



Landscape factors that shape a slow and persistent aquatic invasion: brown trout in Newfoundland 1883–2010

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ABSTRACT

Aim We investigated watershed-scale abiotic environmental factors associated with population establishment of one of the 'world's 100 worst alien invaders' on a temperate Atlantic island. Within the context of the conservation implications, we aimed to quantify (1) the early history and demographics (numbers and origins) of human-mediated brown trout (*Salmo trutta*) introductions, (2) the current distribution of established populations, and (3) the watershed-scale environmental factors that may resist or facilitate trout establishment.

Location Island of Newfoundland, Canada.

Methods We combined field sampling with historical and contemporary records from literature to assemble a presence–absence and physical habitat database for 312 watersheds on Newfoundland. Probability of watershed establishment was modelled with general additive ANCOVA models to control for nonlinear effects of propagule pressure (i.e. the distance to and number of invasion foci within a biologically relevant range) and model performance based on AIC.

Results Between 1883 and 1906, 16 watersheds were introduced with brown trout from the Howietoun Hatchery, near Stirling, Scotland. Since that time, populations have established in 51 additional watersheds at an estimated rate of spread of 4 km per year. We did not detect any obvious abiotic barriers to resist trout establishment, but showed that for a given amount of propagule pressure that relatively large and productive watersheds were most likely to be established.

Main conclusions Brown trout have successfully invaded and established populations in watersheds of Newfoundland and are currently slowly expanding on the island. Populations are more likely to establish in relatively large and productive watersheds, thereby supporting predictions of island biogeography theory. However, we suggest that all watersheds in Newfoundland are potentially susceptible to successful brown trout invasion and that abiotic factors alone are unlikely to act sufficiently as barriers to population establishment.

Keywords

Biological invasions, establishment, exotic, introduced, island introductions, non-native, rate of dispersal, salmonid fishes, straying.

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INTRODUCTION

Island biogeography theory (IBT) predicts that distributions of organisms are maintained by a dynamic balance between local extirpation and colonization (MacArthur & Wilson, 1967). According to classic IBT, the asymptotic number of species (i.e. species richness) should increase with increasing size of an

island or habitat fragment and decrease with greater distance from a colonization source. IBT is elegant in its simplicity, has been supported empirically by iconic experimental manipulation of whole islands (Simberloff & Wilson, 1969) as well as contemporary research in fragmented landscapes (e.g. Leach & Givnish, 1996), and has influenced the contemporary fields of conservation and invasion ecology (Losos *et al.*, 2010).

Humans frequently bridge the barriers to dispersal, thereby facilitating the spread of organisms around the globe (Wilson *et al.*, 2009), inadvertently resulting in large-scale, replicated experiments that can be used to test tenets of IBT (Sax *et al.*, 2005). One of the emerging insights of these imperfectly planned experiments is that ecological systems rarely show signs of saturation and that establishment of non-native species into novel environments is common (Sax *et al.*, 2007). However, the ability to successfully invade varies among taxa (Williamson, 1996; Jeschke & Strayer, 2005) and is context dependent (Korsu *et al.*, 2007), making predictions of which species will become invaders elusive. What is becoming increasingly clear is that vertebrates are exceptionally successful invaders, and once introduced have a high potential to establish populations (Jeschke & Strayer, 2005).

Fish species of the genera *Micropterus* (Warner, 2005), *Oncorhynchus* (Crawford & Muir, 2008), *Salvelinus* (Dunham *et al.*, 2002) and *Salmo* (MacCrimmon & Marshall, 1968) are successful global invaders, having been repeatedly spread through intentional introductions for recreational fishing and aquaculture. Recent years have shown a substantial increase in our understanding of the ecological risk factors (e.g. diet and niche breadth, temperature tolerances and life-history strategies) that likely underpin the success of these species (Kolar & Lodge, 2002; Ruesink, 2005; Olden *et al.*, 2006). Additionally, recent work has highlighted the important role of propagule pressure, the societal motives behind the original introductions, and interactions with abiotic environmental features associated with invasion success (reviewed by Lockwood *et al.*, 2005; Ruesink, 2005; Moyle & Marchetti, 2006). Taken together, these tools have enhanced our ability to understand the patterns and processes behind the successful invasions of these fishes; however, work remains as members of these species are often implicated in the decline or extirpation of local species (McDowall, 2006) and the disruption of ecosystems (Schindler *et al.*, 2001).

Among the most successful freshwater fish invaders is brown trout (*S. trutta*). Brown trout has the ominous distinction as one of the '100 worst invasive alien species' by the Invasive Species Specialist Group (Lowe *et al.*, 2000), and is a current conservation concern in many regions, including New Zealand (McDowall, 2006), the Falkland Islands (McDowall *et al.*, 2001), the Patagonia region of South America (Pascual, 2007), and North America (Waters, 1983; Van Zyll de Jong *et al.*, 2004). One of the first sites of brown trout introduction to North America was to the island of Newfoundland in the late 19th century (Scott & Crossman, 1964; Andrews, 1965; Hustins, 2007). The introduced trout, which were descendants of non-anadromous (i.e. freshwater resident) ancestors, quickly established self-sustaining populations and, as they have in other regions (e.g. Launey *et al.*, 2010), spread to new locations presumably by anadromous (i.e. sea-going) dispersers. However, little is known about the current distribution of brown trout on the island and the physical environmental factors associated with their establishment in watersheds are unknown. Moreover, recent declines in populations of native

salmonids (Atlantic salmon, *S. salar* and brook charr, *S. fontinalis*) in Newfoundland (DFO, 2006) mirror patterns of species displacement and competitive exclusion observed elsewhere (Waters, 1983; Korsu *et al.*, 2007). Thus, a better understanding of the brown trout invasion is urgently needed for planning for conservation of native fishes.

The overarching goal of this paper is to quantify the watershed-scale factors associated with brown trout population establishment with the aim of informing future conservation plans for the long-term persistence of native fish. To meet this objective, we (1) document the early history and demographics (numbers and origins) of human-mediated brown trout introductions, (2) determine the current distribution of established populations, and (3) identify abiotic environmental variables associated with presence of trout populations in an attempt to elucidate the factors facilitating or impeding establishment. Combining field sampling and data assembled from literature and existing government databases, we test the predictions generated from IBT and invasion theory that probability of population establishment is positively correlated with: (1) distance to and total number of potential invasion foci (i.e. propagule pressure), (2) watershed size, and (3) habitat productivity.

METHODS

Species description

Brown trout is a polytypic species with a native Eurasian distribution, which in the course of *c.* 90 years (*c.* 1852–1938) became a successful global invader via extensive intentional introductions (MacCrimmon & Marshall, 1968; Elliott, 1994). The life history of brown trout varies markedly among populations and among individuals within populations, but in general involves fall spawning by mature individuals in flowing waters, parental care by females in the form of egg burial, protracted embryonic development and use of small streams by juvenile trout (Baglinière & Maisse, 1999). Brown trout exhibit two alternative life-history strategies, a complete lifetime in freshwater (freshwater residency) or temporary feeding migrations to sea (anadromy) followed by homing to natal streams for reproduction (Stuart, 1957; Jonsson & Jonsson, 1993; Crisp, 2000). Brown trout are capable of highly accurate homing (Armstrong & Herbert, 1997); however, a small proportion of individuals either fail or 'decide' not to home and stray to other systems to breed. Thus, straying by anadromous brown trout represents a mechanism for invasion of suitable habitat (Launey *et al.*, 2010).

Invasion origins

The brown trout invasion process to Newfoundland follows the archetypal pattern of all successful biological invasions (Kolar & Lodge, 2001): (1) *transport* of propagules and survival upon introduction, (2) *establishment* of populations, (3) *spread* to novel areas and (4) *ecological impact*. A detailed history of

brown trout importation and introductions goes beyond the scope and objectives of this paper, so we only provide a brief overview here. Shipments of trout embryos from the Howietoun hatchery in Stirling, Scotland, began in 1883 and were followed by other importations in 1884, 1892, and 1905–1906 (Frost, 1940; Scott & Crossman, 1964; Andrews, 1965; Hustins, 2007). The majority of imported trout were ‘Scottish’ strain, though latter shipments were comprised of ‘English’ and ‘German’ strains (Hustins, 2007). Imported trout survived well upon introduction and established populations in watersheds in the surrounding vicinity of St. John’s (Maitland, 1887). Brown trout escaped into a watershed with a route to the sea in 1884, representing the first potential source of anadromous colonizers. Straying anadromous fish presumably established populations in subsequent watersheds, though the timing and order of watershed invasion and establishment are unknown. Ecological impacts of the brown trout invasion are not well understood, but likely include competition and displacement of native fish (Gibson & Cunjak, 1986; Van Zyll de Jong *et al.*, 2004) and hybridization with Atlantic salmon (Verspoor, 1988; McGowan & Davidson, 1992). Readers should refer to Hustins (2007) and Fig. 1. for additional details.

Data sources and quality

Database of population establishment

We used multiple sources of data to address the invasion origins, distribution of established populations, and watershed factors associated with brown trout establishment. Data to investigate the historical origins and demographics of early introductions were compiled from Maitland (1887) and Hustins (2007 and references therein). We assembled a database of watersheds with and without established brown trout populations from the Department of Fisheries and Oceans (DFO) Newfoundland Freshwater Salmonid Inventory (<http://public.geoportal-geoportal.gc.ca/dfoGeoPortal/>), which was initiated to provide base line data on all river systems on the island of Newfoundland. We combined these records with historical data from Maitland (1887), Hustins (2007), and the reported distribution of brown trout by DFO’s Angler Guide (DFO, 2010), which lists brown trout watersheds managed for sportfishing. In doing so, we recognized that the numbers and locations of historical stocking, as well as DFO’s data on the current distribution of brown trout are conservative and have associated caveats. Uncertainty in the current known distribution of brown trout arises from a host of complicating factors such as angler effort in certain areas or habitats (e.g. estuaries or salt ponds), misidentifications with the closely related Atlantic salmon, and lack of reporting.

Thus, in an attempt to address the uncertainty in the assembled presence–absence database, we used data from independent field sampling in 2008 and 2010. We selected 24 watersheds to sample within and near the edge of the presumed dispersal range of brown trout (Fig. 2). Our choice of watersheds reflects a desire for geographical coverage, as well

as objectives of other on-going complimentary projects concerning the trout invasion. We employed single-pass, upstream electrofishing with a backpack electrofisher for a minimum of an hour of active shocking time. We focused our sampling in the lower sections (c. 5 km from the mouth) of watersheds assuming that if populations are established, individuals are most likely detected in these parts of the watershed (for empirical examples of this pattern see Korsu *et al.*, 2007; Budy *et al.*, 2008). Moreover, we focused our efforts in habitats associated with brown trout, such as pools, cut banks, and side-channels (Armstrong *et al.*, 2003). Taken together, we are confident that our sampling protocol is sufficient in detecting thoroughly established populations as single-pass electrofishing is frequently used to accurately assess trout populations in streams (e.g. Kruse *et al.*, 1998).

Of 24 watersheds sampled during 2008 and 2010, there was a strong concordance (96%) between the assembled presence–absence database. We found 100% agreement between our sampling and the database, for seven systems reportedly absent of trout and brown trout were encountered in all but one of 17 reportedly established watersheds. This record was retained, given subsequent evidence to support the presence of brown trout in this watershed (e.g. it is a managed brown trout system). Furthermore, we returned to 10 watersheds in 2010 that had been surveyed in 2008 and again found evidence of established populations in all of those systems.

Abiotic environmental factors and propagule pressure

The DFO online database also contained two classes of watershed-scale environmental variables for 312 watersheds, measures of watershed size and water chemistry. The specific variables were watershed area (km²), watershed width (km), watershed length (km), watershed perimeter (km), watershed relief (m), length of mainstem flowing water (km), total length of flowing waters (km), number of tributaries, pH, hardness (ppm), conductivity ($\mu\text{S cm}^{-1}$ at 25°C), turbidity (J.T.U), alkalinity (ppm), calcium (ppm), chloride (ppm) and bicarbonate (ppm). For more information on the collection and measurement of these variables, see Porter *et al.* (1974). Unfortunately, data on watershed obstructions were not sufficiently available for incorporation into our analyses. However, obstructions are only likely to be important when they form a complete barrier at the mouth of a watershed as brown trout are apparently pre-adapted to establishing the lower sections of watersheds (Korsu *et al.*, 2007; Budy *et al.*, 2008). Environmental data were not available for 23 locations of established populations shown in Fig. 2. The locations with missing data result mainly from original stockings into landlocked ponds that were not surveyed by DFO and multiple sites of known populations within watersheds (e.g. six sites within the Rennie’s watershed, Table 2) rather than inherent biases in how the database was assembled.

We attempted to elucidate the association between watershed-scale population establishment and physical environmental

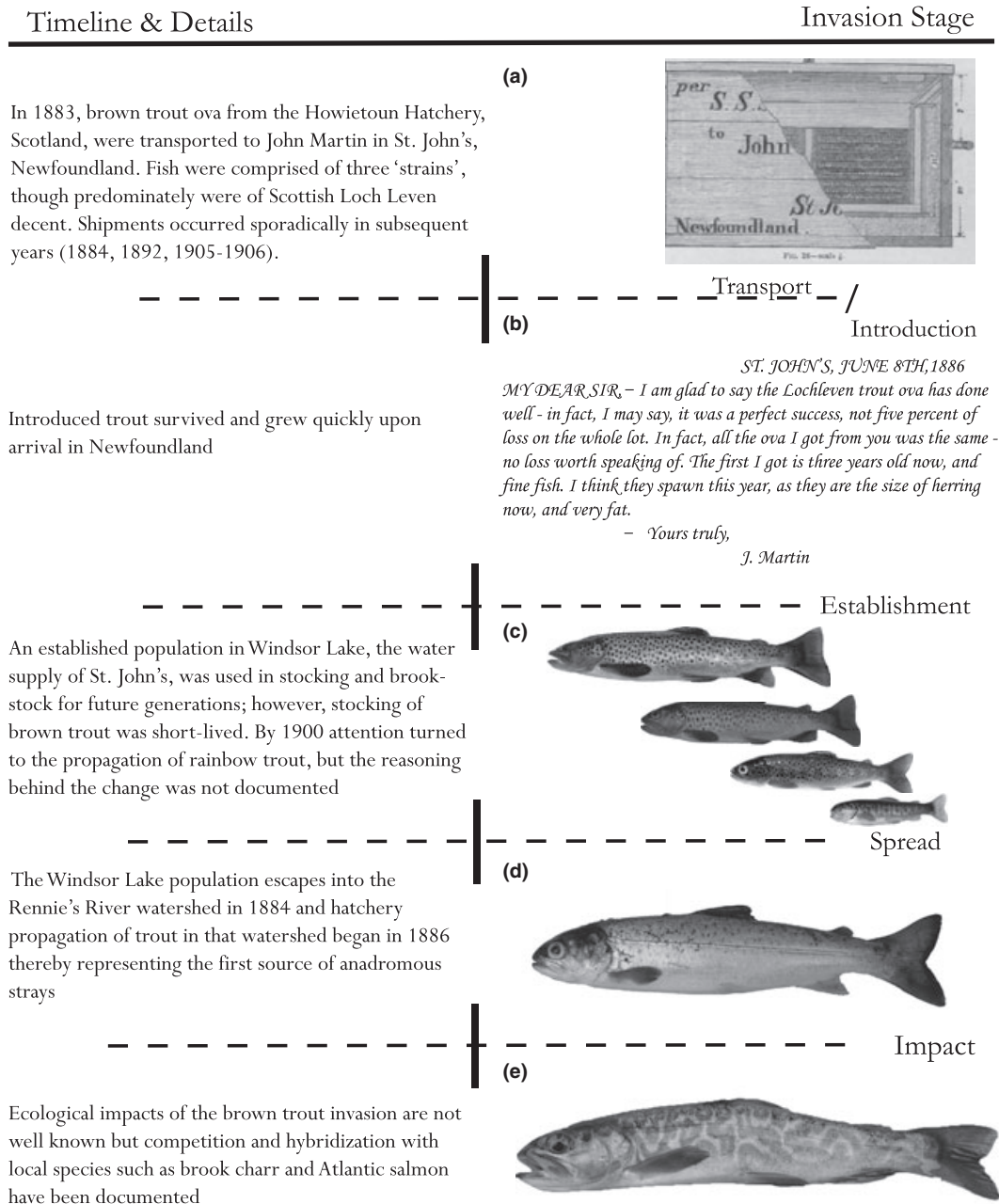


Figure 1 An annotated timeline of the brown trout invasion process to the island of Newfoundland. Discrete stages in the invasion process follow the logic of Kolar & Lodge (2002) and Lockwood *et al.* (2007) and are denoted by dashed horizontal lines. Important dates and details of the invasion are provided on the left side of the figure and supporting images at each stage are provided on the right. (a) Image of the original shipping container for transporting brown trout ova showing its intended destination to John Martin in St. John's, Newfoundland (Maitland, 1887), (b) excerpt from a letter by John Martin where he proclaims successful importation of brown trout (Maitland, 1887), (c) images of representative size and age classes of brown trout, which we take as evidence for population establishment, (d) image of a 115-mm potential anadromous colonizer, and (e) a hybrid between a brook trout and brown trout sampled in a St. John's river. Photographs are provided by the authors.

factors while controlling for distance to and number of nearby invasion foci (a surrogate for propagule pressure). We modelled propagule pressure as the interaction of the distance (km) of the mouth of each watershed to the mouth of the closest source watershed with an established brown trout population *and* the total number of these sources within a 100-km radius of each

watershed. We based the 100-km radius on the typical distance an anadromous brown trout may travel at sea (Klemetsen *et al.*, 2003 and references therein). Distances were calculated using the least cost distance tool in ArcGIS, v. 9.2 (ESRI), which provides a consistent and realistic framework for estimating distance through the ocean. That is, our estimates represent the shortest

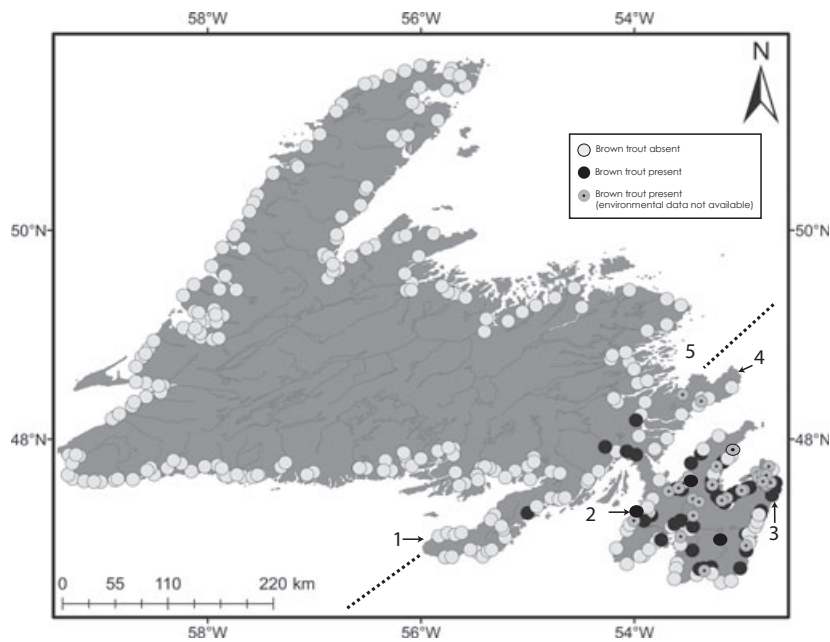


Figure 2 Current distribution of watersheds established by brown trout populations on the island of Newfoundland. The dashed lines denote the apparent dispersal boundary, and thus, only watersheds to the right of the boundary were included in our analyses (see text). Numbers represent locations mentioned in the text: 1) Burin Peninsula, 2) Southeast Placentia River, 3) St. John's, 4) Bonavista Peninsula, and 5) Bonavista Bay. See Fig. 3. for other important locations.

distance of a watershed to a source by excluding travel through land, thereby estimating the shortest distance a sea-going colonist would have to travel from a source to a potential invasion site. This surrogate measure of propagule pressure was applied and incorporated in our models as a smooth nonlinear term following the general approach and logic of Rouget & Richardson (2003).

Data analysis of watershed-scale factors associated with establishment

We investigated the factors associated with population establishment in several steps. First, the relationship between presence and absence of brown trout was investigated using correlation and principal components analysis (PCA) on continuous physical environmental variables that were standardized to account for order of magnitude differences in watershed characteristics such as watershed area. PCA was used to distil a highly correlated set of 16 habitat variables into a less-correlated data set for subsequent use in explaining brown trout establishment. The number of principal components used in interpretation was based on deviations from the broken-stick distribution as described by Peres-Neto *et al.* (2003).

We then used variables from this informative and less correlated data set to investigate brown trout presence and absence using a linear modelling information-theoretic framework. We formulated three a priori candidate models and assessed the weight of support of each model using

(ΔAIC) as our selection metric, which simply represents the difference between the AIC value of a candidate model to the AIC value of the candidate model with the lowest AIC value. We interpreted models with ΔAIC scores of 0–3 to have substantial empirical support, scores of 4–7 to have markedly less support and scores of >7 to have very little support (Burnham & Anderson, 2002). Additionally, we calculated AIC weights as a measure of modelling selection uncertainty and interpret AIC weights as the probability of selecting a candidate model as the best model if the modelling procedure was carried out many times (Hobbs & Hilborn, 2006). We fit binomial ANCOVA models, with binomial error and logit link, using the GAM function in the 'mgcv' library in R v. 2.10.1 to account for auto-correlation and nonlinearity in our covariate surrogate for propagule pressure (Crawley, 2007).

RESULTS

Invasion demographics

The records we have compiled indicate that at least 156 000 juvenile brown trout were introduced across 21 locations in the immediate vicinity of St. John's and to adjacent communities (Table 1, Fig. 3). These records also indicate that the preponderance (93%) of the 156 000 brown trout introduced to Newfoundland waters were of the Scottish Loch Leven-strain originating from the Howietoun hatchery. In contrast, only 7% of the originally introduced trout were of the German von

Table 1 Watershed, waterbody (location within watersheds), destination of water from watersheds or landlocked if water does not drain to sea, geographical coordinates (degrees, minutes, decimal seconds) of waterbody locations, year and number of individuals introduced (when available), and source strain of brown trout introduced to the island of Newfoundland. Data compiled from Hustins (2007).

Watershed	Waterbody	Destination	Latitude	Longitude	Year (number introduced)	Source strain
Bauline	Whiteway's	Landlocked	47 39 52.23	52 45 55.74	1892, 1896 (1000)	German
Brigus	Hodgewater Pond	Conception Bay	47 30 27.73	53 16 17.24	1892	German
Clement	Clement's Pond	Landlocked	47 30 58.28	52 55 31.50	1905–1906	English
Cove Pond	Cove Road Ponds	Landlocked	47 25 02.28	53 09 00.70	1886 (10 000)	Loch Leven
Dildo	South Dildo Pond	Trinity Bay	47 29 46.97	53 32 46.90	1889 (10 000)	Loch Leven
Lee's	Lee's Pond	Conception Bay	47 24 30.92	53 11 35.91	1896 (4000)	German
Lee's	Lee's Pond	Conception Bay	47 24 30.92	53 11 35.91	1905–1906	English
Lower Island	Lower Island Ponds	Landlocked	48 00 13.02	52 59 46.28	1888 (10 000)	Loch Leven
Mundy's	Mundy's Pond	Landlocked	47 33 06.30	52 44 22.10	1886 (5000)	Loch Leven
Murray's	Murray's Pond	Landlocked	47 36 51.69	52 49 13.01	1905–1906	English
Petty Harbour	Petty Harbour Ponds	Atlantic (eastern Avalon)*	47 27 07.41	52 42 35.68	1888 (10 000), 1889 (3000)	Loch Leven
Rennies	Long Pond	St.John's	47 34 40.99	52 44 00.74	1888 (40,000)	Loch Leven
Rennies	Quidi Vidi	St.John's	47 34 52.53	52 41 23.77	1886 (10 000)	Loch Leven
Rennies	Rennie's River	St.John's	47 34 40.45	52 42 57.34	1884	Loch Leven
Rennies	Upper Long Pond	St.John's	47 34 16.08	52 45 46.64	1886 (20 000)	Loch Leven
Rennies	Virginia Lake	St.John's	47 36 24.39	52 42 07.18	1886 (1000)	Loch Leven
Robin's	Robin's Ponds	Landlocked	47 39 25.87	52 45 42.90	1892 (1000)	German
Rocky	Hodge Water Cat Hills	St.Mary's Bay	47 24 46.72	53 31 59.86	1896 (4000)	German
Rocky	Ocean Pond	St. Mary's Bay	47 27 23.13	53 37 45.18	1892	German
Topsail	Topsail Road Ponds	Conception Bay	47 32 03.92	52 56 39.64	1886 (15 000), 1889 (2000)	Loch Leven
Trinity	Trinity Bay Ponds	Trinity Bay	48 22 20.32	53 23 22.84	1889	Loch Leven
Windsor	Windsor Lake	St.John's	47 35 55.07	52 47 34.00	1883 (5000), 1884 (5000)	Loch Leven

*Currently landlocked because of impassable hydropower plant.

Behr-strain. Unfortunately, no records of numbers of stocked English-strain brown trout are known for the stockings that did occur.

Current distribution

The number of watersheds established by brown trout increased fourfold from 16 in 1883 (Table 1) to 68 in 2010 (Table 2). Brown trout populations are currently established in watersheds on the Avalon, Burin and Bonavista peninsulas (Fig. 2).

Environmental factors associated with establishment

The pattern of population establishment observed in (Fig. 2) suggested dispersal limitation by brown trout. Indeed, initial analyses including all 312 watersheds suggested only our measure of propagule pressure had any power to predict population establishment (results not shown), and inclusion of these systems obscured the role of environmental factors associated with establishment elsewhere. Thus, for the remainder of the study, we focused on elucidating watershed-scale environmental factors associated with ($n = 45$) or without ($n = 68$) population establishment within the presumed trout dispersal range (Fig. 2).

Forty per cent (45 of 113) of the watersheds examined were established by brown trout and abiotic environmental variables

varied markedly between these watersheds (Table 3); however, many variables were highly correlated (Table 4). Thus, a principal components analysis (PCA) facilitated the distillation and interpretation of these highly correlated habitat characteristics for quantifying presence or absence of established brown trout populations. The first two axes of the PCA explained 69% of the total variance in the data (Table 5) and were the only axes interpreted based on the broken-stick method. The first axis described a gradient of increasing watershed area, width, length, perimeter, length of mainstem river, total length of flowing waters and number of tributaries. The second axis described a gradient of watersheds with increasing pH, hardness, conductivity, alkalinity, calcium and bicarbonate.

We modelled the importance of watershed area (representing PCA axis 1) and conductivity (PCA axis 2) on predicting brown trout presence or absence while controlling for the nonlinear effect of propagule pressure. We chose to use these important variables from the two axes of the PCA rather than principal component scores in our subsequent modelling to facilitate direct interpretation and to correspond to predictions of biogeography (e.g. larger watersheds should be more likely to be established than smaller ones). Watershed area and conductivity values were logarithmically transformed prior to modelling to meet parametric assumptions. We chose to model the importance of conductivity because conductivity correlates with important biological processes in Newfoundland (Adams,

Table 2 Characteristics of watersheds established with brown trout populations in Newfoundland. Established watersheds (presented in alphabetical order), waterbody (location within watersheds), geographic coordinates, source strain (if known), and applicable reference.

Watershed	Waterbody	Latitude	Longitude	Source strain	References
Aquaforde	Aquaforde River	47 00 17.86	52 59 10.07	Natural colonization (source unknown)	DFO (2010)
Avondale	Avondale River	47 26 07.09	53 12 23.99	Natural colonization (source unknown)	DFO (2010)
Bauline	Whiteway's	47 39 52.23	52 45 55.74	German	Hustins (2007)
Bauline	Whiteway's River	47 41 05.59	53 28 13.50	Natural colonization (source unknown)	DFO (2010)
Biscay Bay	Biscay Bay River	46 47 01.46	53 16 43.93	Natural colonization (source unknown)	DFO (2010)
Brigus	Hodgewater Pond	47 30 27.73	53 16 17.24	German	Hustins (2007)
Cape Broyle	Cape Broyle River	47 05 35.41	52 58 38.33	Natural colonization (source unknown)	DFO (2010)
Chance Cove	Chance Cove Brook	47 38 38.07	53 48 39.73	Natural colonization (source unknown)	DFO (2010)
Chapel Arm	Chapel Arm River	47 31 07.57	53 42 09.20	Natural colonization (source unknown)	DFO (2010)
Clement	Clement's Pond	47 30 58.28	52 55 31.50	English	Hustins (2007)
Colinet	Colinet river	47 13 15.60	53 32 56.26	German	Hustins (2007)
Colliers	Colliers Bay River	47 35 16.04	53 42 37.94	Natural colonization (source unknown)	DFO (2010)
Colliers	Colliers River	47 27 17.76	53 14 07.10	Natural colonization (source unknown)	DFO (2010)
Come by Chance	Come by Chance River	47 50 48.23	53 58 54.65	Natural colonization (source unknown)	DFO (2010)
Cove Pond	Cove Road Ponds	47 25 02.28	53 09 00.70	Loch Leven	Hustins (2007)
Dildo	South Dildo Pond	47 29 46.97	53 32 46.90	Loch Leven	Hustins (2007)
Dildo	South Dildo River	47 32 50.77	53 31 38.99	Natural colonization (source unknown)	DFO (2010)
Green's harbour	Green's Harbour River	47 37 37.20	53.29 36.14	Natural colonization (source unknown)	DFO (2010)
Harbour Main	Gallows Cove	47 27 14.39	53 05 26.14	Natural colonization (source unknown)	DFO Salmonid Fish Inventory
Harry's	Harry's Pond	47 46 53.25	53 11 00.34	Natural colonization (source unknown)	DFO (2010)
Heart's Content	Heart's Content Brook	47 52 39.88	53 20 28.96	Natural colonization (source unknown)	DFO (2010)
Heart's Content	Musquash Pond*	47 52 26.15	53 22 05.66	Loch Leven	Hustins (2007)
Heart's Delight	Heart's Delight River	47 46 10.72	53 27 01.85	Natural colonization (source unknown)	DFO (2010)
Holyrood	Holyrood Pond	46 49 35.72	53 36 27.08	Natural colonization (source unknown)	DFO Salmonid Fish Inventory
Hopeall	Hopeall River	47 36 06.82	53 30 35.12	Natural colonization (source unknown)	DFO (2010)
Indian Pond	Indian Pond	47 27 15.21	53 05 25.17	Natural colonization (source unknown)	DFO (2010)
Island Pond	Island Pond Brook	47 43 59.14	53 13 50.18	Natural colonization (source unknown)	DFO (2010)
Kelligrews	Kelligrews River	47 29 40.21	53 00 32.78	Natural colonization (source unknown)	DFO (2010)
Lee's	Lee's Pond	47 24 30.92	53 11 35.91	German	Hustins (2007)
Lee's	Lee's Pond	47 24 30.92	53 11 35.91	English	Hustins (2007)
Little Salmonier	Little Salmonier River	47 02 43.23	53 44 10.37	Natural colonization (source unknown)	DFO Salmonid Fish Inventory
Lower Gullies	Lower Gullies River	47 28 27.36	53 01 48.30	Natural colonization (source unknown)	DFO (2010)
Lower Island	Lower Island Ponds	48 00 13.02	52 59 46.28	Loch Leven	Hustins (2007)
Manuel	Manuels River	47 30 59.72	52 46 30.97	Natural colonization (source unknown)	DFO (2010)
Mobile	Mobile River	47 15 12.06	52 53 06.83	Natural colonization (source unknown)	DFO (2010)
Mozzen	Mozzen Pond	47 52 26.15	53 22 05.66	Natural colonization (source unknown)	DFO (2010)
Mundy	Mundy's Pond	47 33 06.30	52 44 22.10	Loch Leven	Hustins (2007)
Murray	Murray's Pond	47 36 51.69	52 49 13.01	English	Hustins (2007)
NE Placentia	NE Placentia River	47 13 37.19	53 52 30.66	Natural colonization (source unknown)	DFO (2010)
NE River	NE River	46 45 15.81	53 16 47.27	Natural colonization (source unknown)	Verspoor (1988)
New Harbour	New Harbour River	47 34 38.55	53 32 32.52	Natural colonization (source unknown)	DFO (2010)
North Arm	North Arm River	47 23 34.44	53 09 27.80	Natural colonization (source unknown)	Gibson & Cunjak (1986)
North Harbour	North Harbour River	47 10 55.10	53 37 47.84	German	Hustins (2007)
North River	North River	47 32 27.60	53 18 39.74	Natural colonization (source unknown)	DFO (2010)
Northwest River	Northwest River	46 45 52.76	53 21 05.91	Natural colonization (source unknown)	DFO (2010)
O'Donnells	O'Donnells	46 45 05.12	53 36 10.66	Natural colonization (source unknown)	DFO Salmonid Fish Inventory
Old Shop	Old Shop	47 32 00.40	53 35 47.40	Natural colonization (source unknown)	DFO Salmonid Fish Inventory
Petty Harbour	Petty Harbour Ponds	47 27 07.41	52 42 35.68	Loch Leven	Hustins (2007)
Piper's	Pipers Hole River	47 55 24.89	54 16 26.16	Natural colonization (source unknown)	DFO (2010)

Table 2 (Continued).

Watershed	Waterbody	Latitude	Longitude	Source strain	References
Point Verde	Point Verde	47 13 31.39	54 00 48.75	Natural colonization (source unknown)	DFO Salmonid Fish Inventory
Portugal Cove South	Stoney River	46 47 01.46	53 16 43.93	Natural colonization (source unknown)	Enders <i>et al.</i> 2007
Princeton	Princeton Brook	48 39 33.36	53 06 56.66	Natural colonization (source unknown)	DFO (2010)
Renews	Renews River	46 56 33.03	52 58 32.11	Natural colonization (source unknown)	DFO (2010)
Rennies	Long Pond	47 34 40.99	52 44 00.74	Loch Leven	Hustins (2007)
Rennies	Quidi Vidi	47 34 52.53	52 41 23.77	Loch Leven	Hustins (2007)
Rennies	Quidi Vidi River	47 34 52.53	52 41 23.77	Natural colonization (source unknown)	DFO (2010)
Rennies	Rennie's River	47 34 40.45	52 42 57.34	Loch Leven	Hustins (2007)
Rennies	Upper Long Pond	47 34 16.08	52 45 46.64	Loch Leven	Hustins (2007)
Rennies	Virginia Lake	47 36 24.39	52 42 07.18	Loch Leven	Hustins (2007)
Rexton	Robin Hood Pond	48 23 42.28	53 19 32.12	Natural colonization (source unknown)	DFO (2010)
Robin's	Robin's Ponds	47 39 25.87	52 45 42.90	German	Hustins (2007)
Rocky	Ocean Pond	47 27 23.13	53 37 45.18	German	Hustins (2007)
Rocky	Rocky River	47 13 57.03	53 33 22.01	German	Hustins (2007)
Rocky	Hodge Water Cat Hills	47 24 46.72	53 31 59.86	German	Hustins (2007)
Salmon Cove	Salmon Cove River	47 46 55.43	53 10 30.50	Natural colonization (source unknown)	DFO (2010)
Salmonier	Salmonier	47 10 25.84	53 39 47.84	German	Hustins (2007)
SE Placentia	SE Placentia River	47 13 10.96	53 55 13.49	Natural colonization (source unknown)	DFO (2010)
Seal Cove	Seal Cove River	47 27 59.53	53 04 11.72	Natural colonization (source unknown)	DFO (2010)
Shearstown	Shearstown River	47 35 26.05	53 18 15.23	Natural colonization (source unknown)	DFO (2010)
Shoal Harbour	Shoal Harbour River	48 11 36.66	54 00 58.52	Natural colonization (source unknown)	DFO (2010)
South River	South River	47 32 13.73	53 16 27.39	Natural colonization (source unknown)	DFO (2010)
Spread Eagle	Spread Eagle River	47 31 50.73	53 36 56.52	Natural colonization (source unknown)	DFO (2010)
Stone Ducky	Stone Ducky Brook	47 19 46.39	52 49 14.84	Natural colonization (source unknown)	DFO (2010)
Topsail	Topsail River	47 31 35.38	52 54 19.92	Natural colonization (source unknown)	DFO (2010)
Topsail	Topsail Road Ponds	47 32 03.92	52 56 39.64	Loch Leven	Hustins (2007)
Trinity	Trinity Bay Ponds	48 22 20.32	53 23 22.84	Loch Leven	Hustins (2007)
Waterford	Waterford River	47 32 24.86	52 43 39.12	Natural colonization (source unknown)	DFO (2010)
Windsor	Windsor Lake	47 35 55.07	52 47 34.00	Loch Leven	Hustins (2007)
Witless	Pierre's Brook	47 15 08.18	52 51 40.21	Natural colonization (source unknown)	DFO (2010)

*Evidence for the strain of origin is based on an unsubstantiated historical letter cited in Hustins (2007).

2006) and has been used elsewhere as a surrogate for watershed productivity (Ryder, 1982; Copp, 2003).

Brown trout establishment was positively associated with both watershed area and conductivity. We found strong evidence in favour of a model containing watershed area and conductivity as parametric predictors and a measure of propagule pressure as a smoothed term covariate. This model explained 80% of the observed deviance and received virtually indisputable support based on the model's AIC weight ($w_i = 0.99$). In contrast, we found little support for models containing only conductivity (deviance explained = 66%, $\Delta AIC = 15$, $w_i = 0.01$) or watershed area (deviance explained = 25%, $\Delta AIC = 31$, $w_i \sim 0$), again while controlling for nonlinear effects of propagule pressure.

DISCUSSION

Brown trout have successfully invaded and established populations are slowly expanding on the island of Newfoundland. The initial roots of the trout invasion trace their origins to the

Howietoun Hatchery in Stirling, Scotland, and were predominately descendants of non-anadromous Loch Leven broodstock. Approximately 125 years since their first introduction, brown trout have spread from 16 watersheds of introduction to invade and establish populations in at least 51 additional watersheds. Our results suggest that the brown trout invasion is a contemporary process, as new populations have continued to establish over the past two decades. Modelling the presence-absence of established brown trout populations in Newfoundland indicates that for a given measure of propagule pressure, established watersheds are relatively large and productive compared to unestablished watersheds. Taken as a whole, these results suggest an important role of watershed area and productivity in the dynamics of establishment by brown trout in Newfoundland watersheds.

Invasion origins and current distribution

Documenting the history and demography of a species' introduction is an important first step towards understanding

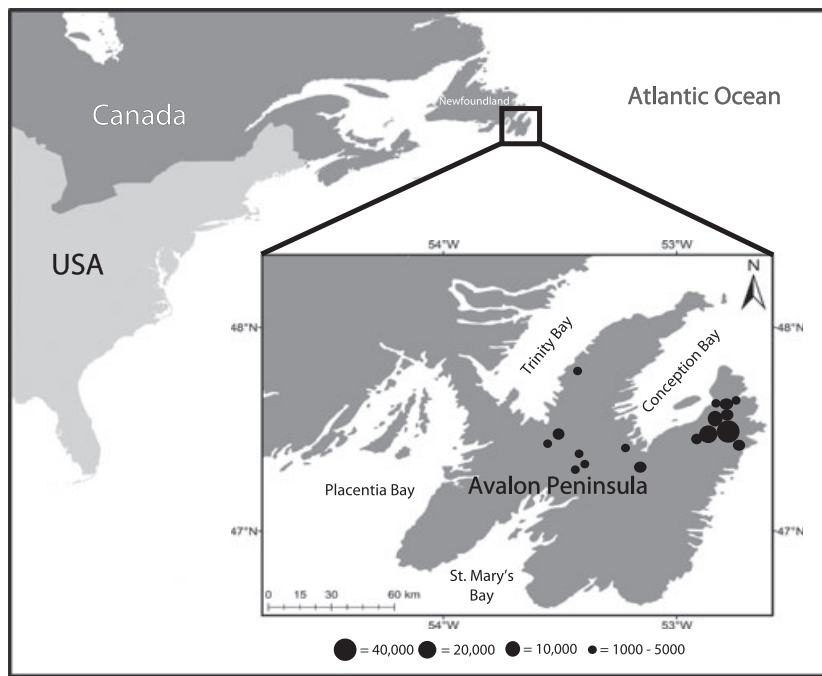


Figure 3 Island of Newfoundland showing watersheds (denoted by filled circles) of brown trout introductions on the Avalon Peninsula, where the size of the circle is roughly proportional to the numbers of trout introduced to a given watershed. See Table 1 for additional information.

Table 3 Factors associated with watersheds that are not established (absent) and established (present) by brown trout populations in Newfoundland. Values represent the mean \pm standard deviation (SD) of each (n) watershed.

	Absent ($n = 68$)	Present ($n = 45$)
Distance to nearest invasion source (km)	18 (20)	11 (14)
Invasion sources within 100 km (n)	13 (8)	14 (7)
Watershed area (km ²)	72 (86)	98 (123)
Watershed width (km)	4 (2)	5 (3)
Watershed length (km)	14 (8)	16 (8)
Watershed perimeter (km)	44 (27)	54 (32)
Watershed relief (m)	243 (53)	259 (60)
Length of mainstem river (km)	12 (10)	13 (9)
Total length of flowing water (km)	64 (76)	66 (81)
Number of tributaries (n)	18 (14)	17 (13)
pH	6.2 (0.4)	6.4 (0.4)
Hardness (ppm)	7.8 (6.5)	6.8 (3.1)
Conductivity ($\mu\text{S cm}^{-1}$ at 25°C)	31.2 (9.4)	40.4 (42.4)
Turbidity (J.T.U)	1.4 (1.0)	1.1 (1.0)
Alkalinity (ppm)	2.9 (1.9)	2.7 (1.4)
Calcium (ppm)	1.4 (1.4)	1.4 (1.0)
Chloride (ppm)	7.4 (2.4)	7.8 (6.4)
Bicarbonate (ppm)	4.3 (2.3)	3.5 (1.7)

the dynamics of a biological invasion. Our documentation of the history surrounding the invasion of brown trout to the island of Newfoundland yields several salient points. We show that the roots of the biological invasion to Newfoundland, like invasions elsewhere, were the result of multiple introductions of three sources of colonists to multiple locations (Wilson *et al.*, 2009). The majority of introduced trout, however, were

descendants of non-anadromous (i.e. freshwater resident) Loch Leven parents (Hustins, 2007) and anadromous (sea-going) populations of brown trout are currently common in Newfoundland watersheds (Van Zyll de Jong *et al.*, 2004). Hatchery propagation of brown trout ceased by the beginning of the 20th century, which makes the current distribution of brown trout populations in watersheds of Newfoundland particularly striking. We suggest, as others have (Bradbury *et al.*, 1999; Van Zyll de Jong *et al.*, 2004), that the majority of watersheds have been established by straying anadromous trout, a pattern documented in other brown trout invasions (e.g. Launey *et al.*, 2010). Fish with anadromous life histories are difficult to transplant outside the native range (Quinn *et al.*, 2001) and anadromy is often implicated in the failure of transplanted species to establish (Quinn, 2005). Brown trout in Newfoundland are thus an exception where anadromy and subsequent straying are primary drivers of invasion success.

Our documentation of the early stages of the invasion also provides insight into dispersal pathways. By combining data sources with our field surveys, we confirmed several systems to be established within a 20-year period. Taken as a whole, the current distribution of established populations is suggestive of a leading-edge pathway of dispersal, where the range is continuously expanding via colonization by individuals from populations at the edge of the range (*sensu* Wilson *et al.*, 2009). For example, the presence of an established population in Bonavista Bay (Fig. 2) is likely now acting as a source of colonists to slowly expand the range westward. Brown trout populations are traditionally cited as being confined to the Avalon Peninsula (Gibson & Cunjak, 1986), but the distribution of populations reported here has clearly expanded to locations off the Avalon. Curiously, we also documented the establishment of a population not along the edge of the range.

Table 4 Pearson correlation values of 16 habitat characteristics used in modelling brown trout population establishment in watersheds on the island of Newfoundland. Correlations between variables >0.5 are highlighted in grey. For description of the variables and units of measure, see Table 3.

	Area	Width	Length	Perim	Relief	Main_len	Tot_len	Num_tribs	PH	Hard	Conduct	Turb	Alk	Cal	chl	bicarb
Drainage area	1															
Axial width	0.85	1														
Axial length	0.86	0.73	1													
Perimeter	0.94	0.84	0.85	1												
Relief	0.47	0.57	0.4	0.52	1											
Mainstem length	0.71	0.48	0.76	0.75	0.29	1										
Total length of flowing water	0.88	0.81	0.74	0.85	0.49	0.6	1									
Number of tributaries	0.61	0.56	0.62	0.68	0.42	0.66	0.61	1								
pH	0.05	0.2	0.09	-0.06	0.13	-0.14	0.01	-0.16	1							
Hardness	0.12	0.27	0.26	0.05	0.34	0.01	0.09	-0.08	0.65	1						
Conductivity	-0.16	-0.08	-0.07	-0.23	0.1	-0.19	-0.19	-0.27	0.57	0.64	1					
Turbidity	0.19	0.19	0.26	0.23	0.57	0.26	0.22	0.26	0.08	0.3	0.35	1				
Alkalinity	0.07	0.19	0.06	0.02	0.29	-0.05	0.05	-0.08	0.66	0.8	0.58	0.24	1			
Calcium	0.08	0.26	0.21	0.01	0.35	-0.08	0.04	-0.13	0.75	0.89	0.79	0.36	0.8	1		
Chloride	-0.31	-0.33	-0.32	-0.33	-0.16	-0.22	-0.29	-0.24	0.11	0.05	0.7	0.18	-0.01	0.21	1	
Bicarbonate	0.08	0.23	0.23	-0.02	0.25	-0.09	0.04	-0.11	0.76	0.89	0.63	0.24	0.87	0.92	-0.04	1

Table 5 Results of a principal components analysis (PCA) on environmental variables of Newfoundland watersheds. For description of the variables and units of measure see Table 3.

	PCI	PCII
Eigenvalues	6.10	5.01
Cumulative % variance	38	69
Eigenvectors		
Drainage area	0.369	-0.105
Axial width	0.357	-0.025
Axial length	0.359	-0.055
Perimeter	0.367	-0.143
Relief	0.267	0.069
Mainstem length	0.290	-0.149
Total length of flowing water	0.347	-0.111
Number of tributaries	0.278	-0.166
pH	0.080	0.345
Hardness	0.150	0.375
Conductivity	-0.003	0.381
Turbidity	0.159	0.119
Alkalinity	0.117	0.364
Calcium	0.132	0.411
Chloride	-0.131	0.154
Bicarbonate	0.130	0.393

Our electrofishing surveys confirmed the presence of an established population in the Southeast Placentia River (Fig. 2). This location had apparently not been established with a population when Verspoor (1988) thoroughly sampled the river, though it is not clear why this watershed resisted population establishment until relatively recently. Combinations of physical environmental factors associated with prob-

ability of population establishment and given levels of propagule pressure may be underlying the recent population establishment in this watershed (see next section below). The Southeast Placentia watershed is relatively large (140 km²) compared to other Avalon watersheds with established trout populations (Table 3), but it is also relatively unproductive (28 $\mu\text{S cm}^{-1}$).

Unfortunately, the data assembled here do not reveal information on the founders of watersheds with established populations and underlying interactions between founders and landscape factors are possible as three 'strains' of trout were originally imported and introduced to Newfoundland waters. It is possible that watersheds in Newfoundland have been colonized by 'favoured founders' who represent non-random, pre-adapted subsets of potential colonists (*sensu* Quinn *et al.*, 2001). In a recent empirical example, Launey *et al.* (2010) show that by combining microsatellite information to assess founder origins with demography they are able to better understand the processes by which brown trout introduced to three rivers on the Kerguelen Islands have successfully colonized 16 additional rivers in *c.* 40 years.

Landscape factors associated with establishment

Population establishment was positively associated with watershed area and conductivity (a surrogate for productivity) while controlling for the influence of propagule pressure. Large watersheds are more likely to receive colonizers based on chance alone (MacArthur & Wilson, 1967), but may also attract roaming potential colonizers, thereby increasing the propagule pressure experienced by these watersheds. This latter scenario is possible, given the observed general pattern that

some watersheds serve as 'magnets' to straying salmonid species, though why some rivers are more attractive than others is not known (reviewed in Quinn, 2005). However, our analysis attempted to control for the effect of propagule pressure and thus suggests that large watersheds are easier to establish relative to smaller watersheds. The positive association between watershed size and establishment is in general agreement with predictions of island biogeography theory and corroborates patterns found in translocated cutthroat trout (*O. clarki*, Haring & Fausch, 2002) and brown trout (Marchetti *et al.*, 2004; Launey *et al.*, 2010) populations. The positive relationship between watershed area and trout invasion are consistent with species saturation and biological resistance to invasion at small scales (Levine, 2000). However, the ability of a biological community to resist invasion varies among scales (Levine & D'Antonio, 1999; Shea & Chesson, 2002). This pattern has received particular attention in plant species, where spatial heterogeneity of resources appears to explain this scale dependence (Davies *et al.*, 2005). Patterns in fish are similar to those observed in plants. At the large scale, watersheds with the most native fish species also contain the most invasive species in California (Marchetti *et al.*, 2004; Moyle & Marchetti, 2006) though biotic interactions, such as predation, may enhance community resistance to invasion within river segments of these watersheds (Harvey *et al.*, 2004).

Watershed productivity, which we modelled with water conductivity as a surrogate (Ryder, 1982), was also an important factor associated with population establishment. This result supports the Subsidized Island Biogeography hypothesis (*sensu* Anderson & Wait, 2001) that suggests an important role of allochthonous inputs in predicting species diversity on small islands or habitat fragments. The low productivity and high acidity of Newfoundland watersheds (Table 3) likely provide a proximate explanation for the relatively slow growth by stream-dwelling Atlantic salmon compared to their European counterparts (Hutchings & Jones, 1998) and have been used to predict fish assemblages in Newfoundland lakes (Van Zyll de Jong *et al.*, 2005). It is possible that low productivity reduces the probability of successful establishment by brown trout via increased inter- and/or intra-specific competition for limited food resources (see Elton, 1958 for similar arguments). Additionally, productivity often correlates with other potentially important variables such as disturbance (Lockwood *et al.*, 2007). Anthropogenic sources of disturbance in watersheds of Newfoundland are minor except for those containing large human populations, such as those near St. John's where streams have been channelized and flow regimes altered. Paradoxically, growth of salmonids in these disturbed city rivers is exceptionally high compared to other watersheds on the island, presumably because of high nutrient input (Gibson & Haedrich, 1988). Thus, productivity and disturbance appeared correlated in some Newfoundland systems, though data deficiencies preclude a formal evaluation of these ideas. Curiously, disturbance does not appear to be a necessary condition for successful salmonid establishment, thereby

suggesting a role of productivity *per se*. For example, brown trout are associated with relatively undisturbed watersheds in California (Marchetti *et al.*, 2004), and Chinook salmon have invaded the virtually pristine region of Patagonia (Correa & Gross, 2008).

Future outlook and conclusions

Brown trout have successfully invaded the island of Newfoundland and in *c.* 125 years established populations in a range of watersheds; however, their apparent rate of spread is comparably slow relative to other documented salmonid invasions. In 25 years, Chinook salmon invaded a large portion of South America (14 degrees of latitude) at a rate of *c.* 54 km per year (Correa & Gross, 2008) and in New Zealand Chinook invaded at a rate of *c.* 13 km per year (Unwin & Quinn, 1993). Similarly, pink salmon (*O. gorbuscha*) have rapidly spread throughout the vast Great Lakes Basin since their introduction into the Current River, a tributary of Lake Superior, in 1956 (Mills *et al.*, 1993). In contrast, brown trout on the Island of Newfoundland have established populations in watersheds within 500 km of the primary introduction sources near St. John's, which translates to a modest 4 km per year invasion rate. Assuming this rate remains constant, the most distant watersheds in Newfoundland would not be expected to be established with populations until the 24th century. Managers should take caution in this latter assumption, however, as many invading species exhibit periods of slow population growth followed by dramatic nonlinear rates of establishment and spread after variable amounts of lag time (Facon *et al.*, 2006).

Previous work on the biology of anadromous brown trout in Newfoundland suggests at least two mechanisms to explain this relatively slow invasion rate. First, O'Connell (1982) reports short (typically <50 km) marine migrations by anadromous trout in Newfoundland, which led him to suggest that these migrations reduced the probability of fish straying into suitable watersheds. Second, O'Connell (1982) reported a high proportion of upstream migrating adults that were not maturing in a given season (*i.e.* skip spawning), thereby slowing the rate of population growth, slowing the time to habitat saturation and potentially reducing the number of strays produced. Brown trout exhibit highly variable life-history traits such as age and size at maturity and skipped spawning between seasons appears common in populations (Klemetsen *et al.*, 2003); however, it is not clear how skipped spawning may alter population dynamics, and in turn, how this may affect the rate of dispersal by brown trout or other invading species (Kot *et al.*, 1996).

In conclusion, our analyses suggest that all watersheds in Newfoundland are susceptible to successful trout invasion as abiotic environmental factors substantially overlap between watersheds with and without established populations (Table 3). That is, we detected no obvious abiotic factors acting as strong barriers to establishment. However, we do show that trout are more likely to establish populations in relatively large and productive watersheds after controlling for

the effect of propagule pressure (i.e. the distance to and the total number of potential nearby sources), and thus, it seems likely smaller and less productive watersheds will become established with trout, given sufficient time and propagule pressure. Although we provide evidence of a dispersal boundary, we suggest it is only a matter of time before distant watersheds beyond this boundary receives brown trout invaders.

ACKNOWLEDGEMENTS

Many people helped during the writing and research for this manuscript, but we would like to make special note of D. Hustins whose work and conversations concerning the history and current status of brown trout in Newfoundland were invaluable. D. Hauser offered guidance on calculating distances to the invasion source in ArcGIS and aided in the production of the maps. We thank G. Pess and D. Scruton for insightful conversations. Logistical support in the field was provided by the Green Team program of the Conservation Corps of Newfoundland and Labrador and we would like to highlight the efforts of H. Cohen, C. Lewis, C. Corcoran, and C. Tobin. The manuscript was greatly improved by the comments of three anonymous reviewers. Funding for this research was provided by the Institute of Biodiversity and Ecosystem Sustainability, Department of Fisheries and Oceans Canada, and the Natural Sciences and Engineering Research Council of Canada. P. Westley was supported by scholarships from Memorial University of Newfoundland and an Olin Fellowship from the Atlantic Salmon Federation.

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Author contributions: P.A.H.W. conceived the analyses and analysed the data. P.A.H.W. and I.A.F. jointly wrote the paper.

Editor: Anthony Ricciardi