Westley and Fleming 2011), with populations reaching the eastern side of the Burin and Bonavista Peninsulas. However, it is unclear exactly what facilitates their spread. There is significant potential for future spread on the island due to the availability of higher productivity watersheds and estuaries in the western part of Newfoundland (Westley and Fleming 2011, Warner et al. 2015).

Predicting the rate of spread using a Reaction-Diffusion model

To test prediction (i) that the model’s predicted rate of spread will approximate the actual spread rate, we parameterized a reaction-diffusion model. Originally used by physicists to model the random movement of particles (Fisher 1937), the reaction-diffusion equation was applied to biology (Skellam 1951, Kierstead and Slobodkin 1953) to mathematically represent a spreading population:

$$\frac{\partial}{\partial t}u = ru + D\frac{\partial^2}{\partial x^2}u \qquad (1)$$

where the change in population density *u* can be estimated as a function of time *t*, space *x*, per capita reproduction rate *r* and diffusion rate *D* (see Andow et al. 1990).

Recently, these models have been used to predict the dispersal of populations (Maciel et al. 2020), the spread of species ranges in the face of climate change (Leroux et al. 2013) and have been increasingly used to estimate invasion (Lubina and Levin 1988, Shigesada and Kawasaki 1997, Bonneau et al. 2016). By assuming that there is a threshold density under which a species cannot be detected within an area, this model predicts that the threshold should move as a front (Ōkubo and Levin 2001). In this context, the above equation can be solved to predict the rate of spread of an introduced species, propagating as an invasion front over a long period of time as:

$$V = \sqrt{4\alpha D} \qquad (2)$$

where the velocity of spread *V* is estimated using only the population growth rate α and diffusion coefficient *D*, the latter being independent from the model (Ōkubo and Levin 2001). This model assumes a homogeneous population that is growing exponentially, with individuals moving independently and randomly in a uniform environment (Andow et al. 1990). Reaction-diffusion equations model spread as occurring radially outward from an introduction point. We examine spread (and later establishment) at the watershed scale because while there may be some freshwater dispersal within watersheds, spread across the 81 watersheds in our system requires movement through a marine coastal environment. To make the model prediction, we obtained independent data on growth rate and movement from the literature for brown trout. Then, to test the prediction (i), we compared it to the observed spread rate (see below). The population growth parameter α is a per capita measure of births, deaths and migration of a population. It can be approximated by the rate of natural increase (or intrinsic growth rate) *r*, which is a measure of the net rate of change in population size, encompassing births and deaths when the local population density is low (Andow et al. 1990). *r* can be measured several ways from a variety of density dependent and independent models (Brook and Bradshaw 2006), life history tables (Grant and Grant 1992, Charles et al. 2000) and abundance time series (Grossman et al. 2017). To obtain an independent estimate of *r*, we conducted a literature review for abundance-time series of brown trout populations (Table 2.6.1). Specifically, we searched for studies examining total abundance, density or population growth of anadromous brown trout or sea trout (both *Salmo trutta*) populations with at least 4 years of continuous population data. We did not find any studies of local Newfoundland trout populations that fit the criteria, though this would result in the most population-specific parameterization (Purchase et al. 2005). Following the methods used by Grossman and colleagues (2017), we used a density-independent equation to approximate the mean intrinsic growth of each population across years:

$$r = \log \frac{N_{t+1}}{N_t} \tag{3}$$

Where the natural rate of increase is the natural log of the total abundance *N* of year *t+1* divided by the that of the previous year *t*. Density *d* can also be used instead of total abundance (Grossman et al. 2017). We then used estimates of *r* from all studies to obtain a mean across studies.

The diffusion parameter, *D*, in eq 2 represents the ability of a population to disperse and is approximated by a mean squared displacement over time (Hastings et al. 2005). Values for diffusion can be difficult to estimate and are commonly calculated from swimming speeds (Grosholz et al. 1996) or mark-recapture studies (Andow et al. 1990). We conducted a literature search on the migration speeds of brown trout populations to obtain values for the diffusion parameter (Table 2.6.2). We searched for studies reporting mean displacement, total displacement over time, or migration speed (measured in body-lengths per second or ground speed) of anadromous brown trout, (known as 'sea trout' in European studies) while in estuaries or the marine environment. We estimated diffusion (in km^2/year) from converting study estimates of mean displacement (in km/day or km/hour) or estimates of swimming speed (in body lengths per second or m/s). Our search obtained a variety of studies on brown trout migration along the fresh water to marine ecotone. Within a population, there exists a wide variation not only in migration strategy (residency vs. anadromy) but also in the dispersal distance once anadromous individuals are in a marine environment (Jonsson and Jonsson 2011). Many individuals maintain close proximity to the mouth of their natal river (within 25km; (Rustadbakken et al. 2004, Veinott et al. 2012, Eldøy et al. 2015, Flaten et al. 2016) while others have been recorded dispersing over 500 kilometres (Degerman et al. 2012, Kristensen et al. 2019). Regardless, the majority (50-75%) of individuals within any population are shorter-distance dispersers with a small minority (<1%) participating in long-distance dispersal (Berg and Berg 1987, Degerman et al. 2012).

Armed with literature-based estimates of *r* and *D*, we estimated spread rate from eq. 2 (Table 2.1). We used a range of values of *r* and *D* to capture the natural range of variability observed in the literature (Figure 2.6.2). Specifically, we used three values of *r* in our model: 1) the mean and 2) median across studies, and 3) the mean of all the positive values. Also, we used four values for the diffusion parameter that reflect the large variation in dispersal distances of brown trout in the ocean, corresponding to the minimum, mean, median and maximum calculated from the distribution of values from our literature search. We then crossed them and used all the 12 possible combinations of these two parameters as inputs to the Reaction-Diffusion equation to obtain estimates of V, velocity of spread.

Measuring the actual rate of spread from the current distribution

To estimate the actual spread of brown trout in Newfoundland, we determined the historic (Maitland 1887, Hustins 2007) and current distribution of brown trout from multiple sources, including: data from a set of previous studies in Newfoundland (see Porter et al. 1974), and validated using more recent, but less comprehensive work (Westley and Fleming 2011) and Fisheries and Oceans Canada (DFO) angler's guide (DFO 2020). We calculated actual spread using distance between the introduction points and the current invasion front, using two methods to measure the distance with the measuring tool on Google Maps (*Google Maps* 2021). Radial distance was measured as the direct line between the mean of the midpoint of the introduction points on the Avalon to the two furthest points of brown trout confirmed presence on each coast, one each in Trinity (north coast) and Placentia (south coast) Bays (Figure 2.6.3). In addition, we calculated the distance following the coast between introduction and the same two furthest points. The coastal distance is likely the shortest and most ecologically relevant as juvenile brown trout generally follow the coast while migrating in the ocean (Labonne et al. 2013, Kristensen et al. 2019).

Validation of salmonid distribution data for establishment analyses

To analyse the environmental correlates of brown trout establishment, we first validated the brown trout, Atlantic salmon and brook charr (*Salvelinus fontinalis*) occurrence data from Porter et al. (1974) and Westley and Fleming (2011). During the summer of 2020, we sampled

21 rivers along the current invasion front, mostly draining into Placentia Bay and Trinity Bay. The choice of sites was informed by previous sampling (including Westley and Fleming 2011, and ongoing government projects), environmental data and using stream length and width to identify rivers large enough to potentially support anadromous salmonids. Stations were within 5 kilometers upstream of the ocean, which is the section brown trout are most likely to be found (Budy et al. 2008) and were within 1 kilometer of a road for accessibility. At each of the 21 rivers, we delineated 2-5 stations, each of which included runs, riffles, and pools to control for the differences in trout, charr and salmon habitat use (Figure 2.6.4).

To best estimate relative population densities of brown trout, as well as local Atlantic salmon and brook charr that co-occur with them, stations were barrier netted on both ends (Budy et al. 2008), we conducted two-pass depletion electrofishing in each station (Budy et al. 2008, Lake 2013) with a Smith-Root LR-24 backpack electro-fisher. Fish were either immobilized or swam directly towards the cathode, depending on the current and their distance from the electro-fisher. We collected the fish using nets and then counted, identified and anaesthetised them with clove oil. We measured the fork length and weight of the fish, and salmon and trout were fin clipped for genetic analysis. A subset of fish caught were sampled for diet as part of another study.

Analysing the environmental correlates of establishment by coast

To test predictions (ii – iv), that abiotic, biotic and landscape environmental variables correlate with the presence of brown trout, we focused on explaining patterns only in the natural establishment of invasive brown trout. Only rivers that are likely to be reached by straying trout (i.e., on the east side of the invasion front; Figure 2.2) were included in the analyses, a total of 165 rivers. We removed any rivers where natural establishment was not possible (n = 11 rivers) due to barriers to dispersal (e.g., high waterfalls). As well, any sites where brown trout were established through human-mediated introductions (another 15 rivers) were not included in the analyses. We extracted data on natural and manmade barriers occurring on rivers in eastern Newfoundland (Porter et al. 1974). An impassable barrier to brown trout dispersal was defined as more than 5 metres in height, based on adult trout's ability to jump over 3m high on average, further if there is high flow. Rivers were then defined as allowing natural establishment if they did not have an impassable barrier at or near the river mouth (Budy et al. 2008, Westley and Fleming 2011). Finally, we removed any rivers from the analyses that had incomplete environmental data in Porter and colleagues' dataset (1974; 86 rivers total). In the end, we were left with 53 rivers in the analysis (Figure 2.6.5).

Based on previous work on salmonids (ex. MacCrimmon and Marshall 1968, Hesthagen and Jonsson 1998, Westley and Fleming 2011) we considered a suite of abiotic, biotic and landscape-level environmental predictors that would likely affect brown trout's ability to establish in a river. For prediction (ii), that abiotic environmental variables will influence trout establishment patterns, we used continuous data on water conductivity, pH, turbidity and calcium for each river (Porter et al. 1974). Related to prediction (iii), the effects of local biotic environmental variables, we obtained salmon occurrence data from Porter et al. (1974) and updated it with recent information from local anglers through a survey. Occurrence of Atlantic salmon is a binary predictor variable coded as being present or absent from a river. Charr presence-absence was not included in the statistical models because they are ubiquitous in rivers on the island of Newfoundland. Next, for prediction (iv) pertaining to the influence of landscape-level environmental variables on brown trout establishment patterns, we again used data from Porter et al. (1974) for watershed relief and area, supplemented by distance to original introduction from Westley and Fleming (2011). We then measured estuary size and distance to nearest introduction using the measurement tool on Google maps. All five landscape-level environmental variables are continuous predictors. Finally, to test prediction (v) that establishment patterns will be explained by different environmental variables depending on the coast, we split the rivers and their corresponding environmental datasets (27 rivers in the north, 26 in the south) and separately analysed them for establishment patterns. We defined the geographic boundary between the north and south coasts as the divide between the Cape Race and Chance Cove watersheds on the Avalon Peninsula (Figure 2.2). This boundary divides the coast based on oceanographic differences caused by currents (i.e., Labrador Current to the north, and North Atlantic Drift to the south – which is an offshoot of the Gulf Stream) and is also used to define local Atlantic salmon population units by Fisheries and Oceans Canada (DFO 2006).

We fitted generalized linear models with a binomial error distribution using a logit link. The response variable was brown trout presence-absence. The ten predictor variables were divided into three environmental categories based on our predictions: abiotic (conductivity, pH, turbidity and calcium), biotic (salmon presence-absence) and landscape-level variables (watershed relief, area, estuary area, distance to original introduction, and distance to nearest introduction point; Table 2.3). These predictors were used to explain the variation in presence-absence of brown trout at 53 rivers within the brown trout invasion range, meaning only within the geographic area that brown trout have currently established. To prevent the occurrence of uninformative parameters in the statistical models (Arnold 2010, Leroux 2019), we then tested each set of explanatory variables for correlations and used Variance Inflation Factor Analysis (*car* package; Fox et al. 2021) to test for multicollinearity. We ran models with all possible combinations of variables within the same environmental categories (abiotic, biotic and landscape), which were each ranked using Akaike's Information Criterion corrected for small sample size, using the *AICcmodavg* package (Mazerolle 2020). AICc ranks models according to their ability to explain the most variation while maintain the fewest number of parameters possible. For each explanatory variable within the model, we calculated the exponent of the model coefficient, called the Odds Ratio. This is used to evaluate the odds that brown trout will be present in a river given a certain explanatory variable.

Finally, based on our results from the above analyses, we 1) estimated how long it will take brown trout to spread to key areas on the Island of Newfoundland, and 2) identified rivers along the south coast that are likely to be established in the future. We used the empirical observation of coastal spread rate to project the extent of spread of brown trout in the next half century. We then used the *predict* function with the top ranked southern linear model to make predictions of which rivers west of the invasion front are likely to be established in the future along the South coast. We did not make predictions about future establishment in the north as we did not identify any environmental variables that could explain establishment patterns in the north. All mathematical and statistical models were run in the statistical software R (R Development Core Team 2021).

2.3 Results

Predicting the rate of spread using a Reaction-Diffusion model

Our literature search for intrinsic population growth parameter values revealed 11 studies that fit the search criteria, Table 2.6.1. The mean across studies, mean of all the positive values and maximum were $r_1 = 0.018$, $r_2 = 0.160$, $r_3 = 0.400$, respectively. Next, we obtained 13 studies from the literature search for diffusion parameter values (Table 2.6.2). The minimum, mean, median and maximum of the distribution of diffusion values were D_{min} = 27.1 km^2/yr, D_{mean} = 630.5 km^2/yr, D_{median} = 1485.5 km^2/yr, D_{max} = 5292.5 km^2/yr, respectively.

Using three values of intrinsic population growth and four values for the coefficient of diffusion for brown trout, we obtained twelve possible combinations of parameter values to be input into the reaction-diffusion model equation and twelve estimates of the rate of spread of brown trout on the Island of Newfoundland (Table 2.1, Figure 2.3). Estimates of rate of spread obtained from the model ranged from 1.4 km/year to 92.0 km/year, with a mean of 27.6 km/year (standard deviation = 26.0) and median of 19.9 km/year.

Measuring the actual rate of spread from the current distribution

The furthest point of the brown trout invasion on the north coast is Princeton Brook on the Bonavista Peninsula (48°39'33.4"N, 53°06'56.7"W), and in the south, Little Salmonier River on the Burin Peninsula (47°04'16.2"N, 55°10'46.8"W). The mean radial estimate of spread to these furthest points is 1.26 km/year (north = 1.03, south = 1.49) whereas the mean coastal estimate is 3.2 km/year (north = 2.5, south = 3.9), Table 2.2.

Validation of distribution data for establishment analyses

Of the 14 rivers we sampled in 2020 that overlapped with Porter et al.'s (1974) dataset for presence absence of brown trout (Table 2.6.3), only one, Renews River (46°56'05.3"N 52°57'14.3"W), revealed conflicting occurrence between the datasets. The other 13 rivers (92.9%) were validated by our sampling.

Analysing the environmental correlates of establishment by coast

Brown trout have been observed in 81 of the 165 watersheds (49.09 %) within the brown trout's current invasion range (Table 2.6.4). Of these, brown trout has naturally established populations in 56 watersheds on the island, which span each of the bays between the first introduction point in St. John's and the current invasion front. Along the north coast, brown trout are present in 63 and absent in 30 watersheds (north total = 93 watersheds) while on the south coast, they are present in 18 and absent in 54 watersheds (south total = 72 watersheds). 11 rivers were excluded from the analysis because barriers to dispersal (dams, waterfalls, etc.) precluded natural establishment. Thus, 53 rivers from different watersheds within this range had complete environmental data and were used in the establishment analyses (Table 2.3).

There were a broad range of measurements for abiotic water variables, though they did not vary greatly between the North and South coasts. The mean water conductivity was 31.5 µmhos/cm (north = 34.7, south = 28.3), mean pH was 6.3 (north = 6.4, south = 6.2), mean turbidity was 1.1 JTU (north = 0.8, south = 1.7), and mean calcium was 1.4 ppm (north = 1.4, south = 1.5). As the biotic environmental variable, Atlantic salmon were present in 42 (79.3 %) of the rivers used in the analysis (north = 18, south = 24), 19 (45.2 %) of which overlapped with the presence of brown trout (north = 13, south = 6). Only 4 (7.6 %) rivers did not contain any brown trout or Atlantic salmon (north = 2, south = 2). In general, the landscape-level environmental variables varied more between coasts. Mean watershed relief was 261.6 metres (north = 259, south = 168). Watershed area averaged 101.0 km^2 (north = 63.5, south = 140). 29 rivers (54.7 %) had significant estuaries measuring at least 2 hectares (north = 13, south = 16), of which the mean size was 71.3 hectares (north = 21.0, south = 123.6). The mean distance to the origin was 268 km from St. John's (north = 132, south = 405) whereas the mean distance to the nearest introduction point was 189 km (north = 41.9, south = 341.7).

Our results do not support our abiotic (ii) or biotic (iii) predictions (Table 2.4). Specifically, the abiotic and biotic models for both North and South datasets all ranked below the intercept according to the AICc. Thus, we found no evidence that conductivity, pH, turbidity, calcium and salmon presence-absence explained the variation in brown trout establishment patterns along the north or south coasts. As well, all landscape variable models were uninformative (i.e., not related to the response) for the north dataset, as were watershed area, relief and distance to the origin in the south. However, three landscape models ranked above the intercept for the south dataset and were Delta AICc < 4 of the top model. The top-ranking model including the predictors estuary and distance to nearest introduction point and explained 38% of the variation in establishment patterns. Estuary, and distance to nearest introduction as separate models make up the second and third ranked models, and explain 24% and 18% of the variation, respectfully. The odds of establishment were positively associated with estuary size (coefficient = 0.004, Odds Ratio (OR) = 1.004) and negatively associated with distance to nearest introduction point (coefficient = -0.04; OR = 0.995, Figure 2.4, Table 2.6.5).

Based on the mean observed coastal spread from the 1880s to present, we calculated that it would take another 45 years for brown trout to spread to Terra Nova National Park, west of the Bonavista Peninsula (48°23'27.1"N 54°11'29.7"W; Table 2.6.6). In approximately 31 years, brown trout could spread around the tip of the Burin Peninsula to Point May (46°53'55.6"N 55°56'13.2"W) and may begin to spread into Fortune Bay. As well, it would take 281 years of spread for brown trout to reach Cape Ray (47°37'12.9"N 59°18'24.6"W) on the southwestern coast of Newfoundland. Next, we applied the top ranked model (using distance to nearest introduction and estuary area as predictors) to rivers directly west of the invasion front on the south coast. The ranked model was unable to identify any rivers on the Burin Peninsula that were likely to be established by brown trout. The mean predicted probability of establishment was 0.04. We did not predict which rivers would be established on the north coast because the predictors were not able to explain establishment along the northern invasion pathway.

2.4 Discussion

Though biological invasions are now ubiquitous with human activity, our understanding of invasion success and our ability to make predictions about future spread and establishment remains uncertain (Cosner 2014, Ricciardi et al. 2017). Here, we integrate a simple mathematical model of spread rate with an analysis of the correlates of establishment to test our ability to make predictions and explain invasion dynamics. First, we observed much slower rates of spread than our Reaction-Diffusion model predicted (Table 2.1, Figure 2.3), and our calculation of the former using coastal spread compared to radial spread seemed to be most similar to the reaction-diffusion model predicted spread (Table 2.2). Second, two of our landscape-level variables explained some of the variation in occurrence patterns of brown trout, though only along one of the coastal pathways of the invasion (Figure 2.4).

Predicting the rate of spread using a Reaction-Diffusion model

Our data suggests that brown trout on the Island of Newfoundland are spreading at a rate of 3.2 km/year. This remains a slow estimate of observed spread, comparable to the 4 km/year estimated in a previous study on the Island of Newfoundland (Westley and Fleming 2011). In Newfoundland, brown trout has naturally established at least 51 watersheds in 125 years (0.4 watersheds per year; Westley and Fleming 2011), compared to a rate of 0.8 watersheds/year in the Kerguelen Islands in the Southern Indian Ocean (Lecomte et al. 2013). There are likely many ecological and environmental factors that can limit the growth and dispersal of non-native individuals, resulting in slow spread rate (Johnson et al. 2006, Goldstein et al. 2019b). This gradual spread can occur when there are low rates of population growth and egg deposition or low dispersal due to few straying individuals (O’Connell 1982). Specifically, the density of salmonids in a river may need to pass a certain threshold for significant spread of individuals to occur. Newfoundland rivers are generally less productive than other areas with brown trout (Randall et al. 2017), which can reduce the rate of natural increase of fish populations (Lyon et al. 2019). Moreover, angling pressure on returning adults, which in Newfoundland is significant in estuaries where brown trout are known to frequent (Warner et al. 2015) could also limit the number of adults returning to fresh water to spawn and maintain low densities (Hard et al. 2008). However, angling may be a selective-pressure on non-native fish species and increase their fitness (Evangelista et al. 2015). Angling could select for traits that not only make fish harder to catch, but also make them more successful invaders or stronger competitors. The presence of other salmonids in Newfoundland waters could also limit brown trout's spread. For example, in New Zealand, non-native brown trout were extremely successful invaders, possibly due to the absence of native salmonids in the southern hemisphere and the corresponding presence of a 'vacant' niche (Townsend 1996). On the Island of Newfoundland, native Atlantic salmon and brook charr have life-history strategies that considerably overlap with those of brown trout and so may slow the latter's invasion according to the 'biotic resistance hypothesis' (Olden et al. 2006). Thus, the presence of native salmonids, as well as low population growth and rates of straying may contribute to the slow rate of spread we observed.

This simple reaction-diffusion model only predicted spread rates near our empirically observed spread when dispersal and population growth were at the low end of the gradients observed in the literature. The reaction-diffusion model assumes that the population is unstructured, that its growth is exponential and that diffusion occurs in a uniform and one dimensional environment (Andow et al. 1990). However, these assumptions may not be supported by the data in Newfoundland (Purchase et al. 2005), producing predictions that disagree with observed spread. Models that take into account the stage-structure of populations demonstrate that intrinsic growth rate can sometimes decrease in relation to the rate of spread, contrary to the monotonic relationship described by the reaction-diffusion model (Neubert and Caswell 2000). On the other hand, classic diffusion is based on an assumption of drawing distance from a normal dispersal kernel (Neubert and Parker 2004). The dispersal kernel is a probability density function of possible dispersal distances, from which values are randomly drawn to inform diffusion (Ōkubo and Levin 2001). In reality the shape of the dispersal kernel seems to most often be leptokurtic, a distribution that affects the speed of invasion and its potential acceleration over time (Kot et al. 1996), thus overestimated spread suggests a linear approximation of the rate of spread may be inappropriate (Neubert and Parker 2004). Slower rates of observed spread than are predicted by a reaction-diffusion model can also indicate the influence of the Allee effect (Lewis and Kareiva 1993, Kot et al. 1996), which is a relationship between the fitness and size or density of a population (Allee et al. 1949). One possible mechanism of the Allee Effect is the decrease in available mates that can occur at lower population densities (Lewis and Kareiva 1993). Such low densities are often found at the front of an invasion, may directly slow the rate of spread (Hurford et al. 2006) and facilitate hybridization with other species (Quilodrán et al. 2020). Hybridization between brown trout and Atlantic salmon, or brook charr occurs naturally in Newfoundland, and may result in lower fitness of all species involved (Verspoor 1988). A number of methods can refine the predictions of spread obtained from a reaction-diffusion model, including the way parameter values are estimated. When the rate of spread and intrinsic growth is known for a specific population, more informative diffusion values can be calculated using the reaction-diffusion velocity equation, and so can reveal the dispersal required to maintain a certain rate of spread (Leroux et al. 2013). As well, parameterizing the model using a density-dependent method of calculating intrinsic rate of growth (for example see Ricker 1954) can lead to lower and more accurate estimates of population growth. As such, future models should incorporate population-specific parameter estimates (Purchase et al. 2005) that take into account such density-dependent mechanisms to avoid making predictions that overestimate spread (Hastings et al. 2005).

Finally, the reaction-diffusion model assumes environmental homogeneity. The spread of brown trout in the Kerguelen Islands was initially fast, but slowed somewhat after 30 years according to an ecological gradient at the front of the invasion (Labonne et al. 2013). The more westward the invasion front moved, the more unhospitable the landscape became, and the fewer resources available to juvenile brown trout. This suggests that perhaps the rate of spread in our system could not be modelled accurately as independent from the characteristics of the receiving ecosystem, as the simple reaction-diffusion models assumes, and that spread in Newfoundland is in some way influenced by environmental conditions, such as fishing pressure, estuary size or biotic interactions. Additionally, Marco et al. (2011) found that habitat heterogeneity only influenced models of short distance dispersal, and that it directly lowered the estimated spread velocity. If spread in Newfoundland is largely due to shorter distance dispersal, than perhaps environmental conditions need to be considered to make more accurate predictions of slower spread. Such environmental heterogeneity may affect dispersal while in freshwater as well as in marine and estuarine environments. Indeed, recent work has integrated environmental heterogeneity into reaction-diffusion models to study dispersal in patchy landscapes (Maciel et al. 2020) and the effect of spatial variation, competition and individual movement on spread (Maciel and Lutscher 2018, Wang et al. 2019, Lutscher et al. 2020). Given multiple components of environmental heterogeneity in Newfoundland waters as discussed above, future models of spread should integrate the environmental characteristics of the receiving ecosystem that may facilitate or limit growth and dispersal in the landscape to test the importance of these phenomena in this system.

Analysing the environmental correlates of establishment by coast

We found no evidence that any of the abiotic or biotic variables that we analysed were correlated with establishment patterns of brown trout in Newfoundland. First, our sampling generally validated the occurrence data we obtained from the literature, except for at Renews River, where we did not observe brown trout. However, significant research conducted on this river indicates there is high confidence that brown trout are present there (Warner 2013, Warner et al. 2015). This mismatch between our sampling and previous studies is likely due to the yearly and seasonal differences in salmonid densities (MacIsaac 2010) that likely contributed to our inability to detect brown trout during a one-time sampling event. Though there is evidence that some water chemistry variables influence salmonid behaviour (Sweka and Hartman 2001), physiology (Oduleye 1975, Liebich et al. 2011) and density (Hesthagen et al. 1999, Enge and Kroglund 2011) in different ecological contexts, there exists no real consensus in the literature on the importance of abiotic variables in structuring trout establishment. Temperature and stream flow discharge may be important for determining fish distribution within streams (de la Hoz Franco and Budy 2004), while substratum heterogeneity and slope may also be influential (Hasegawa et al. 2016). The lack of evidence supporting our abiotic predictions could also reflect the coarse resolution of our data (Fernandez et al. 2017), as our measurements are a snapshot of the environmental conditions at one time and spatial scale, or else averaged over the summer. However, measuring water chemistry values at specific times of year (i.e. at spawning; Beechie et al. 2008) and incorporating abiotic and biotic factors at multiple spatial scales (Rich et al. 2003) may be more relevant than an average seasonal value. Counter to our prediction, studies have demonstrated that competition between brown trout and Atlantic salmon in rivers is limited by habitat segregation according to their preferences for different depths and water velocities (Bietz et al. 1981, Gibson and Cunjak 1986) thus this corroborates our finding that salmon presence has no effect on trout establishment. Though Bietz and colleagues (1981) found that resource competition increases between the salmonids within smaller river systems, it is likely that this does not have a measurable effect on the occurrence of brown trout in the rivers included in our study. Perhaps some abiotic and biotic environmental variables can help explain the establishment dynamics of brown trout, however it could be that they are discernible only when taking into account temporal dynamics as colonization rates may not stay constant in time or space (Labonne et al. 2013). Future work should use temporal sampling at multiple spatial scales to verify whether these environmental variables can explain any patterns in establishment of brown trout.

On the other hand, our analyses provided weak evidence that two landscape variables influence establishment. It is important to note, however, that there was considerable residual variation in the relationship between both predictors (estuary presence and distance to nearest introduction point) and the occurrence of brown trout (Table 2.4). There is consensus in the literature that landscape variables structure establishment patterns of invaders, though the key variables differ somewhat from those in our study (Suarez et al. 2001, Launey et al. 2010, Westley and Fleming 2011, Labonne et al. 2013, Alharbi and Petrovskii 2019). Consistent with our predictions, shorter distance to nearest introduction point and larger estuary areas are associated with brown trout presence. Labonne et al. (2013) found that distance between established and non-established rivers directly influenced the probability of the latter’s establishment in a study of invasive brown trout in the Kerguelen Islands (Labonne et al. 2013).

That estuaries are important for brown trout in Newfoundland is well understood (Veinott et al. 2012, Warner et al. 2015), likely because estuaries provides trout with feeding opportunities, protection from predators and a transition zone in which to undergo the physiological changes required when entering or leaving a saline marine environment (McDowall 1976). Overall, our analyses of establishment dynamics suggest that brown trout may be more likely to establish rivers with significant estuarine areas that are close to a source population.

The ability of some landscape-scale variables to explain variation in southern establishment patterns but not in the North is likely due to the vastly different introduction histories and marine environments between the coasts. Launey et al. (2010) found that patterns of genetic diversity of brown trout were best explained by the introduction history, whereby each established population was directly able to act as a source of colonization for the nearby rivers in the Kerguelen Islands. This generally corroborates the stepping-stone pattern found in Newfoundland by O'Toole and colleagues (*in press*). They further found that within each establishment foci (or source), landscape factors such as river mouth accessibility, coastal characteristics, river length and distance between rivers influenced the direction and rate of migration (Launey et al. 2010). Thus, perhaps the importance of landscape level variables is moderated by the introduction history of the coast, or else is only discernible on the scale of each source population. Along the northern coast of Newfoundland, there were many introductions dispersed throughout the range and thus, potentially many established foci from which migration could occur, moderating the importance the landscape. However, along the southern coast, there existed only two introduction points. Successful establishment of new rivers in the South could be influenced by the landscape factors that shaped migration from these foci and explain the differential importance of the landscape between the coasts. As well, coastal marine differences have been shown to affect the distribution and richness of non-native species (Ruiz et al. 2013). For example, level of international shipping in estuaries (Ruiz et al. 2013) and oceanic currents (Bishai 1960) can affect the distribution and marine migration patterns of fish species while in the ocean. Such differences between the north and south coastal marine environments of Newfoundland, and resulting climates, may influence the differential influence of landscape variables between the two invasion pathways. Labonne and colleagues (2013) also found patch size, defined as the main river stem length and connectivity to lakes, was positively correlated with colonization probability. This is contrary to our finding that watershed size does not explain any establishment variance. Westley and Fleming (2011) found that watershed area in concert with conductivity best explained brown trout establishment in Newfoundland, though neither variable performed well alone. We may not have obtained the same evidence due to our division of datasets by invasion pathway, because we did not run models with combined abiotic and landscape predictors or else because other landscape variables not measured in this study may correlate with brown trout occurrence. Launey et al. (2010) surmised that an established population may only become a relevant source of migration once a certain population density threshold has been surpassed. Thus, if some of the introduction points in Newfoundland still had very low densities and low amount of straying, they may not actually be a source for migrating individuals. Furthermore, the differences in human settlements and anthropogenic activity between the North and South pathways of the Newfoundland invasion could potentially explain the differences in environmental variables’ ability to explain establishment between the coasts.

Based on the current observed coastal spread rate of 3.2 km/yr, within the next 50 years brown trout will likely spread around the tip of the Burin Peninsula into Fortune Bay, and in the North, will spread to Terra Nova National Park, west of the Bonavista Peninsula. However, our top ranked model does not reveal that any rivers on the Burin Peninsula are at risk of being established by brown trout, due to their generally smaller estuaries and extreme distance (over 700 km) from the introduction points on the Avalon Peninsula. Comparatively, the most western introduction point on the north coast is located on the Bonavista Peninsula. However, the inclusion of any of the factors previously discussed could improve or even change the predictions of future establishment in Newfoundland rivers. Though brown trout spread on the Island of Newfoundland is indeed slower than elsewhere and establishment is likely limited, it is paramount that we continue to synthesize information and make predictions about their invasion to mitigate any future ecological consequences. Atlantic salmon and brook charr populations in Newfoundland have suffered decline in the last century (DFO 2006), and as important economic and cultural resources, it is vital that future research integrates studies of brown trout invasion with an analysis of their impacts on local salmonids.

Our study has revealed the complexity of mechanisms that interact to structure spread and establishment dynamics of non-native species. We tested a classic reaction-diffusion model's ability to make predictions of spread, and the results point to the need for parameterization that includes environmental heterogeneity, while remaining simple and replicable. Our analysis of establishment dynamics emphasizes how the landscape structures the direction and strength of propagule movement and suggests that finer temporal resolution of environmental data may help future studies further untangle the mechanisms of establishment. This project contributes to the growing body of invasion science that is seeking to refine knowledge, improve predictions and explain patterns in order to minimize the introduction, establishment and spread of current and future non-native species.

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Table 2.1 Rate of spread *V*, obtained from 12 combinations of literature sourced intrinsic growth rate *r* values (Table 2.61) and diffusion *D* values (Table 2.6.2).

PARAMETERS		**MODEL OUTPUT**
Intrinsic growth *r* yr^{-1}	**Diffusion *D*** km^2yr^{-1}	**Predicted Velocity *V*** $km \cdot yr^{-1}$
0.0183	27.12	1.41
0.16	27.12	4.17
0.4	27.12	6.59
0.0183	630.54	6.79
0.16	630.54	20.09
0.4	630.54	31.76
0.0183	1485.54	10.43
0.16	1485.54	30.83
0.4	1485.54	48.75
0.0183	5292.51	19.68
0.16	5292.51	58.20
0.4	5292.51	92.02

Table 2.2 The values of actual spread we calculated using current and historic distribution data of brown trout. Radial spread was obtained using the distance measurement tool on Google Maps and was defined as the shortest distance between the coastal midpoint of origin and each of the furthest brown trout presence points, divided by the number of years since the first introduction. Coastal spread, measured with the same tool, was defined as the distance using the least cost path along the coast from the same origin to the same two furthest points on the north and south coasts. The mean estimates are the average of the spread rates in along each coast.

	River/ Location	**Latitude**	**Longitude**	**RADIAL**		**COASTAL**	
Origin	Coastal midpoint	47.522969	-52.969084	**Distance (km)**	**Spread rate ($\text{km}\cdot\text{yr}^{-1}$)**	**Distance (km)**	**Spread rate ($\text{km}\cdot\text{yr}^{-1}$)**
North	Princeton Brook	48.659278	-53.115750	121	1.03	394	2.46
South	Little Salmonier	47.071158	-55.179675	174	1.49	628	3.93
				radial mean	**1.26**	**coastal mean**	**3.20**

Table 2.3 Average measurements of the environmental variables used as explanatory variables in the logistic regressions, a series of generalized linear models with a binomial error structure and logit link. The variables are divided by category (abiotic, biotic and landscape), and the units are specified below each variable. Mean values are given (with the exception of salmon river counts), with standard deviation in parentheses. Values for each variable are divided based on coast and by the presence-absence of brown trout.

Category	**Environmental variables**	**NORTH**		**SOUTH**		**COMBINED**
		Absent	**Present**	**Absent**	**Present**	**Overall Mean**
Abiotic	pH	6.37 (0.5)	6.42 (0.3)	6.20 (0.3)	6.32 (0.3)	6.32 (0.4)
	Conductivity µmhos/cm	31.14 (4.9)	35.9 (27.5)	28.05 (9.7)	29.0 (9.5)	31.53 (18.3)
	Turbidity JTU	0.73 (0.2)	0.90 (0.8)	1.30 (1.0)	1.84 (1.8)	1.25 (1.1)
	Calcium ppm	1.11 (0.4)	1.48 (1.3)	1.55 (1.9)	1.23 (0.4)	1.43 (1.4)
Biotic	Salmon rivers count	7	20	20	6	53
Landscape	Watershed area km^2	55.43 (24.1)	66.35 (28.7)	114.95 (96.8)	223.33 (284.7)	101.02 (118.9)
	Watershed maximum relief metres	248.0 (79.3)	254.95 (43.4)	263.6 (59.7)	292.67 (64.6)	261.57 (57.2)
	Distance to original introduction km	161.57 (49.1)	121.45 (55.3)	414.2 (112.6)	374.0 (112.8)	310.44 (242.7)
	Distance to nearest introduction point km	36.57 (49.1)	43.8 (45.1)	386.35 (268.1)	193.0 (121.8)	189.0 (234.4)
	Estuary size hectares	43.48 (107.8)	13.15 (23.7)	52.97 (149.7)	359.01 (507.3)	71.34 (213.5)

Table 2.4 Subset of AIC outputs for a series of generalized linear models obtained for north and south datasets. Only the models with 1 parameter are shown. K is the number of independently adjusted parameters for the model (Akaike 1974). AICc, Akaike's Information Criterion corrected for small sample size, is a measure of the fit of the model against the number of estimated parameters. Delta AICc is a relative measure of how each model ranks against the top model, AICcWt is the probability that model is the best model given the data and compared to the other ranked models, LL is the log-likelihood ratio, and Nagelkerke's R^2 is an adjusted measure of the variation in the data explained by the model parameters. All models in the north dataset ranked below the intercept, meaning they are *pretending variables* and do not explain any of the variation (Leroux 2019), as did all of the abiotic and biotic models in the South dataset. However, two single parameter landscape models explain variation in the South, as well as the top ranked model which is a combination of the same two parameters.

Coastal Pathway	Model parameters	K	AICc	Delta AICc	AICc Wt	LL	R^2
NORTH	**- ABIOTIC -**						
	intercept	1	33.06	0	0.29	-15.45	0
	calcium	2	34.6	1.54	0.14	-15.05	0.04
	turbidity	2	35.07	2	0.11	-15.28	0.02
	conductivity	2	35.13	2.07	0.1	-15.31	0.01
	pH	2	35.32	2.26	0.09	-15.41	0
	- BIOTIC -						
	intercept	1	33.06	0	0.75	-15.45	0
	salmon presence-absence	2	35.31	2.24	0.25	-15.4	0.01
	- LANDSCAPE -						
	intercept	1	33.06	0	0.2	-15.45	0
	estuary area	2	34.11	1.04	0.12	-14.8	0.07
	watershed area	2	34.53	1.46	0.09	-15.01	0.05
	distance to nearest introduction point	2	35.26	2.2	0.07	-15.38	0.01
	watershed relief	2	35.31	2.25	0.06	-15.41	0
	distance to original introduction	2	35.36	2.29	0.06	-15.43	0
SOUTH	**- ABIOTIC -**						
	intercept	1	30.26	0	0.31	-14.05	0
	pH	2	31.94	1.68	0.13	-13.71	0.04
	calcium	2	32.41	2.15	0.11	-13.94	0.01
	turbidity	2	32.47	2.21	0.1	-13.97	0.01
	conductivity	2	32.56	2.31	0.1	-14.02	0
	- BIOTIC -						
	intercept	1	30.26	0	0.65	-14.05	0
	salmon pa	2	31.51	1.26	0.35	-13.5	0.06
	- LANDSCAPE -						

distance to nearest introduction point + estuary area	3	27.77	0	0.39	-10.34	0.38
estuary area	2	28.12	0.35	0.32	-11.8	0.24
distance to nearest introduction point	2	29.33	1.56	0.18	-12.4	0.18
intercept	1	30.26	2.49	0.11	-14.05	0
watershed area	2	30.74	4.43	0.01	-13.11	0.11
watershed relief	2	31.5	5.19	0.01	-13.49	0.06
distance to original introduction	2	31.82	5.51	0.01	-13.65	0.05

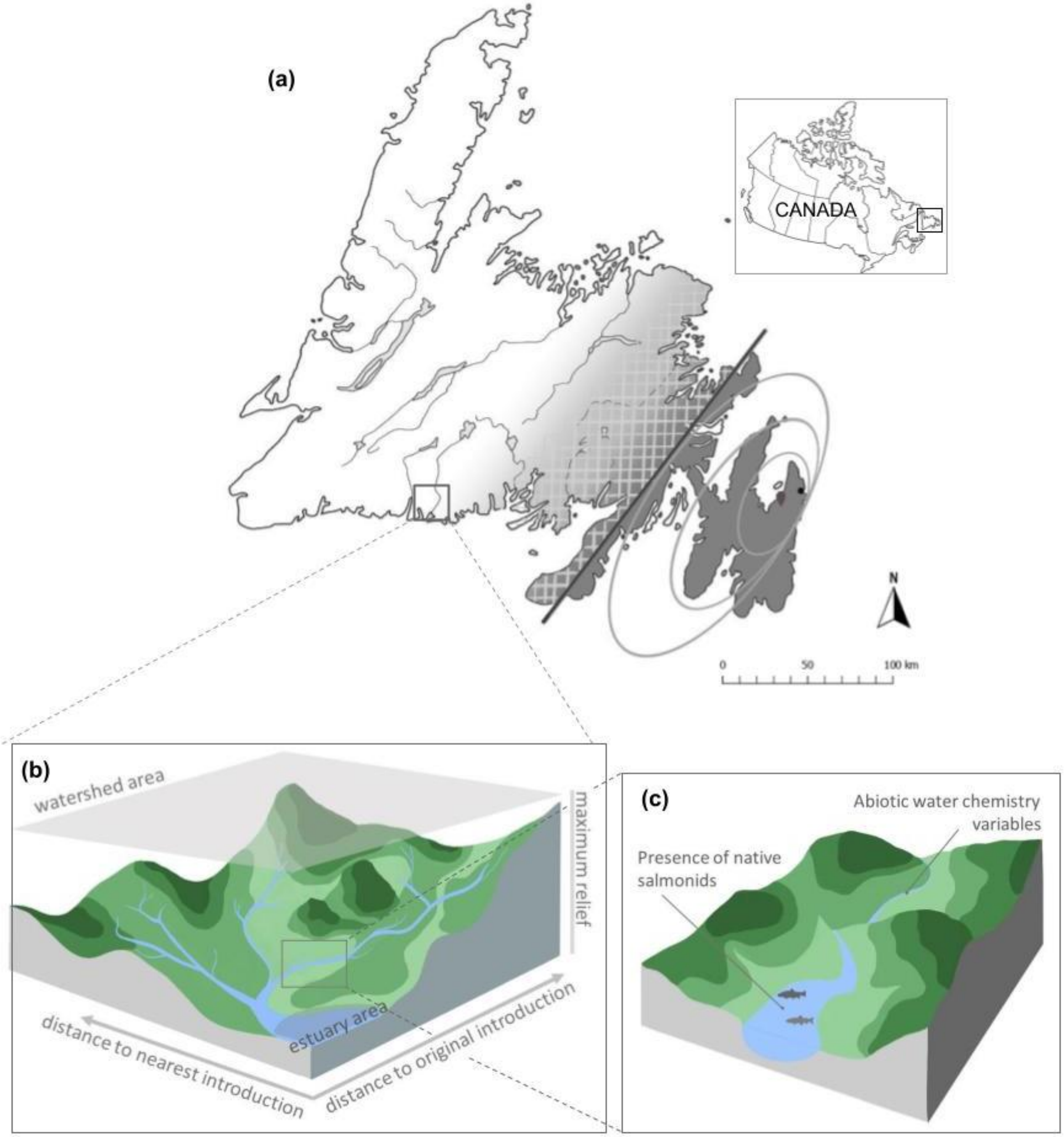

Figure 2.1 Conceptual overview of the study. Brown trout were introduced to the Island of Newfoundland (a) and have since spread westward. The ellipses represent the gradual spread of brown trout since their introductions on the Avalon Peninsula in the 1880s. The front of the invasion (dark grey line) is currently the furthest point westward brown trout have reached. The

shading represents the future spread and establishment of brown trout on the island. The Reaction-Diffusion model predicts the average rate of spread (symbolized by cross-hatching) to be further West than the actual front. We hypothesized that this difference in spread rate and the patterns in the establishment of populations can likely be explained by a number of watershed level variables (b) and local abiotic and biotic environmental variables at the river-scale (c).

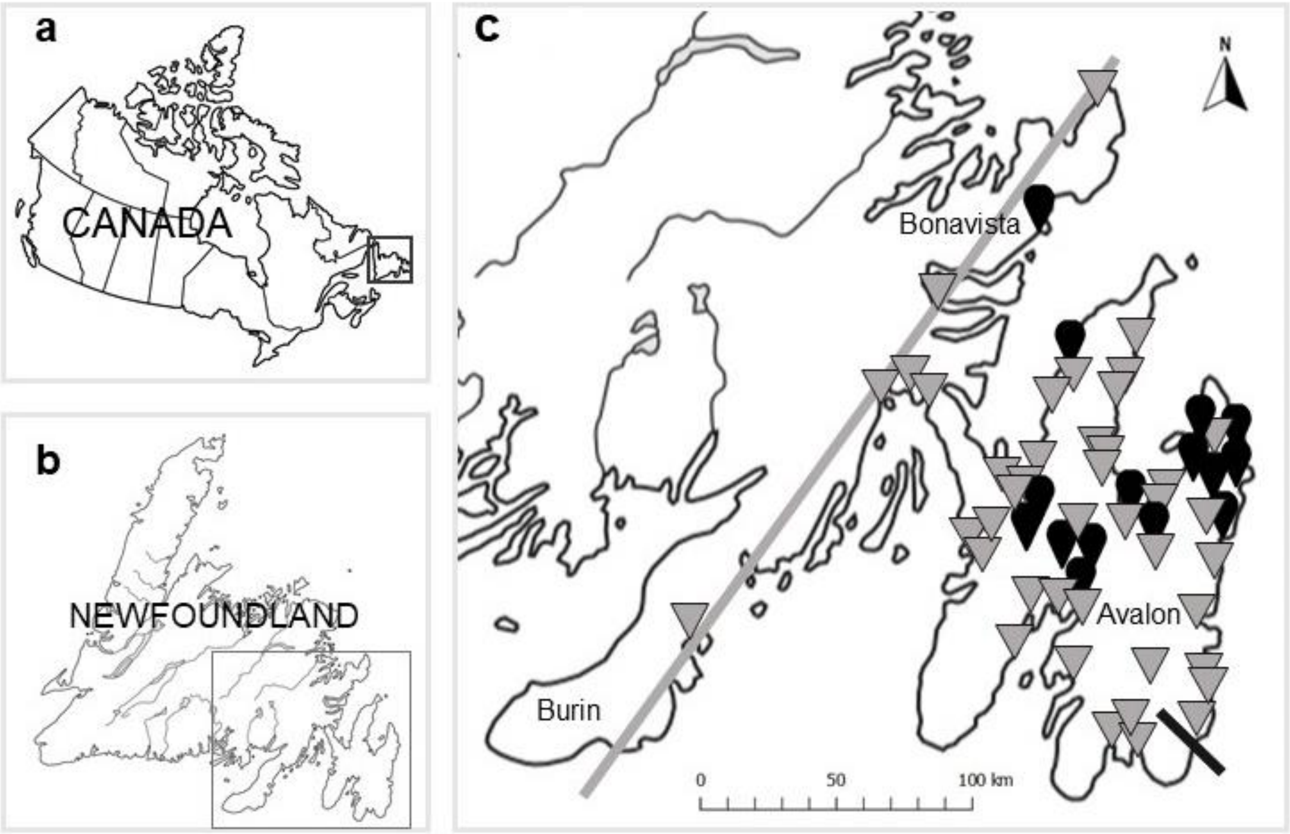

Figure 2.2 Map of the invasion range of brown trout on the Island of Newfoundland (b), Canada (a). The front of the invasion (grey line) is located along the Burin and Bonavista Peninsulas (c). Black location markers represent the introduction points, and grey triangles indicate the places where brown trout have naturally established populations. The establishment statistical analyses only considered rivers East of this line and split the datasets between north and south coasts along the black boundary line between Cape Race and Chance Cove watersheds.

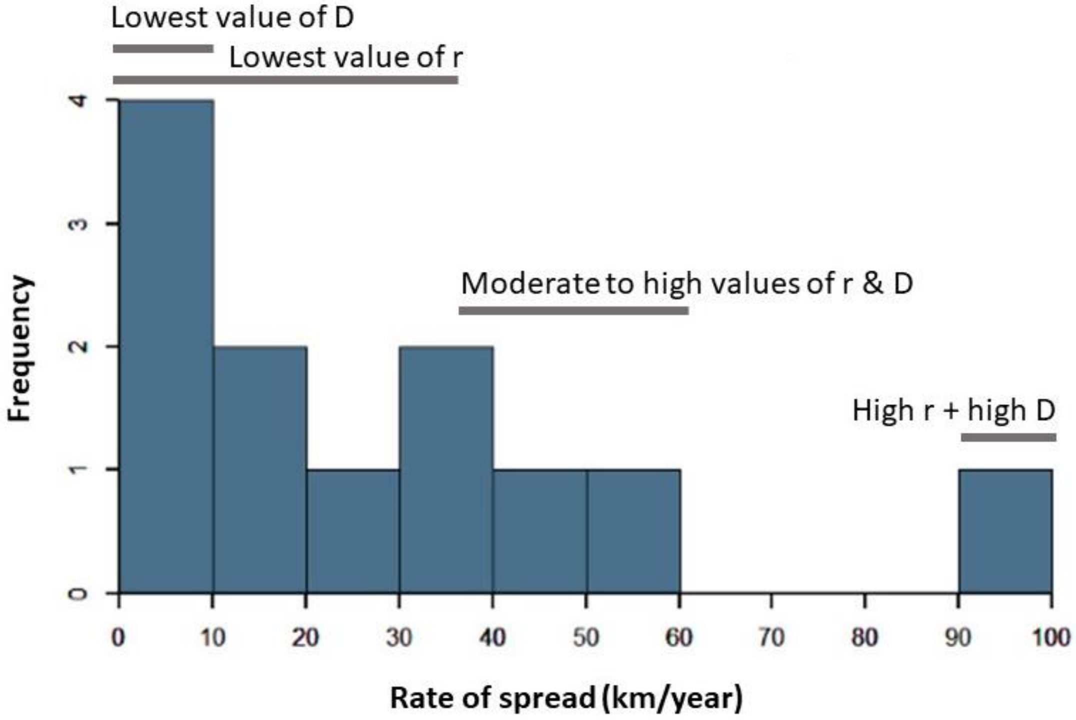

Figure 2.3 Using twelve combinations of values for growth *r* and diffusion *D* parameters (see Table 2.1), we obtained twelve estimates of rate of spread *V* from the Reaction-Diffusion model. This histogram shows the frequency distribution of these spread predictions (blue bars), along with the distribution of the parameter values used as the inputs (grey lines).

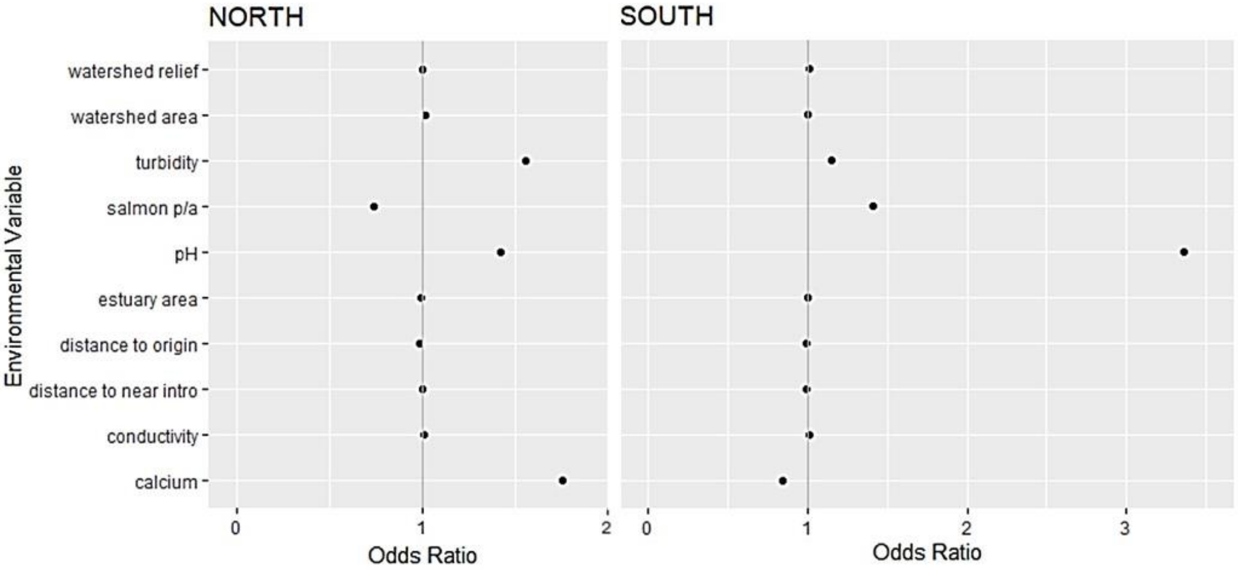

Figure 2.4 We ran a series of logistic regression models, generalized linear models with binomial error and logit link, with different environmental variables and for each model, calculated the Odds Ratio (OR, exponent of the model coefficient). Represented by the black points, the Odds Ratio is the odds of brown trout being present at a river under each environmental regime. The line at OR = 1 represents the threshold for the direction of the relationship of brown trout presence with each variable, with OR < 1 corresponding to a negative relationship, and OR > 1 a positive relationship with trout presence.

2.6 Appendices

Table 2.6.1 Results of a literature search for population growth values, each of the papers below having fulfilled the search criteria. The type of data we used to calculate r from each paper varied from estimates of abundance or density (which we input into equation 3) to values of intrinsic growth calculated by the authors. The time series is the number of consecutive years that the paper provided data for the population. We calculated the intrinsic growth value r (except for Grossman et al. 2017) for each of these studies and then used the distribution of values to inform our independent values for the Reaction-Diffusion model (Figure 2.6.1).

Citation	**Original Data Type**	**Time Series**	**Population Location**	**Intrinsic Growth Value *r***	**Full Reference**
Elliot 1984	Abundance/m^2	16 years	(Black Brows Beck) Lake District, UK	**-0.013**	Elliott, J. M. 1984. Numerical Changes and Population Regulation in Young Migratory Trout Salmo trutta in a Lake District Stream, 1966-83. Journal of Animal Ecology 53:327–350.
Elliot 1987	Abundance/ 60 m^2	7 years	(Wiflin Beck) Lake District, UK	**0.400**	Elliott, J. M. 1987. Population Regulation in Contrasting Populations of Trout Salmo trutta in Two Lake District Streams. Journal of Animal Ecology 56:83–98.
Thorpe 1974	Total abundance	4 years	Loch Leven, UK	**-0.292**	Thorpe, J. E. 1974. Estimation of the number of brown trout Salmo trutta (L.) in Loch Leven, Kinross, Scotland. Journal of Fish Biology 6:135–152.
Wolff et al. 1990	Abundance/ mile	3 years	Douglas Creek, WY USA	**-0.400**	Wolff, S., T. Wesche, D. Harris, and W. Hubert. 1990. Brown Trout Population and Habitat Changes Associated with Increased Minimum Low Flows in Douglas Creek, Wyoming:25.

O'Neal 2008	Total abundance	2 years	Patagonia, Chile	**0.376**	O'Neal, S. L. 2008. Lessons to learn from all out invasion: life history of brown trout (Salmo trutta) in a Patagonian River.43.
Unfer and Pinter 2018	Total abundance	8 years	Ois river, Austria	**0.122**	Lobón-Cervía, J., and N. Sanz, editors. 2017. Brown trout: biology, ecology and management. Wiley, Hoboken, NJ.
Unfer et al. 2011	Total abundance	12 years	Ybbs River, Austria	**0.011**	Unfer, G., C. Hauer, and E. Lautsch. 2011. The influence of hydrology on the recruitment of brown trout in an Alpine river, the Ybbs River, Austria. Ecology of Freshwater Fish 20:438–448.
Bagliniere et al. 1989	Total abundance	4 years	Scorff River, France	**-0.072**	Bagliniére, J. L., G. Maisse, P. Y. Lebail, and A. Nihouarn. 1989. Population dynamics of brown trout, Salmo trutta L., in a tributary in Brittany (France): spawning and juveniles. Journal of Fish Biology 34:97–110.
Olsson and Greenberg 2004	Total abundance	2 years	Greåna River, Sweden	**0.033**	Olsson, I. C., and L. A. Greenberg. 2004. Partial migration in a landlocked brown trout population. Journal of Fish Biology 65:106–121.
Grossman et al. 2017	Intrinsic growth	25 years	Spruce Creek, PA USA	**0.018**	Grossman, G. D., R. F. Carline, and T. Wagner. 2017. Population dynamics of brown trout (Salmo trutta) in Spruce Creek Pennsylvania: A quarter-century perspective. Freshwater Biology 62:1143–1154.
Carline 2009	Abundance/ hectare	18 years	Spruce Creek, PA USA	**-0.021**	Carline, R. F. 2006. Regulation of an Unexploited Brown Trout Population in Spruce Creek, Pennsylvania. Transactions of the American Fisheries Society 135:943–954.

Table 2.6.2 Results of literature search for diffusion parameter values, each of the papers below having fulfilled the search criteria of anadromous brown trout population movement. We used the original data from the study to calculate ground speed and Diffusion *D*. for each of these studies and then used the distribution of values to inform our independent values for the Reaction-Diffusion model (Figure 2.6.2).

Citation	**Original Data Type**	**Ground Speed (km/day)**	**Diffusion D (km^2/day)**	**Full Reference**
Davidsen et al. 2014	Mean progression rate (bl·s−1)	0.3	**27.1**	Davidsen, J. G., M. Daverdin, J. V. Arnekleiv, L. Rønning, A. D. Sjursen, and J. I. Koksvik. 2014. Riverine and near coastal migration performance of hatchery brown trout Salmo trutta. Journal of Fish Biology 85:586–596.
Finstad et al. 2005	Mean speed (bl·s−1)	1.7	**156.9**	Finstad, B., F. Økland, E. B. Thorstad, P. A. BjØrn, and R. S. McKinley. 2005. Migration of hatchery-reared Atlantic salmon and wild anadromous brown trout post-smolts in a Norwegian fjord system. Journal of Fish Biology 66:86–96.
Aldven et al. 2015	Average ground speed (bl·s−1)	2.5	**224.5**	Aldvén, D., R. Hedger, F. Økland, P. Rivinoja, and J. Höjesjö. 2015. Migration speed, routes and mortality rates of sea trout Salmo trutta during outward migration through a complex coastal habitat. Marine Ecology Progress Series 541.
Thorstad et al. 2004	Mean migration speed (bl·s−1)	4.8	**433.6**	Thorstad, E., F. kland, B. Finstad, R. Sivertsgrd, P. Bjorn, and R. McKinleyd. 2004. Migration speeds and orientation of Atlantic salmon and sea trout post-smolts in a Norwegian fjord system. Environmental Biology of Fishes 71:305–311.
Serrano et al. 2009	Migration speed (bl·s−1)	5.7	**520.1**	Serrano, I., S. Larsson, and L.-O. Eriksson. 2009. Migration performance of wild and hatchery sea trout (Salmo trutta L.) smolts—Implications for compensatory hatchery programs. Fisheries Research 99:210–215.
Berg and Berg 1987	Mean distance of daily travel (km·day−1)	6.0	**547.5**	Berg, O. K., and M. Berg. 1987. Migrations of sea trout, Salmo trutta L., from the Vardnes river in northern Norway. Journal of Fish Biology 31:113–121.

Aldven et al. 2015	Average ground speed (bl·s−1)	6.9	**630.5**	Aldvén, D., R. Hedger, F. Økland, P. Rivinoja, and J. Höjesjö. 2015. Migration speed, routes and mortality rates of sea trout Salmo trutta during outward migration through a complex coastal habitat. Marine Ecology Progress Series 541.
Serrano et al. 2009	Migration speed (bl·s−1)	12.0	**1095.0**	Serrano, I., S. Larsson, and L.-O. Eriksson. 2009. Migration performance of wild and hatchery sea trout (Salmo trutta L.) smolts—Implications for compensatory hatchery programs. Fisheries Research 99:210–215.
Kristensen et al. 2019	Mean daily migration speed (km·day−1)	16.0	**1460.0**	Kristensen, M. L., M. W. Pedersen, U. H. Thygesen, D. del Villar-Guerra, H. Baktoft, and K. Aarestrup. 2019. Migration routes and habitat use of a highly adaptable salmonid (sea trout, Salmo trutta) in a complex marine area. Animal Biotelemetry 7:23.
Berg and Berg 1987	Mean distance of daily travel (km·day−1)	20.0	**1825.0**	Berg, O. K., and M. Berg. 1987. Migrations of sea trout, Salmo trutta L., from the Vardnes river in northern Norway. Journal of Fish Biology 31:113–121.
Serrano et al. 2009	Migration speed (bl·s−1)	33.1	**3020.4**	Serrano, I., S. Larsson, and L.-O. Eriksson. 2009. Migration performance of wild and hatchery sea trout (Salmo trutta L.) smolts—Implications for compensatory hatchery programs. Fisheries Research 99:210–215.
Finstad et al. 2005	Maximum speed in body lengths (bl·s−1)	44.7	**4078.9**	Finstad, B., F. Økland, E. B. Thorstad, P. A. BjØrn, and R. S. McKinley. 2005. Migration of hatchery-reared Atlantic salmon and wild anadromous brown trout post-smolts in a Norwegian fjord system. Journal of Fish Biology 66:86–96.
Kristensen et al. 2019	Maximum daily speed of migration (km·day−1)	58.0	**5292.5**	Kristensen, M. L., M. W. Pedersen, U. H. Thygesen, D. del Villar-Guerra, H. Baktoft, and K. Aarestrup. 2019. Migration routes and habitat use of a highly adaptable salmonid (sea trout, Salmo trutta) in a complex marine area. Animal Biotelemetry 7:23.

Table 2.6.3 Rivers we sampled during the summer and fall of 2020 and the resulting presence absence of brown trout, as well as the occurrence assigned by Westley and Fleming (2011). This table is used to validate the brown trout occurrence data we obtained from Westley and Fleming and used for our analysis of the correlates of establishment. Note all river occurrences match except for Renews River, where our sampling did not reveal any brown trout but other studies have extensively sampled and found brown trout (see Warner et al. 2015).

River Name	Latitude	Longitude	Author Sampling 2020	Porter et al. 1974
West Lawn River	46.92681	-55.47864	absent	absent
Rushoon River	47.35879	-54.91614	absent	absent
Rattle Brook	47.45026	-54.85330	absent	absent
Little Barasway	47.17996	-54.03387	absent	absent
Great Barasway	47.12762	-54.06967	absent	absent
L'anse au Loup Brook	47.08376	-55.68154	absent	absent
Renews River	46.93392	-52.95256	absent	present
Northeast Placentia River	47.27174	-53.84261	present	present
Piper's Hole River	47.92677	-54.27469	present	present
Little Salmonier Brook	47.07244	-55.17574	present	present
Southeast Placentia River	47.22243	-53.89573	present	present
Chapel Arm Brook	47.51922	-53.67300	present	present
New Harbour Brook	47.58194	-53.54124	present	present
Old Shop Pond Brook	47.52355	-53.57359	present	present

Table 2.6.4 River dataset used for the analysis of the correlates of establishment. 165 rivers are east of the invasion front, meaning they are within the invasion range of the brown trout. Rivers that did not fit the analysis criteria (Figure 2.6.5) were removed from the analysis before they were coded according to their invasion pathway (north and south coasts). Each river is coded as either having brown trout (present) or absent. Sites where brown trout are absent have not been established. Sites where brown trout are present were either due to introductions or natural establishment.

Name	Bay	Latitude	Longitude	Site Type	Coast	Brown trout occurrence	Inclusion in Analyses
Aquaforte River	Aquaforte	47.00496	-52.9861	Natural Establishment	south	present	No
Arnold's Cove Brook	Placentia	47.77194	-53.9751	Natural Establishment	south	present	No
Avondale River	Conception	47.42229	-53.1956	Natural Establishment	north	present	Included
Bay Bulls River	Bay Bulls	47.31298	-52.8052	Natural Establishment	south	present	No
Bay de l'Eau River	Placentia	47.43937	-54.7822	Not established	south	absent	Included
Beachy Cove Brook	Conception	47.61716	-52.8703	Not established	north	absent	No
Beckford River	St. Mary's	46.88714	-53.9194	Not established	south	absent	Included
Bellevue Brook	Trinity	47.60929	-53.7663	Not established	north	absent	No
Big Barachois River	St. Mary's	47.04989	-53.7753	Not established	south	absent	Included
Big Brook	Trinity	48.03004	-53.2102	Not established	north	absent	No
Big River	Flat rock	47.7086	-52.7082	Not established	north	absent	No
Big Salmonier Brook	Placentia	47.06066	-55.211	Not established	south	absent	Included
Biscay Bay River	Biscay	46.77539	-53.2811	Natural Establishment	south	present	No
Black River	West Placentia	47.58837	-54.4438	Not established	south	absent	Included
Black River	North Placentia	47.88233	-54.1676	Not established	south	absent	No
Blackhead Brook	Conception	47.8459	-53.0923	Not established	north	absent	No
Branch River	St. Mary's	46.88272	-53.9499	Not established	south	absent	Included
Bristy Cove River	Bristy	46.63158	-53.1885	Not established	south	absent	No
Broad Cove Pond	Conception	47.59159	-52.8848	Natural Establishment	north	present	No

Broad Cove River	Conception	47.59159	-52.8848	Not established	north	absent	No
Broom River	Trepassy	46.70319	-53.4156	Not established	south	absent	No
Cape Broyle River	Cape Broyle	47.09121	-52.9561	Natural Establishment	south	present	Included
Cape Roger Brook	Placentia	47.4272	-54.7035	Not established	south	absent	No
Chance Cove Brook	Chance Cove	46.76609	-53.009	Natural Establishment	north	present	Included
Chapel Arm River	Trinity	47.51877	-53.7026	Natural Establishment	north	present	No
Clement's Pond	Conception	47.63438	-52.8246	Introduction	north	present	No
Colinet River	St. Mary's	47.21665	-53.5539	Introduction	south	present	No
Collier Bay River	Long Cove	47.60795	-53.7204	Not established	north	absent	No
Colliers River	Conception	47.45406	-53.2249	Natural Establishment	north	present	Included
Come By Chance River	Placentia	47.8523	-53.985	Natural Establishment	south	present	Included
Cove Road Ponds	Conception	47.4173	-53.1502	Introduction	north	present	No
Crossing Place River	St. Mary's	46.93711	-53.4581	Not established	south	absent	No
Cuslett Brook	Placentia	46.95578	-54.1685	Not established	south	absent	Included
Deer Harbour River	Trinity	47.90682	-53.8103	Not established	north	absent	No
Deer River	St. Mary's	46.81435	-53.5994	Not established	south	absent	No
Flinn River	St. Mary's	47.16259	-53.6534	Not established	south	absent	No
Fluospar	Placentia	46.93217	-55.4734	Not established	south	absentA	No
Freshwater River	Cape Race	46.64607	-53.0944	Not established	south	absent	No
Gallows Cove	Conception	47.44397	-53.1566	Natural Establishment	north	present	No
George's Brook	Trinity	48.23326	-53.9662	Not established	north	absent	No
Glenden's Brook	Placentia	47.14984	-55.22	Not established	south	absentA	No
Gooseberry Cove Brook	Placentia	47.06918	-54.0928	Not established	south	absentA	No
Great Barasway Brook	Placentia	47.12762	-54.0697	Not established	south	absent	Included
Green's Harbour River	Trinity	47.627	-53.4934	Natural Establishment	north	present	No
Harricott River	St. Mary's	47.176	-53.5239	Not established	south	absent	No
Harry’s Pond	Conception	47.78146	-53.1834	Natural Establishment	north	present	No
Heart's Content Brook	Trinity	47.86229	-53.376	Natural Establishment	north	present	Included
Heart's Content River	Trinity	47.8695	-53.3639	Natural Establishment	north	present	Included
Heart's Delight Brook	Trinity	47.77121	-53.4686	Natural Establishment	north	present	Included
Hickman's Harbour River	Trinity	48.21455	-53.5786	Not established	north	absent	No
Hodge Water Cat Hills	St. Mary's	47.41298	-53.5333	Introduction	south	present	No

Hodgewater Pond	Conception	47.5077	-53.2715	Introduction	south	present	No
Holyrood Pond	St. Mary's	46.82659	-53.6075	Natural Establishment	south	present	No
Hopeall River	Trinity	47.6075	-53.514	Natural Establishment	north	present	No
Horse Chops River	Cape Broyle	47.0955	-52.9309	Not established	south	absent	No
Horse Cove Brook	Conception	47.57307	-52.904	Not established	north	absent	No
Indian Pond	Conception	47.45423	-53.0903	Natural Establishment	north	present	No
Island Pond brook	Conception	47.73309	-53.2306	Natural Establishment	north	present	Included
Kelligrews River	Conception	47.49968	-53.0199	Natural Establishment	north	present	No
La Manche River	Cape Broyle	47.16625	-52.8667	Not established	south	absent	No
Lance River	Lance	46.80768	-54.0714	Not established	south	absent	No
Lawn River	Lawn	46.92681	-55.4786	Not established	south	absent	Included
Lee's Pond	Conception	47.40859	-53.1933	Introduction	north	present	No
Little Barachois River	St. Mary's	47.01648	-53.7974	Not established	south	absent	Included
Little Barasway River	Placentia	47.1826	-54.0431	Not established	south	absent	No
Little Harbour River	St. Mary's	47.13359	-53.4782	Not established	south	absent	No
Little Hearts Ease Brook	Trinity	48.0072	-53.6968	Not established	north	absent	No
Little Lawn River	Lawn	46.94521	-55.5387	Not established	south	absent	No
Little Rattling Brook	Placentia	47.37291	-53.8781	Not established	south	absent	No
Little Salmonier River	St. Mary's	47.03743	-53.7499	Natural Establishment	south	present	Included
Lockston River	Trinity	48.39872	-53.3738	Not established	north	absent	Included
Long Pond	Quidi Vidi	47.57805	-52.7335	Introduction	south	present	No
Lower Gullies River	Conception	47.49599	-53.0342	Natural Establishment	north	present	No
Lower Island Ponds	Conception	48.00362	-52.9962	Introduction	north	present	No
Mahers River	Conception	47.38697	-53.1251	Not established	north	absent	Included
Mall Bay Brook	St. Mary's	46.99296	-53.5688	Not established	south	absent	No
Maloney's River	Conception	47.43277	-53.1591	Not established	north	absent	Included
Manuels River	Conception	47.5286	-52.9513	Natural Establishment	north	present	Included
Maturin Brook	Placentia	47.42896	-53.8295	Not established	south	absent	No
Mizzen Pond	Trinity	47.87231	-53.3584	Natural Establishment	north	present	No
Mobile River	Mobile	47.24833	-52.8424	Natural Establishment	south	present	Included
Mundy’s Pond	St. John's	47.55175	-52.7395	Introduction	south	present	No
Murphy's Brook	Trinity	47.57385	-53.6748	Not established	north	absentA	No
Murray’s Pond	Conception	47.61436	-52.8203	Introduction	north	present	No
Musquash Pond	Trinity	47.88249	-53.354	Introduction	north	present	No
New Chelsea	Trinity	48.02821	-53.2184	Not established	north	absent	No

New Harbour River	Trinity	47.58284	-53.5406	Natural Establishment	north	present	No
New Perlican River	Trinity	47.90554	-53.3541	Not established	north	absent	No
Nonsuch River	Placentia	47.44214	-54.6498	Not established	south	absent	No
North Arm River	Conception	47.39338	-53.157	Natural Establishment	north	present	Included
North East Brook	Trepassy	46.76667	-53.3528	Natural Establishment	south	present	Included
North Harbour River	Placentia	47.88436	-54.0721	Not established	south	absent	Included
North Harbour River	St. Mary's	47.1888	-53.6246	Introduction	south	present	No
North River	Conception	47.54979	-53.2821	Natural Establishment	north	present	Included
Northeast River	Placentia	47.27174	-53.8426	Natural Establishment	south	present	Included
Northwest Brook	Trepassy	46.7589	-53.3896	Not established	south	absent	Included
Northwest Brook	Trinity	48.03025	-53.9584	Not established	north	absent	Included
Northwest River	Trepassy	46.76544	-53.3526	Natural Establishment	south	present	No
O’Donnells Brook	St. Mary's	46.75142	-53.603	Natural Establishment	south	present	No
Ocean Pond	St. Mary's	47.40878	-53.4322	Introduction	south	present	No
Old Shop Pond Brook	Trinity	47.52206	-53.5739	Natural Establishment	north	present	No
Paradise River	Placentia	47.61765	-54.4317	Not established	south	absent	No
Patrick's Cove Brook	Placentia	47.03769	-54.1167	Not established	south	absentA	No
Peter's River	St. Mary's	46.76269	-53.6097	Not established	south	absent	Included
Petty Harbour River	Maddox	47.46464	-52.711	Natural Establishment	south	present	No
Pierre's Brook	Witless	47.28651	-52.8191	Natural Establishment	south	present	No
Pipers Hole Brook	Placentia	47.92677	-54.2747	Natural Establishment	south	present	Included
Placentia Sound River	Placentia	47.30561	-53.8688	Not established	south	absent	No
Point Verde	Placentia	47.22539	-54.0135	Natural Establishment	south	present	No
Popes Harbour River	Trinity	48.23782	-53.5589	Not established	north	absent	No
Port Union River	Trinity	48.49778	-53.0893	Not established	north	absent	No
Portugal Cove Brook	Trepassy	46.71427	-53.2734	Not established	south	absent	No
Princeton Brook	Bonavista	48.64994	-53.1142	Natural Establishment	north	present	No
Quidi Vidi Lake	Quidi Vidi	47.58098	-52.6903	Introduction	south	present	No
Quidi Vidi River	Quidi Vidi	47.58239	-52.6778	Introduction	south	present	No
Rattle Brook	Placentia West	47.43468	-54.8372	Not established	south	absent	No
Red Harbour River	Placentia	47.294	-55.0002	Not established	south	absent	Included
Red Head River	St. Mary's	46.94674	-53.8647	Not established	south	absent	No

Renews River	Renews	46.93392	-52.9526	Natural Establishment	south	present	Included
Rennie's River	Quidi Vidi	47.5779	-52.7159	Introduction	south	present	No
Robin Hood Ponds	Robinhood	48.39508	-53.3256	Natural Establishment	north	present	No
Robin's Ponds	Torbay	47.65719	-52.7619	Introduction	north	present	No
Rocky River	St. Mary's	47.22359	-53.5667	Introduction	south	present	No
Rushoon River	Placentia	47.35879	-54.9161	Not established	south	absent	Included
Ryans Brook	Conception	47.59827	-53.2842	Not established	north	absent	No
Ryders Brook	Trinity	48.23486	-53.9398	Not established	north	absent	No
Salmon Cove River	Trinity	48.39343	-53.3053	Not established	north	absent	Included
Salmon Cove River	Conception	47.78111	-53.1699	Natural Establishment	north	present	Included
Salmonier River	Lamaline	46.8734	-55.7743	Not established	south	absent	Included
Salmonier River	St. Mary's	47.16571	-53.4512	Natural Establishment	south	present	Included
Salt Cove Brook	Placentia	46.88012	-55.4216	Not established	south	absent	No
Sandy Harbour River	Placentia	47.69623	-54.3357	Not established	south	absent	Included
Seal Cove Brook	Conception	47.47188	-53.0819	Natural Establishment	north	present	Included
Shalloway Pond Brook	Placentia	47.29595	-53.9035	Not established	south	absent	No
Shearstown brook	Conception	47.59862	-53.2757	Natural Establishment	north	present	No
Ship Harbour Brook	Placentia	47.3509	-53.8756	Not established	south	absent	No
Shoal Harbour River	Trinity	48.18216	-53.9862	Natural Establishment	north	present	Included
South Dildo Brook	Trinity	47.51778	-53.5564	Introduction	north	present	No
South Dildo Pond	Trinity	47.49638	-53.5464	Introduction	north	present	No
South River	Conception	47.66743	-53.2586	Not established	north	absent	Included
South River	Conception	47.54098	-53.2724	Natural Establishment	north	present	Included
Southeast River	Placentia	47.2198	-53.9107	Natural Establishment	south	present	No
Spout Cove Brook	Conception	47.81678	-53.1268	Not established	north	absent	No
Spout River	Aquaforte	47.0102	-52.9263	Not established	south	absent	No
Spread Eagle River	Trinity	47.52659	-53.6074	Natural Establishment	north	present	Included
St. Lawrence River	St. Lawrence	46.93108	-55.3728	Not established	south	absent	No
St. Shores River	St. Mary's	46.66509	-53.625	Not established	south	absent	No
St. Shott's River	St. Mary's	46.63368	-53.5923	Not established	south	absent	Included
Stone Ducky Brook	Bay Bulls	47.32955	-52.8208	Natural Establishment	south	present	No
Taylor Bay Brook	Taylor	46.87576	-55.7112	Not established	south	absent	Included
Tides Brook	Mortier	47.13869	-55.2314	Not established	south	absent	Included
Topsail River	Conception	47.54046	-52.9195	Natural Establishment	north	present	Included

Topsail Road Ponds	Conception	47.52148	-52.9025	Introduction	north	present	No
Tors Cove River	Ferryland	47.21053	-52.8484	Not established	south	absent	No
Trinity Bay Ponds	Trinity	48.37472	-53.3891	Introduction	north	present	No
Trouty River	Trinity	48.32841	-53.4009	Not established	north	absent	Included
Upper Long Pond	Quidi Vidi	47.57113	-52.763	Introduction	south	present	No
Virginia Lake	Quidi Vidi	47.60678	-52.702	Introduction	south	present	No
Waterfall Brook	Placentia	46.9434	-55.3388	Not established	south	absent	No
Waterford River	St. John's	47.55464	-52.7112	Natural Establishment	south	present	Included
West Brook	Mortier	47.1695	-55.2467	Not established	south	absent	No
Whiteway's Pond	Torbay	47.66451	-52.7655	Introduction	south	present	No
Whiteway's River	Trinity	47.68489	-53.4704	Natural Establishment	north	present	No
Windsor Lake	Conception	47.59785	-52.7958	Introduction	north	present	No
Witless Bay River	Witless	47.27888	-52.8334	Not established	south	absent	No

Table 2.6.5 Landscape models that rank above the intercept according to AICc for the South dataset. The model coefficient is a measure of the relationship between the response (brown trout presence-absence) and the explanatory variable (s) in the model. The Odds Ratio is the exponential of the model coefficient and represents the odds that trout are present in an area under a certain explanatory variable's regime.

	MODEL COEFFICIENTS			ODDS RATIOS	
Variables	**Intercept**	**Distance to nearest introduction**	**Estuary**	**Distance to nearest introduction**	**Estuary**
intercept	-1.204				
estuary	-1.727		0.003		1.003
distance to nearest intro + estuary	-0.476	-0.005	0.004	0.995	1.004
distance to nearest intro	-0.037	-0.004		0.996	

Table 2.6.6 The predicted probability of brown trout establishing future rivers on the Burin Peninsula, using the top ranked south regression model (distance to nearest introduction and estuary size). Each river is west of the furthest point of invasion. The predicted probability is the likelihood of brown trout being present at the river in the future, where a value closer to 1 means higher likelihood. The Odds Ratio represents the odds that trout are present in an area under a certain explanatory variable's regime.

River	Latitude	Longitude	Distance Nearest Intro (km)	Estuary Area (km^2)	Predicted Probability	DISTANCE TO NEAREST INTRO		ESTUARY AREA	
						Coefficient	Odds Ratio	Coefficient	Odds Ratio
Scott's Barasway	47.369902	-55.285739	675	1.38	0.02	-1.59	0.39	-0.54	0.66
Hay Brook	47.345809	-55.297745	672	1.06	0.02	-1.57	0.36	-0.54	0.58
Brown's Harbour brook	47.275145	-55.309033	665	0	0.03	-1.54	0.35	-0.54	0.59
Brown's Harbour Pond	47.27147	-55.310211	664	7.5	0.03	-1.53	0.50	-0.51	0.59
Garnish	47.234748	-55.357725	658	3.2	0.03	-1.51	0.33	-0.53	0.58
Seal Cove Brook (Fortune)	47.191113	-55.435431	645	8.79	0.03	-1.44	0.32	-0.51	0.59
Piker	47.151418	-55.483006	641	10.91	0.03	-1.43	0.31	-0.5	0.58
Unamed (Fortune)	47.094887	-55.671379	626	1.18	0.03	-1.35	0.28	-0.54	0.61
Unamed (Fortune)	47.116861	-55.616157	630	6.43	0.03	-1.37	0.27	-0.52	0.59
Muddy Hole brook	47.099673	-55.667847	627	4.55	0.03	-1.36	0.26	-0.52	0.58
L'anse au Loup brook	47.092385	-55.695745	624	1.91	0.03	-1.34	0.26	-0.54	0.67
Grand Bank	47.101433	-55.749852	618	3.92	0.03	-1.32	0.26	-0.53	0.58
Little Barasway (Fortune)	47.109278	-55.629762	629	21.62	0.03	-1.37	0.26	-0.45	0.59
Fortune	47.076131	-55.828542	609	10	0.03	-1.27	0.25	-0.5	0.64
L'anse au Loup Barasway brook	47.092399	-55.680923	625	31.08	0.04	-1.35	0.25	-0.41	0.60
Point Crewe	46.948579	-55.9808	588	0	0.04	-1.17	0.24	-0.54	1.67
Point May	46.899007	-55.936031	581	2.09	0.04	-1.14	0.24	-0.54	0.61
High Beach River	46.889348	-55.893518	576	0.67	0.04	-1.12	0.24	-0.54	0.60
Salmonier River	46.8734	-55.774334	565	5.58	0.04	-1.06	0.23	-0.52	2.09
Taylor Bay Brook	46.875764	-55.71121	559	0	0.04	-1.03	0.22	-0.54	0.59
Lawn River	46.926809	-55.478641	537	28.31	0.05	-0.93	0.22	-0.42	0.60
Great Salmonier River (Lewin's Cove)	47.059686	-55.215747	487	3.4	0.06	-0.69	0.21	-0.53	0.58
Grand Beach	47.13738	-55.503182	639	239.46	0.08	-1.42	0.21	0.51	0.58
Frenchman's Cove brook	47.218484	-55.404605	653	290.61	0.09	-1.48	0.20	0.74	0.58

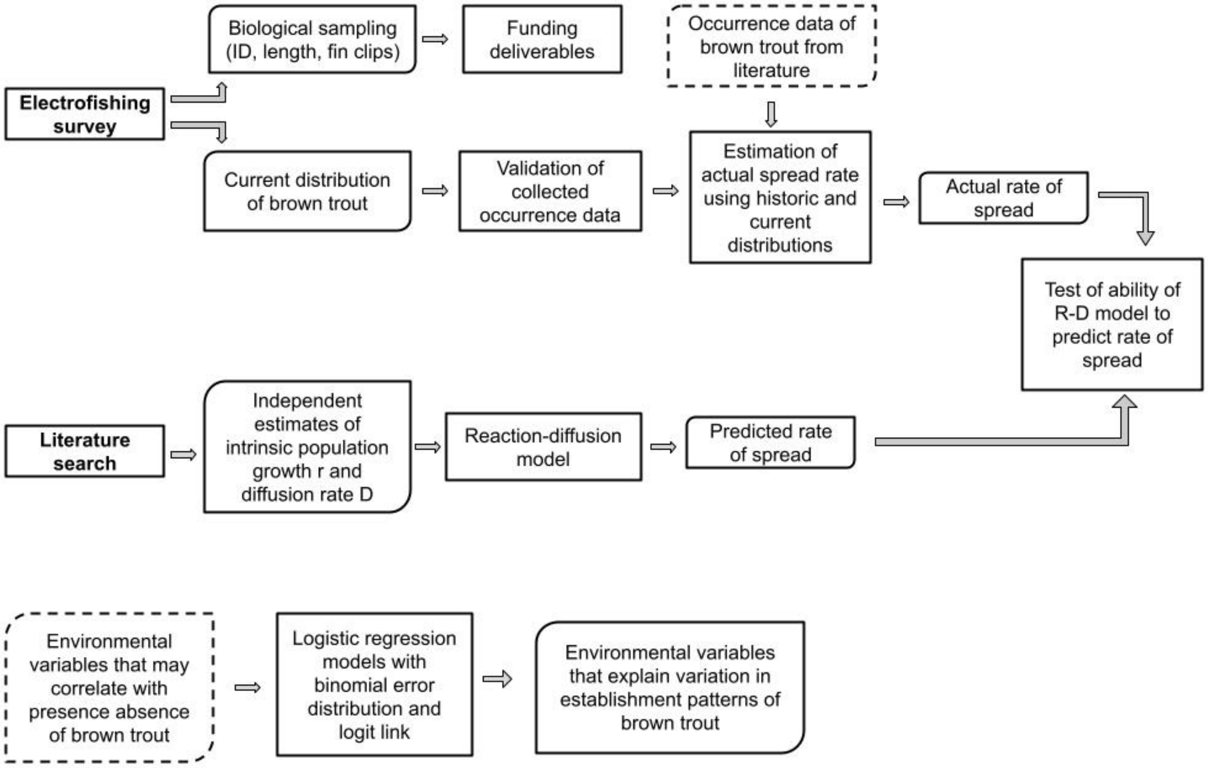

Figure 2.6.1. Methodological overview of chapter 2. Using contemporary occurrence data (Porter et al. 1974) and historic distribution data (Maitland 1887, Hustins 2007, Westley and Fleming 2011) from past research in Newfoundland, we were able to estimate the actual rate of spread of brown trout in Newfoundland. We used this to test the ability of a Reaction-Diffusion model, parameterized using independent values from the literature, to predict the spread. We then analysed the environmental variables that explain establishment dynamics using local abiotic, biotic (Porter et al. 1974) and landscape-level environmental data (Westley and Fleming 2011).

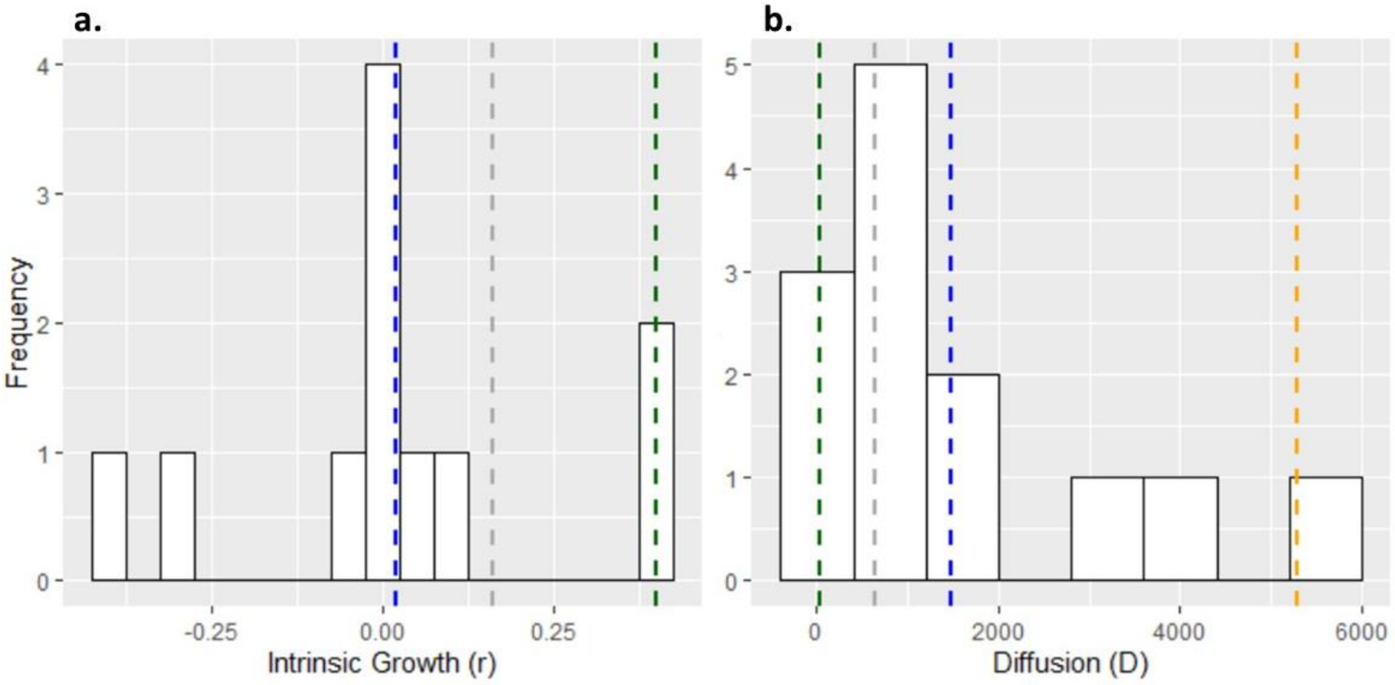

Figure 2.6.2 Results of the literature search for a. intrinsic growth rate values and b. diffusion parameter values. The values for intrinsic growth r in panel a. are the 1) the mean across studies in blue, 2) the maximum across all studies in green, and 3) the mean of all the positive values in grey. The values for diffusion in panel b. correspond to 1) the minimum in green, 2) the mean in grey, 3) the median in blue and 4) the maximum of the distribution across all studies in yellow.

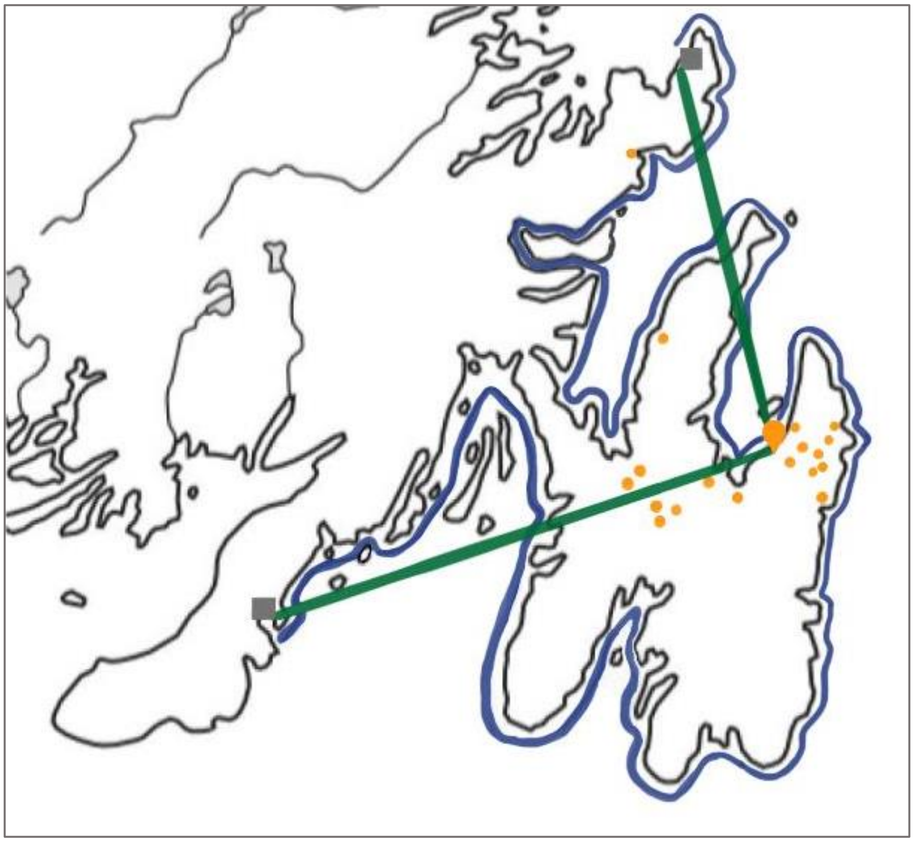

Figure 2.6.3. Methods of calculating actual spread as the mean value of the distances between the midpoint (orange location icon) of the introduction points (orange points), to the two furthest locations of brown trout presence (grey squares). The actual spread distance was measured radially (green lines) and along the coast (blue lines).

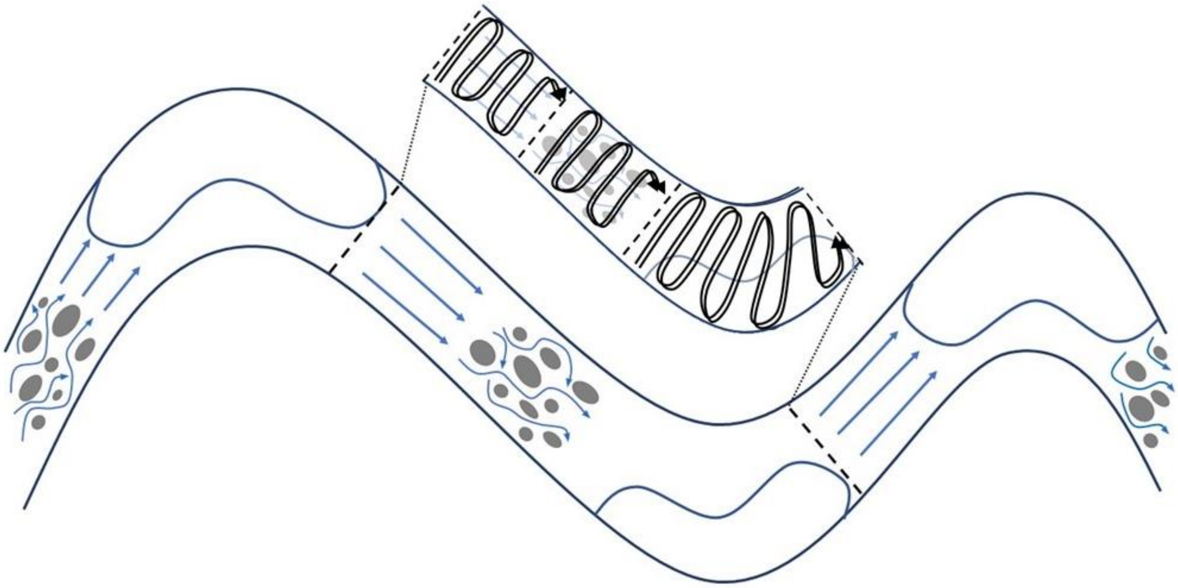

Figure 2.6.4 Salmonid stream sampling design. We designated 2-5 stations at each river, each of which contained several river habitats: runs (straight blue lines representing fast unbroken flow), riffles (curved arrows, broken flow around rocks) and pools (white polygons representing deeper, slower flow). After installing block nets at the upstream and downstream edges of the station, we conducted two-pass electrofishing using a backpack electro-fisher to estimate presence-absence and relative abundance of salmonids.

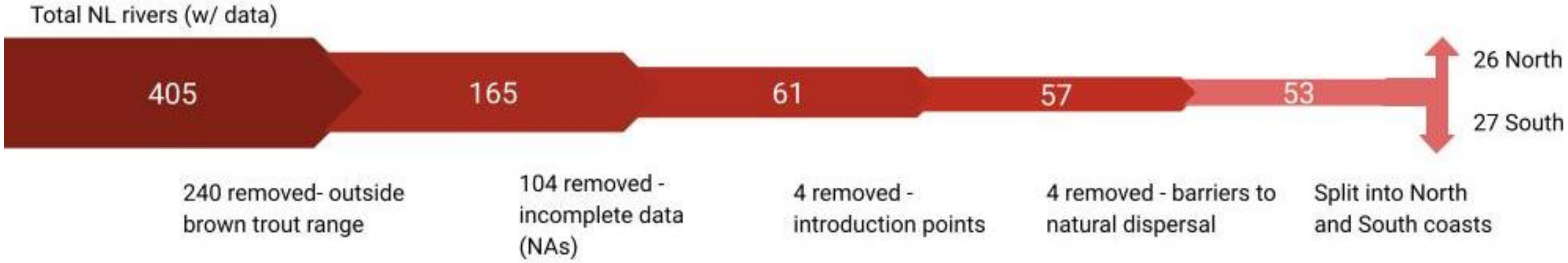

Figure 2.6.5 Visualisation of the preparation of data prior to running the generalized linear models with binomial error and logit link for establishment patterns. Only rivers where natural establishment was possible were included in the analyses, thus we removed those outside the invasion range, where brown trout were introduced, and absences where it was likely barriers prevent dispersal. Finally, we split the datasets by coast to analyse whether different environmental variables were responsible for explaining presence-absence between the north and south invasion pathways.

CHAPTER 3: Summary and Discussion

3.1 Predictions of spread and explanation of establishment patterns using a case study

Species undergo range shifts as a response to changing environmental conditions (Gaston 2009) and as they evolve new adaptations (Tomiolo and Ward 2018), however these shifts are increasing in frequency and magnitude due to large scale changes in climate and anthropogenic activity (Gaston and Gaston 2003). These range shifts are intensified by human-mediated introductions of species outside of their natural ranges, which if successful, can result in the establishment and spread of invasive populations that have the potential to cause irreversible impacts on the receiving ecosystem (Jeschke 2014). Though the components of invasion have been extensively studied, our ability to make predictions of spread and explain establishment of invasive species remain highly context dependent.

Spread is defined as an expansion in the geographic range of a species and is a function of their species-specific dispersal mechanism and their interaction with the local environment (Johnson et al. 2006). Once a species spreads to a novel area, their establishment of self-sufficient populations depends on their ability to overcome environmental barriers to successfully grow and reproduce (Richardson et al. 2000). There is a need in invasion ecology for simple models that can accurately predict an invasion's rate of spread and explain what environmental variables can limit or facilitate the establishment of non-native species. Only then can we begin to disentangle the mechanisms that interact to produce a successful invasion. Our study used a unique combination of introduction history, establishment and spread data to understand the complex dynamics of an anadromous invader in a boreal ecosystem. We integrated a classic model of spread rate and correlative statistical models of establishment using extensive brown trout occurrence and environmental data from the Island of Newfoundland.

First, we tested a classic reaction-diffusion model's ability to predict spread by comparing it to observed spread velocities from the system. We hypothesized that the model would be able to make predictions of spread comparable to what was observed, using only population-level characteristics of brown trout. We parameterized the model with brown trout demographic and dispersal data from a literature search and obtained a range of predicted spread values. We then compared these predictions to the observed rate of spread estimated using historic and current occurrence data, obtaining the following results:

a. The observed spread of brown trout in Newfoundland is relatively slow compared to brown trout invasions elsewhere
b. The coastal observed spread is on the lower end of range of predictions made by the reaction-diffusion model
c. The model predicts brown trout spread similar to the observed spread rate only when population growth and diffusion are low

The reaction-diffusion model's lowest predictions of velocity of spread, which is in the range of observed spread, stem from the smallest population growth and diffusion parameter values. This may suggest that there is likely low population growth and slow (or short-distance) dispersal of brown trout in this system. That spread in Newfoundland is slow is logical; being an island with relatively low species richness and low productivity rivers, there are fewer resources for invaders than on a temperate mainland region. The invasions of brown trout in New Zealand and in the Kerguelen Islands were arguably more successful, as these island's watersheds are larger and more productive and their location in the southern hemisphere means a lacks native salmonids whose presence could potentially exclude trout (Townsend 1996). The range of predictions made by the reaction-diffusion model is wide and many of the moderate and higher predictions of spread vastly overestimate empirical spread in Newfoundland, counter to our hypothesis. This indicates that many of the parameter values we obtained from the literature are not applicable to the system or else brown trout spread in Newfoundland violates key assumptions made by the model. The reaction-diffusion model has made accurate spread predictions for the small cabbage white butterfly (*Pieris rapae)* invasion of North America, the muskrat (*Ondatra zibethica*) invasion of Europe (Andow et al. 1990), and the invasive grass *Microstegium vimineum* in the United States (Huebner 2010), and was adapted to measure the range shifts of butterflies northward under climate change (Leroux et al. 2013). However, it may also overestimate spread if the dispersal kernel of the population is non-normal (Kot et al. 1996), if intrinsic population growth doesn't take into account density-dependence (Hastings et al. 2005) or stage-structure (Neubert and Caswell 2000), or if there is presence of an Allee Effect (Hurford et al. 2006). Regardless, while the lowest predictions made by the model accurately describe the slow observed spread in the Newfoundland system, more precise parameterization of the model is needed to disentangle the drivers behind these predictions and how they fit this particular system.

Second, we ran a series of logistic regression models to determine how several environmental variables at the river and landscape level may explain the variation of brown trout presence-absence data in Newfoundland. We divided the predictors into three categories: abiotic (pH, conductivity, turbidity and calcium content), biotic (Atlantic salmon presence-absence), and landscape (watershed area, maximum relief, estuary size, distance to nearest introduction point and distance to original introduction point). The following results did not support our hypotheses:

i. There was evidence that stream pH, water conductivity, turbidity or calcium content were not correlated with brown trout presence/absence
ii. There was evidence that Atlantic salmon presence was not correlated with brown trout presence/absence
iii. There was evidence that watershed area, maximum watershed relief or distance to original introduction point were not correlated with brown trout presence/absence

We tested a series of abiotic environmental variables, none of which correlated with brown trout presence, which could indicate their low relative impact in the system or else that their influence was not detectable using the scale and resolution of our data. Studies differ in the method they use to measure water chemistry variables, as well as the temporal and spatial resolution of their sampling events (Hesthagen et al. 1999, de la Hoz Franco and Budy 2004, Fernandez et al. 2017). Brown trout are highly adaptable salmonids that generally have wide tolerance limits, thus perhaps abiotic environmental variables are important to determine trout presence in a region, they may not determine presence or absence at the river level (Cushman and McGarigal 2004). That Atlantic salmon had no effect on the occurrence patterns of brown trout was contrary to our hypothesis that according to the theory of Limiting Similarity, the presence of Atlantic salmon, a closely related species to brown trout, would exclude the latter (Abrams 1983, Adams 1999). However, within rivers, studies have demonstrated that salmon and trout tend to spatially segregate enough to allow coexistence at smaller densities (Gibson and Cunjak 1986), while there is more spatial overlap between brown trout and brook charr (*Salvelinus fontinalis*). Contrary to our findings, another study found that watershed area correlated with the establishment of brown trout, but only when combined with conductivity to act as a proxy for watershed productivity (Westley and Fleming 2011), thus our analyses reveal that watershed area alone may not influence establishment, which is contrary to the Theory of Island Biogeography. As well, distance to the original introduction point, St. John's, was likely not an important predictor of establishment as the nearest established populations are the most likely to act as a source of migrants to colonize new rivers (Launey et al. 2010). Overall, while landscape influences migration and establishment, the high acidity and low productivity of Newfoundland rivers is hypothesized to be a important factor limiting the available food resources, heightening competition and thus, limiting establishment on the island (Westley and Fleming 2011).

While we did not find that any of the abiotic or biotic and three of the landscape environmental variables showed any evidence of influencing brown trout establishment, the following results were in support of our hypotheses:

i. There was weak evidence that estuary size was positively correlated with brown trout presence/absence

ii. There was weak evidence that distance to nearest introduction point was negatively associated with brown trout presence/absence

iii. The ability of the environmental variables to explain establishment patterns differed between the coastal pathways of invasion (i.e., North vs South spread)

Estuaries are used by anadromous fishes as a transition zone in which to undergo the physiological changes that allows them to adjust from freshwater to saltwater habitats and vice versa (Björnsson et al. 2011). Brown trout also spend a large portion of their time while in the ocean feeding in estuaries (Etheridge et al. 2008), which are productive and shallow waters that provide ample cover from predators (Pritchard 1967) and an osmoregulatory refuge from cooler saltwater during the winter (Jonsson and Jonsson 2011), making them an important habitat for brown trout populations. The other important landscape variable, distance to nearest introduction point, determines the number of propagules reaching a new river and thus is an indicator of brown trout presence. Overall, it seems that brown trout are more likely to establish a river that is close to one with a self-sufficient population that provides migrators, and one that has a large estuary to support their physiological and dietary needs. Other landscape factors not measured in our study, including river mouth accessibility and coastal characteristics may also be influential in determining the direction and rate of migration (Launey et al. 2010). As aquatic invaders that use anadromy to spread while in the ocean, brown trout must navigate a matrix of unsuitable habitat (land) interspersed with small sections of invadable waterbodies (rivers). Thus, the landscape plays an important role in determining where and how anadromous can migrate, as well as the likelihood that enough fish will reach a given area to allow for colonization. Our result that the environmental predictors differed in their ability to explain establishment along the different coasts suggests the complexity of the different mechanisms that structure invasions. Often non-native populations may be faced with different environmental conditions depending on where they were introduced or the direction of their spread (Macgregor et al. 2021). Some landscapes are more conducive to navigating and establishing populations (Labonne et al. 2013) or the introduction history of the area results in a higher propagule pressure for establishment that moderates the importance of the landscape. An area with many established populations may have migrants from several directions, increasing the likelihood of overcoming environmental barriers of establishment. The results of our study indicate that landscape environmental factors contribute to establishment patterns, though the role of other mechanisms in moderating them are still unclear. Important landscape factors may be those specific to the biology of the invader, such as estuary size, or may be more general to all invasions, such as the distance to the nearest introduction point. Finally, the environmental variables that affect establishment may differ depending on the direction of spread or be moderated by the introduction history.

The slow spread and limited establishment of brown trout may indicate their interaction within this system. Slow spread suggests that there may be few individuals straying to new areas, which could decrease their ability to find mates and establish spawning populations in new rivers. Establishment in this system is limited by the introduction history and landscape factors, which moderates the direction of movement and number of strayers. As well, brown trout likely overlap significantly with brook charr, which are likely present in most watersheds in Newfoundland and represent the potential for both habitat competition (Fausch and White 1981) and hybridization (Poulos 2019, Lantiegne 2021). Thus, if there are strict conditions required for establishment, limited resources and mates due to the presence of local brook charr, and it takes many generations for enough strays to disperse in the environment, the result is slow spread, limited establishment opportunities and overall, a very gradual biological invasion on the Island of Newfoundland.

3.2 Limitations, future directions, and implications

Mathematical models must be parsimonious yet remain complex enough to be representative in order to make inferences about biological phenomena (Mollison et al. 1986). The act of simplifying a biological system and attempting to make predictions can allow us to elucidate important mechanisms and indicates directions that future models should take to improve results while remaining parsimonious. Like many species, demographic and dispersal data of brown trout is readily available for populations within their natural range (concentrating heavily in the Nordic countries and Scotland; such as Berg and Berg 1987, Elliott 1987, Bagliniére et al. 1989, but see Grossman et al. 2017). However, species transplanted from their native range face a diversity of demographic and environmental challenges, and so may adapt their growth and reproductive strategies in a way that would make predictions based on native population parameter overestimate non-native spread (Cooke 2016). The most straightforward way to counteract this is to parameterize the model using only values from invasive brown trout populations, or from the specific system being studied. As well, assessing the proportion of anadromous individuals in this population may help untangle the mechanism of spread, as anadromy is hypothesized to drive spread but particularly high mortality while in the ocean (including known targeted angling of larger individuals in estuaries) may opposingly reduce the spread rate. However, the more specific to the system we make this model (i.e., parameterization using values from Newfoundland populations), the less transferable this model's outputs become to other brown trout invasions. Alternatively, one may use more robust methods of estimating intrinsic growth and diffusion coefficient such as incorporating the stage-structure (Caswell et al. 2003) or density dependence of populations (reviewed by Brook and Bradshaw 2006). With finer resolution occurrence data, we can also estimate local spread patterns use local spread in several directions to make an average spread rate, taking into account the variation in spread rate throughout a heterogeneous landscape (Shigesada et al. 1987, Havel et al. 2002). Regardless, it seems that obtaining precise predictions of spread from the reaction-diffusion model likely requires either more complex or system-specific parameterization.

Like all studies that use statistical models, we are limited to making inferences only about the predictors for which we have data, however the value of a null result should not be discounted. There is currently a lack of agreement on which environmental variables affect the distribution of salmonids, which could be a result of the often confounding temporal, spatial and environmental variability of occurrence datasets (Anderson and Cribble 1998). However, that our study ruled out some of the most obvious environmental variables indicates that establishment patterns may be more complex than we thought, or else may only be detectable at finer temporal or spatial resolutions. Future studies should examine brown trout establishment patterns over several biological invasions to determine which environmental variables are ubiquitous across them and which are more regionally influential. Further analyses of establishment should categorize the influence of environmental variables into those that are specific to the study organism, and those that are more generally applicable to a range of invaders. Establishment success may also be highly dependent on the traits of the originally imported stock (Moodley et al. 2013). Thus, a comprehensive comparison of the genetic and phenotypic composition of donor populations with the invasive populations could reveal the adaptations that allow some to succeed and others to fail (O'Toole et al. *in press*). Finally, a fine scale temporal study of an uncolonized patch near an established one could reveal the variability of populations attempting to colonize a new area, and the number of individuals needed to establish a self-sufficient population. We suggest that comparative studies of establishment across biological invasions combined with the analysis of environmental and demographic data throughout the establishment process will allow us to identify the specific environmental mechanisms that determine the colonization of non-native species.

My study is unique in that it combines empirical data with independent parameterization, a classic mathematical model and statistical models in order to elucidate the importance of invader characteristics in predicting spread and of environmental variables in determining establishment patterns. Since establishment is required for spread to happen and once introduced, the opposite is true, future studies should analyse invasion holistically in order to infer not only specific processes but also broader scale mechanisms that may influence the success of invasion as a whole. In order to measure the interactive effects of spread and establishment, future research should run computer simulated invasions (e.g. cellular automaton model, see Marco et al. 2002) in various environments and at different scales to determine how varying the rate of spread of an invasion drives the establishment success. Our study is a step towards understanding how the characteristics of the invader and the receiving environment interact to produce a successful, but slow invasion. Only once we clearly identify the mechanisms through which biological invasions function can we begin to mitigate their effects and prevent future non-native species introductions.

Darwin (1859) has been attributed with declaring that it is not the strongest nor the most intelligent species that survive, but those that are most adaptable. Indeed, in this time of unprecedented climatic change, if a species cannot react or adapt to changing environmental conditions, it will not survive and will likely be replaced by those who can. A century after Darwin, Elton made observations about the larger implications of biological invasions. Since Elton published those observations, the number of biological invasions has increased in all environments and across all taxonomic groups (Butchart et al. 2010), and we have only just begun to understand their impacts on native biodiversity. In this search for knowledge and for ecological solutions, it is important to remember that no invasion is too small to study. The alternative, allowing the results of anthropogenic activity to run rampant without interference, is too frightening to even consider.

3.3 References

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