

# Landscape, demographic, and dispersal parameters influence the spread and establishment dynamics of an aquatic biological invasion

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## Research Article

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# Abstract

Human-mediated species introductions have provoked innumerable biological invasions, which are contributing to the biotic homogenization of global flora and fauna. Despite extensive research, we lack simple methods of predicting how and where an introduced species will spread and establish. We predict that spread can be modelled simply using the characteristics of the invading population, while 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, we fit a reaction-diffusion model to brown trout population data to predict expected spread and test these predictions against extensive occurrence data. Next, we use statistical models to assess the influence of several environmental variables on brown trout establishment patterns. We find that observed spread in Newfoundland is slow and that it lies on the lower end of the range of predictions made by the reaction-diffusion model. Two landscape-level environmental variables explain establishment patterns, but their influence is likely moderated by other factors. The wide range of predictions made by the model point to the importance of using population-specific parameterization and the intricate interplay of environmental variables that influence establishment illustrates the need to consider both landscape factors that are generally applicable across biological invasions, and those that are more specific to the ecology of the invader. Our study contextualises the mechanisms that contribute to a slow aquatic invasion and reveals that studies need to integrate a variety of methods to elucidate the processes governing invasions.

# Introduction

Understanding the mechanisms governing the distribution of species in space and time is essential to ecology (Hutchinson, 1959; 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 (each can be modified by humans): 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). Though a biological invasion can be broken into these three components, it is often difficult to disentangle them (Catford et al. 2009). What is more, the success of these components 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). Understanding the relationship between invader and ecosystem 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).

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. 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). The reaction-diffusion model, a partial differential equation commonly used in invasion ecology, uses 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 spatially explicit and is simple enough to be 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), but the framework is likely relevant to aquatic ecosystems.

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). 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). These 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 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 influence the establishment of aquatic invasive populations illustrates the need to not only ask where an invader is spreading but also how they are able to establish there.

Here, we integrate modelling and empirical data to study the rate of spread and the mechanisms of establishment of a pervasive invader. Brown trout (*Salmo trutta*) have been introduced globally and their life history variability makes predicting invasion and the accompanying ecological impacts complex (see review in Buoro et al. 2016). Using the introduction of brown trout to the Island of Newfoundland as a case study, 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 it 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 differs along two coastal pathways of 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 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 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 (*Salmo salar*), will negatively correlate with brown trout establishment (Bietz et al. 1981; Korsu et al. 2007), and vi) 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 more dramatic marine environmental differences than implied by latitude, and different trout introduction histories and established populations that are genetically different (O'Toole et al. 2021), we hypothesize that the brown trout invasion has split into two pathways, with differential establishment dynamics. We then predict that v) different environmental variables will be responsible for explaining establishment patterns between the north and south coasts.

## Methods

### Study System

The introduction history of non-native salmonids on the Island of Newfoundland is well-documented (Westley and Fleming 2011), 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 island (Protected Areas Association of Newfoundland and Labrador 2008), making it both an ideal landscape for freshwater studies, and a potentially hospitable place for an anadromous invader (one that uses both freshwater and marine environments over the course of its life-cycle). 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 via migration through the marine environment. 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 2013).

## 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:

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

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:

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

where the velocity of spread  $V$  is estimated using only the population growth rate  $\alpha$  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 examined spread (and later establishment) at the watershed scale because while spread in fresh water occurs within watersheds, large scale 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  $\alpha$  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. Specifically, we searched Google Scholar and the Memorial University Centre for Newfoundland Studies sites 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:

$$r = \log \frac{N_{t+1}}{N_t} \quad (3)$$

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 in aquatic systems are commonly calculated from swimming speeds (Grosholz et al. 1996) or more generally from 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. We searched Google Scholar and the Memorial University Centre for Newfoundland Studies 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  $\text{km}^2/\text{year}$ ) from converting study estimates of mean displacement (in  $\text{km}/\text{day}$  or  $\text{km}/\text{hour}$ ) or estimates of swimming speed (in body lengths per second or  $\text{m}/\text{s}$ ). Our search obtained a variety of studies on brown trout

migration along the freshwater 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; Eldøy et al., 2015; Veinott et al., 2012) 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 equation no. 2 (Table 1). We used a range of values of  $r$  and  $D$  to capture the natural range of variability observed in the literature. 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. As a type of sensitivity analysis, 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), Fisheries and Oceans Canada (DFO) angler's guide (DFO 2020), and our own sampling. 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 (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. 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 brown trout generally follow the coast while migrating in the ocean (Labonne et al. 2013; Kristensen et al. 2019).

To analyse the environmental correlates of brown trout establishment and to verify whether brown trout have spread to new watersheds since Westley and Fleming's study in 2010, 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 using barriers nets, each of which included runs, riffles, and pools to control for the differences in trout, charr and salmon habitat use. We used a Smith- Root LR-24 backpack electro-fisher to conduct two-pass depletion at each station. We used counts of salmonids caught by electrofishing to estimate occurrence and relative abundance.

## **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) were included in the analyses, a total of 165 rivers (Online Resource 1). We extracted data on natural and human made barriers occurring on rivers in eastern Newfoundland (Porter et al. 1974). An impassable barrier to brown trout dispersal was defined as more than 5m in height, based on adult trout's ability to jump over 3m high on average (Reiser and Peacock 1985), 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). We removed 11 rivers where natural establishment was not possible due to such barriers. As well, any sites where brown trout were established through human-mediated introductions (n = 15 rivers) were not included in the analyses. Finally, we removed any rivers from the analyses that had incomplete environmental data in Porter and colleagues' dataset (1974; n = 86 rivers). In the end, we were left with 53 rivers in the analysis (Online Resource 2).

Based on previous work on salmonids (i.e. 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. Brook 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 were 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 1 panel a). 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 at 53 rivers within the invasion range. 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). We used Variance Inflation Factor Analysis (*car* package; Fox et al. 2021) to test for multicollinearity among covariates. 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 estimated how long it will take brown trout to spread to key areas on the Island of Newfoundland. All mathematical and statistical models were run in the statistical software R (R Development Core Team 2021).

## Results

### Predicting the rate of spread using a reaction-diffusion model

Our literature search for parameter values revealed 11 studies that fit the search criteria for intrinsic population growth and 15 studies for diffusion. For intrinsic growth (Online Resource 3), 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. The minimum, mean, median and maximum of the distribution of diffusion values (Online Resource 4) were  $D_{min} = 27.1 \text{ km}^2/\text{yr}$ ,  $D_{mean} = 630.5 \text{ km}^2/\text{yr}$ ,  $D_{median} = 1485.5 \text{ km}^2/\text{yr}$ ,  $D_{max} = 5292.5 \text{ km}^2/\text{yr}$ , respectively.

Using three values of intrinsic population growth (i.e.  $r$ ) and four values for the coefficient of diffusion (i.e.  $D$ ) 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, Online Resource 5). 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 4.4 km/year (north = 3.4, south = 5.4), Table 2. Of the 14 rivers we sampled in 2020 that overlapped with Porter et al.'s (1974) dataset for presence absence of brown trout, only one, Renew's 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. Other recent studies ((Westley and Fleming 2011; Warner et al. 2015) confirmed the presence of brown trout in Renew's River, therefore we use this river as a presence point.

## Analysing the environmental correlates of establishment by coast

Brown trout have been observed in 81 of the 165 watersheds (49%) that are located within the brown trout's current invasion range. Of these, brown trout have 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. Fifty-three rivers from different watersheds within this range had complete environmental data and were used in the establishment analyses.

There were a broad range of abiotic freshwater variables, though they did not vary greatly between the North and South coasts (Table 3). The mean water conductivity was 31.5  $\mu\text{mhos/cm}$  (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  $\text{km}^2$  (north = 63.5, south = 140). Twenty-nine 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 first introduction location in St. John's was 268 km (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 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 included the predictors estuary size and distance to nearest introduction point, and explained 38% of the variation in establishment patterns. Estuary, and distance to nearest introduction as separate models made up the second and third ranked models, and explained 24% and 18% of the variation, respectively. The odds of establishment in this top ranked model of south coast river 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, Online Resource 6). Based on the mean observed coastal spread from the 1880s to present, we calculated that it would take another 33 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). In approximately 23 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 103 years of spread for brown trout to reach the Conne River (47°47'40.5"N 55°49'39.9"W) and 206 years to reach Cape Ray (47°37'12.9"N 59°18'24.6"W) on the southwestern coast of Newfoundland.

## Discussion

Though biological invasions are 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. We observed much slower rates of brown trout spread on the Island of Newfoundland than the majority of predictions made by the reaction-diffusion model. 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.

## Predicting the rate of spread using a reaction-diffusion model

Our data suggests that brown trout on the Island of Newfoundland are spreading at an average rate of 4.4 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 have naturally established at least 56 watersheds in 125 years (0.4 watersheds per year; Westley and Fleming 2011), compared to a rate of 0.8 watersheds per 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. 2019). 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). The presence of other salmonids in Newfoundland waters could also limit brown trout's spread. For example, in New Zealand and the Kerguelen Islands, non-native brown trout are 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 natural histories 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 that we observed.

The simple reaction-diffusion model's lowest predictions of spread were comparable to those observed in our study system. Thus, the 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, producing predictions that disagree (Purchase et al. 2005) 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 (i.e., distribution with a heavy positive tail), 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 an 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 inhospitable 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 migration while in fresh water as well as marine and estuarine dispersal. 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. 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. 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; Labonne et al. 2013). 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 provide trout with feeding opportunities and a transition zone in which to undergo the physiological changes required when entering or leaving a saline marine environment (McDowall 1976). 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 and overall, landscape factors that influence invasion dynamics 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.

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 (2021). Launey and colleagues (2010) 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. 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 4.4 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. 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, such as ability to hybridize (Lantiegne and Purchase 2021). 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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## Declarations

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## Tables

**Table 1** Rate of spread  $V$ , obtained from 12 combinations of literature sourced intrinsic growth rate  $r$  values and diffusion  $D$  values.

**Table 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 along each coast.

**Table 3** Average measurements of the environmental variables used as explanatory variables in the series of generalized linear models. 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 occurrence (presence-absence) of brown trout.

**Table 4** Subset of AIC outputs for a series of generalized linear models obtained for north and south datasets.  $K$  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.

**Table 1**

PARAMETERS		MODEL OUTPUT
Intrinsic growth $r$ $\text{yr}^{-1}$	Diffusion $D$ $\text{km}^2\text{yr}^{-1}$	Predicted Velocity $V$ $\text{km yr}^{-1}$
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

	River/ Location	Latitude	Longitude	RADIAL		COASTAL	
Origin	Coastal midpoint	47.522969	-52.969084	Distance (km)	Spread rate ( $\text{km/yr}^{-1}$ )	Distance (km)	Spread rate ( $\text{km/yr}^{-1}$ )
North	Princeton Brook	48.659278	-53.115750	121	1.03	394	3.37
South	Little Salmonier	47.071158	-55.179675	174	1.49	628	5.37
				<b>radial mean</b>	<b>1.26</b>	<b>coastal mean</b>	<b>4.37</b>

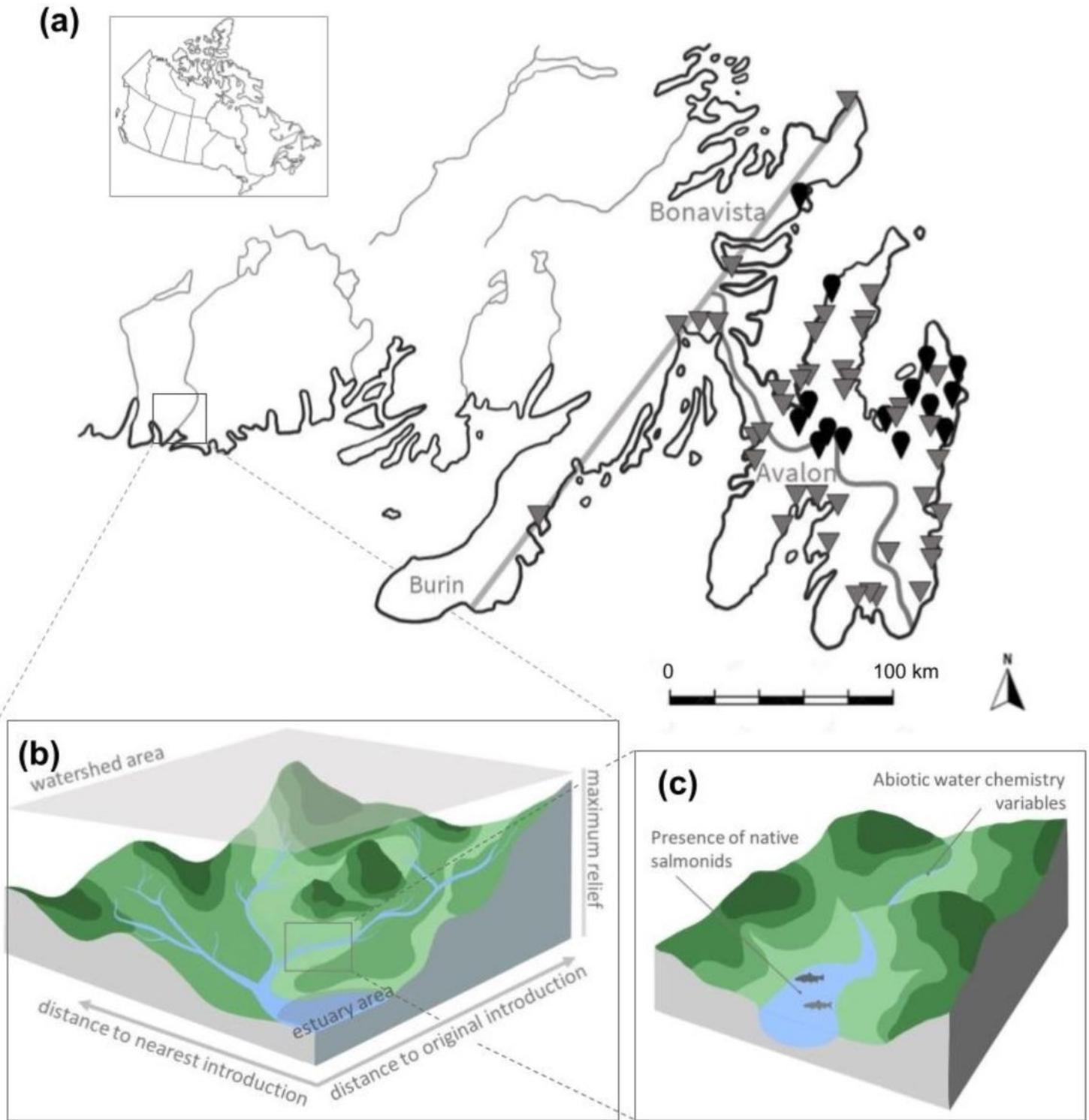
Table 3

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 <i>μmhos/cm</i>	31.14 (4.9)	35.9 (27.5)	28.05 (9.7)	29.0 (9.5)	31.53 (18.3)
	Turbidity <i>JTU</i>	0.73 (0.2)	0.90 (0.8)	1.30 (1.0)	1.84 (1.8)	1.25 (1.1)
	Calcium <i>ppm</i>	1.11 (0.4)	1.48 (1.3)	1.55 (1.9)	1.23 (0.4)	1.43 (1.4)
Biotic	Salmon rivers <i>count</i>	7	20	20	6	53
Landscape	Watershed area <i>km<sup>2</sup></i>	55.43 (24.1)	66.35 (28.7)	114.95 (96.8)	223.33 (284.7)	101.02 (118.9)
	Watershed maximum relief <i>m</i>	248.0 (79.3)	254.95 (43.4)	263.6 (59.7)	292.67 (64.6)	261.57 (57.2)
	Distance to original introduction <i>km</i>	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 <i>km</i>	36.57 (49.1)	43.8 (45.1)	386.35 (268.1)	193.0 (121.8)	189.0 (234.4)
	Estuary size <i>ha</i>	43.48 (107.8)	13.15 (23.7)	52.97 (149.7)	359.01 (507.3)	71.34 (213.5)

Table 4

Coastal Pathway	Model parameters	K	AICc	Delta AICc	AICc Wt	LL	R <sup>2</sup>	
NORTH	<b>- ABIOTIC -</b>							
	intercept	1	33.06	0	0.29	-15.45	0	
	<i>calcium</i>	2	34.6	1.54	0.14	-15.05	0.04	
	<i>turbidity</i>	2	35.07	2	0.11	-15.28	0.02	
	<i>conductivity</i>	2	35.13	2.07	0.1	-15.31	0.01	
	<i>pH</i>	2	35.32	2.26	0.09	-15.41	0	
	<b>- BIOTIC -</b>							
	intercept	1	33.06	0	0.75	-15.45	0	
	<i>salmon presence-absence</i>	2	35.31	2.24	0.25	-15.4	0.01	
	<b>- LANDSCAPE -</b>							
	intercept	1	33.06	0	0.2	-15.45	0	
	<i>estuary area</i>	2	34.11	1.04	0.12	-14.8	0.07	
	<i>watershed area</i>	2	34.53	1.46	0.09	-15.01	0.05	
	<i>distance to nearest introduction point</i>	2	35.26	2.2	0.07	-15.38	0.01	
	<i>watershed relief</i>	2	35.31	2.25	0.06	-15.41	0	
	<i>distance to original introduction</i>	2	35.36	2.29	0.06	-15.43	0	
	SOUTH	<b>- ABIOTIC -</b>						
		intercept	1	30.26	0	0.31	-14.05	0
		<i>pH</i>	2	31.94	1.68	0.13	-13.71	0.04
		<i>calcium</i>	2	32.41	2.15	0.11	-13.94	0.01
		<i>turbidity</i>	2	32.47	2.21	0.1	-13.97	0.01
<i>conductivity</i>		2	32.56	2.31	0.1	-14.02	0	
<b>- BIOTIC -</b>								
intercept		1	30.26	0	0.65	-14.05	0	
<i>salmon pa</i>		2	31.51	1.26	0.35	-13.5	0.06	
<b>- LANDSCAPE -</b>								
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	
<i>watershed area</i>		2	30.74	4.43	0.01	-13.11	0.11	
<i>watershed relief</i>		2	31.5	5.19	0.01	-13.49	0.06	
<i>distance to original introduction</i>		2	31.82	5.51	0.01	-13.65	0.05	

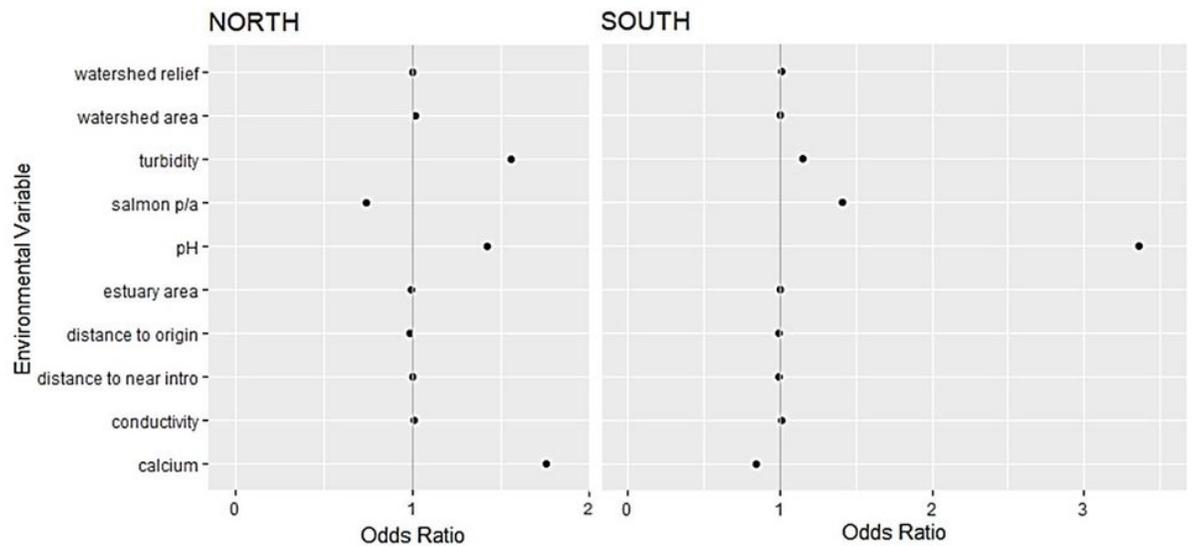
## Figures



**Figure 1**

Conceptual overview of the study. Brown trout were introduced to the Island of Newfoundland (black locator symbols; panel a) and have since spread westward, and have naturally established new rivers (grey triangles). The front of the invasion (light grey line) is now located along the Burin and Bonavista peninsulas. 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) The establishment statistical analyses only considered rivers East of the invasion front and split the datasets between north and south coasts along the dark grey boundary line dividing the Avalon. Figure created using Google Draw and MS PowerPoint



**Figure 2**

We ran a series of 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. Figure created in the statistical software R (R Development Core Team 2021)

## Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [OR1RiversDatasetFull14Mar2022.pdf](#)
- [OR2EstablishmentAnalysesRivers14Mar2022.csv](#)

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