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ARTICLE

Rainbow trout (*Oncorhynchus mykiss*) habitat overlap with wild Atlantic salmon (*Salmo salar*) and brook trout (*Salvelinus fontinalis*) in natural streams: do habitat and landscape factors override competitive interactions?

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Abstract: The purpose of this study was to update rainbow trout (*Oncorhynchus mykiss*) invasion status, delineate factors that increase the invasion probability, and quantify habitat overlap between invasive rainbow trout and native Atlantic salmon (*Salmo salar*) and brook trout (*Salvelinus fontinalis*) on Prince Edward Island, Canada. Analysis of landscape-level variables in 26 watersheds (14 with and 12 without rainbow trout) demonstrated that watershed slope, percent agricultural land use, and distance to the nearest rainbow trout population significantly increased the probability of rainbow trout establishment. Two independent reach-level fish community surveys were conducted by electrofishing in combination with habitat surveys. Reaches with rainbow trout had higher stream slope, Atlantic salmon were found in wider reaches with larger substrate, and brook trout were typically dominant in headwater reaches with finer substrate. Findings at multiple ecological scales illustrated that rainbow trout invasion success is positively influenced by the presence of high-slope habitat. Habitat separation of the three salmonid species indicates that competition with introduced rainbow trout may not be the most significant threat to native salmonid populations.

Résumé : Le but de l'étude était d'actualiser l'état des envahissements de truites arc-en-ciel (*Oncorhynchus mykiss*), circonscrire les facteurs qui accroissent la probabilité d'envahissement et quantifier le chevauchement d'habitats entre la truite arc-en-ciel envahissante et le saumon atlantique (*Salmo salar*) et l'omble de fontaine (*Salvelinus fontinalis*), deux espèces indigènes, dans l'île du Prince Édouard (Canada). L'analyse de variables du paysage dans 26 bassins versants (14 avec des truites arc-en-ciel et 12 sans) démontre que la pente du bassin versant, la proportion de sols agricoles et la distance par rapport à la population de truites arc-en-ciel la plus proche accroissent significativement la probabilité d'établissement de truites arc-en-ciel. Deux relevés indépendants des communautés de poissons à l'échelle du tronçon ont été menés par pêche électrique de concert avec des inventaires des habitats. Les tronçons comptant des truites arc-en-ciel avaient des pentes plus fortes, les saumons atlantiques se trouvaient dans des tronçons plus larges présentant un substrat plus grossier et les ombles de fontaine étaient typiquement dominants dans les tronçons d'amont caractérisés par un substrat plus fin. Des observations à différentes échelles écologiques indiquent que le succès d'envahissement des truites arc-en-ciel est positivement influencé par la présence d'habitats de forte pente. La séparation des habitats des trois espèces de salmonidés indique que la concurrence avec des truites arc-en-ciel introduites pourrait ne pas être la plus grande menace pour les populations de salmonidés indigènes. [Traduit par la Rédaction]

Introduction

The global stocking of rainbow trout (*Oncorhynchus mykiss*) makes them among the most ubiquitously introduced fish species (Fausch et al. 2001; Marchetti et al. 2004; Crawford and Muir 2008). As an invading species, rainbow trout are known to interact with native species via direct predation and competition for prey and as a dominant character in interspecific interactions (Lowe et al. 2000; Baxter et al. 2007; Elkins and Grossman 2014). While rainbow trout are often viewed as drivers of native species declines, Didham et al. (2005) suggested that invasive species can be "passengers" in human-mediated loss of biodiversity. Therefore, studies on distributions of non-native species and their impacts would benefit from consideration of both anthropogenic activities and direct interspecific interactions to determine whether invasives are a symptom of ecological changes or a cause in native species declines.

Rainbow trout have established self-sustaining populations in many areas of eastern Canada where there is concern over effects on native salmonids (Thibault et al. 2009; Madden et al. 2010; Thibault and Dodson 2013). Studies of interspecific competition between rainbow trout and Atlantic salmon (*Salmo salar*) have shown that they occupy similar riffle habitats where rainbow trout tend to dominate in interspecific interactions (Hearn and Kynard 1986; Blanchet et al. 2007; Houde et al. 2016). Brook trout (*Salvelinus fontinalis*), also widespread in the region, have been shown to exhibit diet and habitat overlap with rainbow trout. However, brook trout tend to numerically dominate headwater assemblages and thus may be less affected by rainbow trout incursions (Johnston 1980; Magoulick and Wilzbach 1998; Thibault and Dodson 2013).

There is a general lack of information on how individuals in wild fish populations interact with rainbow trout following their

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establishment in natural streams. While there has been considerable research in controlled streams and laboratory aquaria (Blanchet et al. 2007; Houde et al. 2015), extrapolating to natural stream channels has inherent challenges. Spatially restricted studies or those using individuals of hatchery origin may fail to mimic natural interactions and may magnify the amplitude of competitive interactions (Korsu et al. 2010). Recent research has emphasized the importance of understanding interspecific competition under realistic stream conditions (Thibault and Dodson 2013; Johnson and Chalupnicki 2014; Johnson and McKenna 2015). One of those studies demonstrated that rainbow trout presence caused changes in habitat use by native brook trout and Atlantic salmon in situ (Thibault and Dodson 2013).

On Prince Edward Island (PEI), in eastern Canada, anthropogenic modification to the landscape and historical overharvest has led to declines in native salmonids, particularly Atlantic salmon (Cairns 2002; Cairns and MacFarlane 2015). Following an era of widespread introduction, over 1 000 000 rainbow trout were stocked, and they have now established naturally reproducing populations in many PEI rivers (MacCrimmon 1971; Guignion et al. 2010). It has been reported that Atlantic salmon populations in all PEI rivers with rainbow trout are below conservation requirements (Cairns et al. 2012). With many watersheds in a relatively limited geographical area, PEI represents a unique opportunity to study rainbow trout incursion at the landscape, watershed, and reach scale to investigate their influence on native salmonids.

The objectives of this research are (1) to characterize the status of rainbow trout invasion on PEI, (2) to investigate the factors leading to successful rainbow trout invasion, and (3) to establish the degree of habitat overlap between rainbow trout and native salmonids. It is hypothesized that rainbow trout thrive in anthropogenically modified watersheds, whereas Atlantic salmon prefer less impacted habitat and brook trout would associate with headwater habitats. Habitat variables and salmonid community composition were examined across multiple ecological scales. At the landscape scale, watersheds with and without rainbow trout invasion were used to determine the influence of variables such as discharge, temperature, watershed slope, and land-use patterns on rainbow trout establishment. At both the watershed and the reach scale, surveys were conducted to examine the relationship between salmonid communities and instream habitat variables such a substrate, stream width, and slope. We sought to contribute to the understanding of the ecological space where non-native rainbow trout thrive and to improve the understanding of potential for competitive interactions with Atlantic salmon and brook trout in natural streams.

Methods

Study design

The study was comprised of a rainbow trout distribution update from Guignion et al. (2010), a landscape-scale study investigating if there are habitat differences between invaded and uninvaded rivers, and two reach-scale studies exploring habitat use and spatial overlap between native salmonids (Atlantic salmon and brook trout) and rainbow trout. In the distribution and landscape-scale studies, watersheds were selected based on angler capture reports, proximity to aquaculture, and stocking activity (Fig. 1; supplemental material Fig. S1[1]; Table S1). In the landscape survey, watershed attributes including distance to the nearest source population, land use, watershed slope, stream discharge, and stream temperature were monitored to investigate if there were underlying trends in the success of rainbow trout across the province. In two independent reach-scale surveys, salmonid densities were evaluated by electrofishing, and a suite of habitat features were evaluated at each site. The first survey in 2001–2002 examined salmonid communities across a gradient of agricultural land use. We reevaluated this data set in an effort to elucidate the degree of habitat overlap between rainbow trout and native salmonids. In the second survey (2014), salmonid species composition was evaluated on three rivers across an upstream–downstream longitudinal gradient. Both reach-scale surveys included assessment of hydrological variables including discharge, particle size distribution, and stream channel slope.

Study system

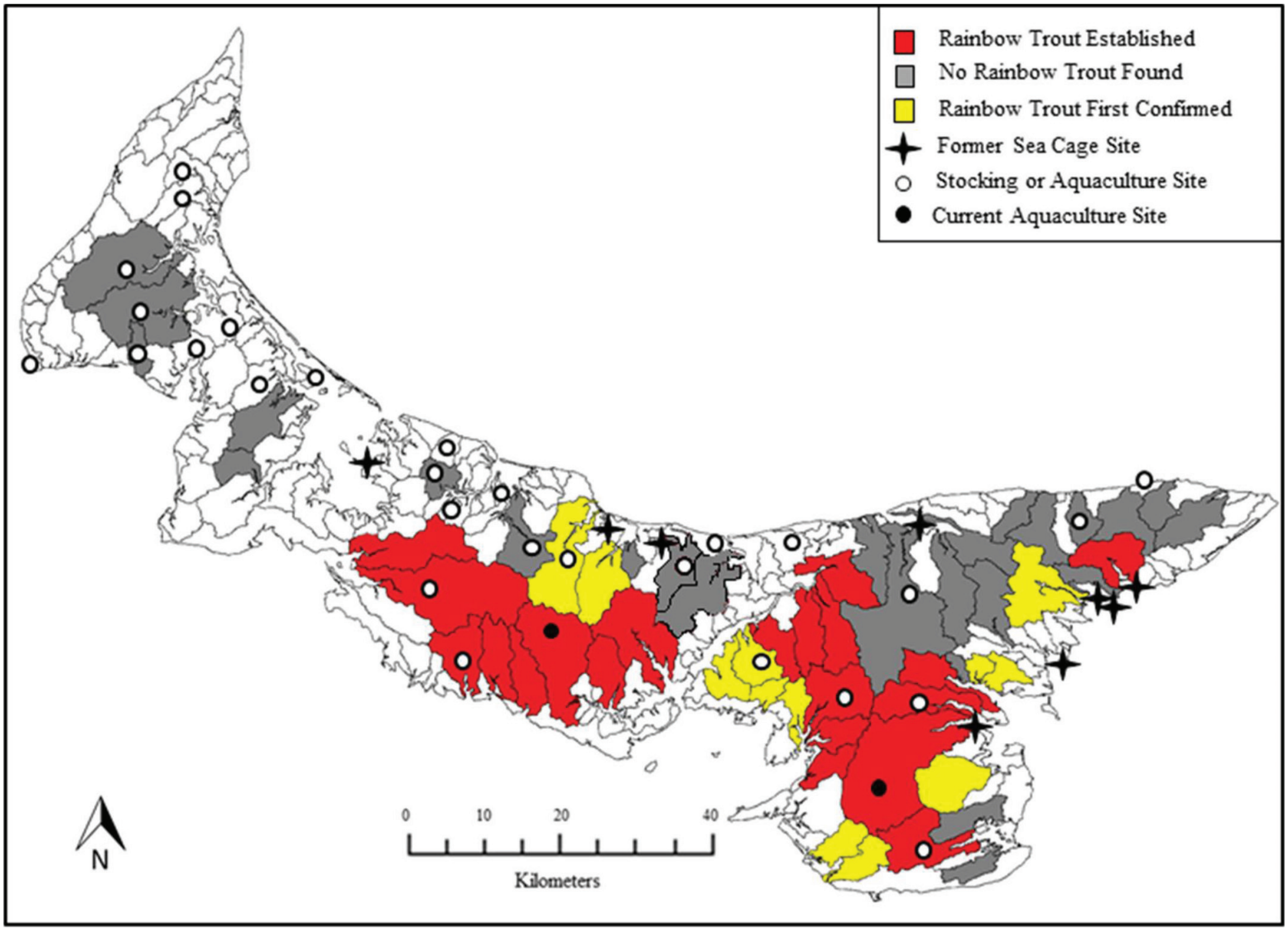
PEI is Canada's smallest province with an area of 5560 km^2. The island is in the southern Gulf of St. Lawrence and comprised of carbo-permian sandstone deposits overlain by glacial till (van der Poll 1983). The present-day Island was revealed approximately 7000 – 10 000 years ago as Pleistocene glaciers receded (Miller 2010). Holocene sea level rise has resulted in short rivers on PEI (e.g., Shaw 2005), which are spring fed from groundwater sources (Jiang and Somers 2009; Knysh et al. 2016). Land use is dominated by agriculture with approximately 50% of the land base in agricultural production province-wide (PEI Department of Agriculture and Forestry 2015). Brook trout are common in all watercourses across the province. Atlantic salmon were widespread prior to European colonization, but habitat modification (deforestation, dam construction) and overharvest have eradicated Atlantic salmon from much of its original distribution (Cairns et al. 2012; Cairns and MacFarlane 2015). Conversely, rainbow trout have been widely introduced over the last century and now have established naturalized populations in many areas of the province (MacCrimmon 1971; Cairns and MacFarlane 2015). Historically, the introduction of rainbow trout was viewed as an opportunity to promote recreational fisheries and their introductions went largely undocumented for decades. While Guignion et al. (2002) synthesized known stocking totals and aquaculture sites (sea cages and land based), the total numbers and locations of rainbow trout introductions on PEI are unknown (but see Fig. S1; Table S1).

Rainbow trout distribution survey

The aim of the distribution survey was to update the status of rainbow trout in the province, particularly in areas with recent anecdotal reports. To date, a province-wide survey of rainbow trout distribution has not been conducted, and routine monitoring of salmonid populations tends to focus on larger watersheds and those known to contain Atlantic salmon (see Guignion et al. 2010). Due to a lack of prior information in many watersheds, new records of rainbow trout were not necessarily indicative of a recent dispersal or invasion. Nonetheless, the survey will form the basis to monitor future dispersal and invasion. Electrofishing surveys were conducted on 37 rivers in two time periods (19–21 September 2011 and 13 August – 4 October 2013). Surveys were conducted with a backpack electrofisher (Smith-Root, Mode LR-24 POW) using a single-pass spot check. Electrofisher power was set at the factory default (400 W) and conductivity ranged from 142 to 370 μS/cm in the study rivers. A single survey date with multiple 200 m reaches per system was conducted; however, remote access, unsuitable habitat, and the relatively short length of several coastal streams often restricted sampling to one or two sites. Sites were selected based on angler reports, previous stocking records, and proximity to established populations. Currently, there are two active rainbow trout culture operations on PEI, but both are in watersheds where rainbow trout have established. Given that there was no active rainbow trout stocking of eggs or juveniles on any of the watersheds in the survey, the presence of juvenile rainbow trout was used as an indicator of a naturally established population. In 2016 and 2017, unrelated electrofishing surveys and an instream

[1]Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2017-0342.

Fig. 1. Watersheds assessed in the distribution survey with red indicating a previously established population, yellow indicating areas where rainbow trout (*Oncorhynchus mykiss*) were first confirmed in this study, and grey indicating that no rainbow trout were found. Locations with a record of stocking or aquaculture are indicated by circles and locations of former sea cage aquaculture operations are shown by star symbols. [Color online.]



counting fence yielded additional observations of rainbow trout in new watersheds; these findings are reported below.

Landscape-scale study

The landscape-scale survey of watershed characteristics included 14 watersheds where rainbow trout have established and 12 without established populations but all with some degree of prior introduction of varying intensity. Watersheds without rainbow trout were chosen based on historical information of previous stocking activity or proximity to former rainbow trout aquaculture operations (Fig. 1). Watersheds were characterized for land use and mean watershed slope using the PEI land use layer and digital elevation models with Arc GIS (v. 10.2) (ESRI, Redlands, California, USA, Corporate Land Use Inventory 2010) (PEI Department of Environment, Energy and Forestry 2010). Continuous temperature data were obtained by deploying a thermal logger (Onset Hobo Tidbit or Hobo Water Temp Pro 2) on the mainstem of each river and maintained year-round during 2013–2014 (3 h logging interval). Aperiodic gaps at some sites were caused by equipment failure or environmental conditions; these were resolved by establishing a linear regression relationship using two central sites with complete temperature profiles (Pisquid River, 13 sites, adjusted R^2 = 0.90–0.99 and Trout River, five sites, adjusted R^2 = 0.95–0.99). Temperature profiles were used to generate various cumulative degree-day based metrics:

$$\text{(1)} \qquad \mathrm{DD} = \left(\left(\frac{T_{\max} + T_{\min}}{2}\right) - T_0\right)$$

where $T_{\max}$ and $T_{\min}$ are the maximum and minimum daily temperatures and T_0 is the temperature threshold for subsequent metrics. Cumulative degree-days (DD) was calculated with a T_0 of 0 °C, as it is a common metric for embryonic development (Jonsson et al. 2005). Effective growing degree-days (EGDD) were calculated with a T_0 of 5 °C, as this metric may have implications for juvenile growth (Fausch 2007; Thibault et al. 2010*a*). Groundwater, which is discharged at approximately 7 °C throughout the year (Knysh et al. 2016), may warm the stream water during winter months, which may influence upstream movements or the timing of spawning period. Thus, another metric considering degree-days during winter (between 1 January and 31 March) was generated (winter DD) (T_0 = 0 °C). We also quantified the degree-days during the potential egg incubation period (1 April to 31 June) and defined it as incubation degree-days (incubation DD) (T_0 = 0 °C), and spawning period was determined from several years of the authors' observations of actively spawning rainbow trout. This corroborates with documented spawning periods of rainbow trout in their native range during increasing water levels (Muhlfeld et al. 2009). Peak annual flows on the West River (Environment Canada Gauge 01CC005) occurred in late March or April 16 times from

1989 to 2012 (67% of years). Discharge was surveyed using a Flo-Mate (model 2000 portable flowmeter, Marsh-McBirney, Inc., Frederick, Maryland, USA). Flow monitoring occurred during 2013 and 2014 during the full range of flow conditions. Discharge was calculated (Q = velocity × area) and hydrographs were modeled for each site by comparing with nearby Environment Canada gauging stations (01CA005, 01CB002, 01CC002, 01CA003, and 01CB004) or the gauging stations used in Alberto et al. (2016). Gauge-level data was compared with flow measurements via linear regression of log-transformed discharge data and the predictive equation of the line was applied to stream gauge data to predict study site discharge throughout the year (average daily cubic metres per second). The r^2 value was set to >0.7; only two sites fell below this threshold (North Lake Creek 0.66 and Vernon River 0.65), which may be attributed to a missed sampling event or watershed-specific features. Hydrographs from the study were standardized by watershed area (cubic metres per hectare per year) to generate a standardized value for the landscape multivariate analysis. At each flow monitoring event, conductivity, pH, and salinity of river water were recorded using a YSI V2 6600 multiparameter sonde (Yellow Springs, Ohio, USA) to document abiotic stream characteristics.

Reach-scale studies

The first reach survey conducted at the watershed scale was part of a 2001–2002 survey that examined 13 watersheds (32 sites) and the second occurred in 2014 on three watersheds (42 sites). The original study aimed to assess how varying land-use intensity (highly agricultural to highly forested) affected salmonid populations (Gormley 2003). The second reach survey (17 July 2014 – 9 September 2014) used a similar methodological framework but examined three watersheds along an upstream–downstream gradient. In the latter reach survey, Pisquid River and West River have naturally coexisting rainbow trout and Atlantic salmon. The other watershed (Cross River) has a productive population of Atlantic salmon but no rainbow trout. This site was selected to gather reference data on Atlantic salmon distribution and habitat use in the absence of rainbow trout.

In 2001–2002, site selection was based on surrounding land use, visual inspection of the suitability of salmonid spawning habitat (shallow riffle areas and gravel–cobble substrate with minimal interstitial sediment and some pools), and site accessibility (Gormley 2003). Sampling reaches were then randomly selected in the region of stream selected. In the 2014 survey, sites were stratified into three reach types: mainstem, tributary, and headwater. We considered the area between the head of tide (tidal limit) and the first fork to be the mainstem (Reach 1), tributary habitats to be major branches off the mainstem (Reach 2), and headwaters to be the most upstream areas above Reach 2 that still maintain passage for migrating fish (Reach 3). In several areas, access was limited by landowner permission or general accessibility of the watercourse. Within the areas that were identified as accessible, starting locations were randomly selected on GIS software prior to the survey. In the field, the electrofisher operator began the survey at the bottom of the riffle that was nearest to the predetermined point. In total, Cross River had seven sites, Pisquid River had 19, and West River had 17.

The two reach surveys employed slightly different electrofishing methods. In 2001–2002, electrofishing surveys were conducted with barrier nets (upstream barrier on all sites and a downstream barrier on sites >4 m width). Each sampling event consisted of three passes and sites were chosen to be approximately 100 m² of stream area. Each site was surveyed throughout 2001 and 2002 (July, August, and September) for a total of six sampling events at each site. The mean density of each species was taken over the entire time series. In 2014, a stream length of approximately 50 m was paced off and marked at the top and bottom. The area of the site was calculated by measuring the surface width (metres) at three evenly spaced locations and the total site length (metres). The locations of each sampling reaches are shown in Fig. 2. A single-pass backpack electrofishing survey (without barrier nets) was used to sample the fish assemblage. This strategy allowed the survey of a greater number of reaches within the limited period of study and allowed greater access to remote locations where logistics prohibit the use of barrier nets (Foley et al. 2015). The operator of the electrofisher applied current in short bursts to avoid herding fish upstream (Thibault and Dodson 2013). Electrofisher power was set at the factory default (400 W) and conductivity ranged from 142 to 180 μS/cm. Fish density (individuals per square metre) was calculated from the number of juveniles found in the reach. While this method differed from the approach in the first survey (three passes with barrier nets), it permitted more rapid sampling in sites where Atlantic salmon is a species of conservation concern. In both surveys, once the sweep was complete, all fish were identified to species and measured (±1 mm fork length). Given that the goal was to explicate competitive interactions between juveniles (age 0–2), larger fish (>17.5 cm) were assumed to be smolts or post-smolts (rainbow trout and Atlantic salmon) or adults (stream resident brook trout (as in Thibault et al. 2010; Thibault and Dodson 2013).

In both reach surveys, an assessment of hydrological variables including substrate composition, stream slope, and discharge was conducted. The substrate was examined by a random walk Wolman pebble count over the erodible channel of the site; 100 randomly selected particles were measured on the x-, y-, and z-axes to the nearest 0.1 cm (Wolman 1954; Newbury 1996). The three axes were averaged to standardize substrate size as the mean particle size. The proportion of cobble (>6.4 cm mean width) and fine pebble (0.2–1.6 cm) in the site was determined (Reynoldson et al. 2012). To ensure consistent sampling, one surveyor measured substrate at all sites. Stream bed slope (metres per metre) was determined at each site with a surveyor's level by evaluating the change in elevation over the length of the site (Giberson and Caissie 1998). Discharge, bankfull width, and cross-sectional area were measured at three representative locations along the reach. The tractive force equation in Giberson and Caissie (1998) was used to calculate bed sheer stress:

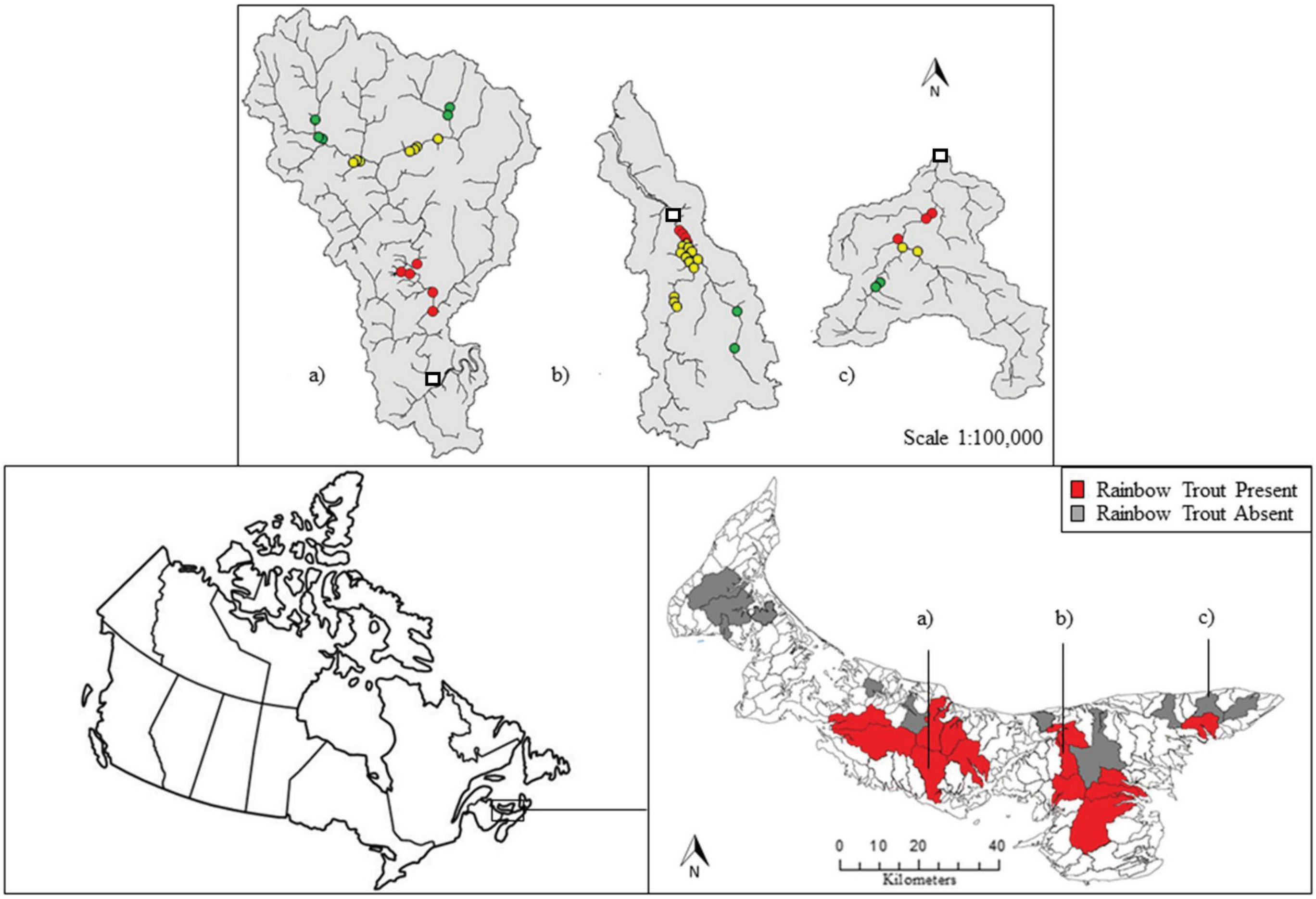
$$\tau(\mathrm{kg/m^2}) = 1000\ \mathrm{kg/m^3} \times D \times S \qquad (2)$$

where D is the mean depth (metres) and S is the water surface slope (metres per metre). From the tractive force equation, τ is considered equal to the intermediate axis of the substrate that would be in motion at a given discharge. The tractive force and bed in motion were calculated for the flow condition at the time of the survey and bankfull stage to generate a bankfull bed in motion variable.

Statistics

Landscape and reach-scale surveys were evaluated using a combination of univariate (STATISTICA v.8; Stat Soft 2007, Tulsa, Oklahoma) and multivariate statistics (PRIMER v.6 and PRIMER v.6 with PERMANOVA + v.1; PRIMER-E Ltd., Plymouth, UK). At the landscape scale, land-use and habitat variables were compared between watersheds to establish whether there are any differences between watersheds where rainbow trout have been successful or unsuccessful. Land-use and habitat variables were evaluated using ANOVA with rainbow trout presence and absence as a categorical variable. All data were tested for the assumptions of parametric statistics using normal probability plots and the Brown–Forsythe test for homogeneity of variance; variables that were not normally distributed were log (agriculture, wetland, conductivity, slope, DD, EGDD, and incubation DD) or square root transformed (watershed area, distance to source, residential area, and discharge). The critical level of significance was $p < 0.05$ for all

Fig. 2. Watersheds involved in the landscape-scale habitat assessment indicating study rivers with rainbow trout (*Oncorhynchus mykiss*) (red) and those without (grey). Reach locations are shown for three rivers involved in the fine-scale habitat survey: (*a*) West River, (*b*) Pisquid River, and (*c*) Cross River. Colored circles indicate reach designation with mainstem (red), tributary (yellow), and headwater (green). In both Pisquid River and West River, the drainage map contained a substantial portion of tidal water (Pisquid River 2.9 km and West River 2.8 km); the head of tide locations (squares) is identified on the map. [Color online.]



analyses. Landscape-scale abiotic variables and land-use data were also evaluated using principal components analysis (PCA).

In the reach-scale analyses, habitat variables were associated with fish densities using a distance-based linear model (DistLM) (Anderson et al. 2008). This DistLM is a multivariate multiple linear regression using association indices. Both reach surveys analyses were using Bray–Curtis similarity as a measure of association (Anderson et al. 2008). In both reach surveys, a Bray–Curtis resemblance matrix was generated from square root transformed fish density. In the earlier survey, environmental data that were not normally distributed were log transformed (percent forest, mean depth, mean width, and tractive force) or square root transformed (wetland, agriculture, percent fines and sand, percent fine pebble, percent cobble, slope, and upstream distance). In the latter survey, variables were log transformed (mean width, upstream distance, bankfull bed in motion, mean depth, hydraulic radius, tractive force, and bankfull tractive force) or square root transformed (percent bed in motion, slope, percent cobble, percent fine pebble, and percent fines and sand) to achieve normal distribution. Environmental variables were used as the predictor variables in the model. The process consists of performing an ordination of the community similarity matrix followed by generation of a model to determine what variables predict that community best. The model was run with 9999 permutations with model type based upon Anderson (2001) and Anderson et al. (2008). Environmental data in the DistLM were based on the adjusted R^2 selection criteria and a stepwise selection procedure. Model selected environmental data were used in a constrained ordination to illustrate fish–environment relationships using distance-based redundancy analysis (dbRDA). Strength of relationship between fish species and dbRDA axes are reported as Pearson correlation coefficients.

Results

Distribution

Many of the watersheds in the distribution survey had not been recently surveyed; therefore, it was not possible to confirm that a new record was indicative of an active invasion into new watersheds. Nonetheless, 12 new watersheds were found to have juvenile rainbow trout, bringing the total to 32 rivers with confirmed reproduction. This represents the first confirmation of rainbow trout establishment in two northside watersheds. The greatest increase was on the south shore of PEI with six new watersheds containing rainbow trout. The remaining four new documentations of rainbow trout establishment were on the east side of PEI. There has been no indication of expansion to the western extent of PEI. Following the conclusion of the distribution survey, independent surveys (2016 and 2017) found juvenile rainbow trout in three additional systems, Winter River, Cow River, and North Lake Creek, all along the north shore of the province. A partially spent female rainbow trout (46 cm, 1.15 kg) was captured heading

Table 1. Summary of variables used in the landscape-scale survey.

	Rainbow trout present (n = 14)			Rainbow trout absent (n = 12)				r			
	Median	Mean	SD	Median	Mean	SD	p	PC 1 = 30.1%	PC = 23.1%	PC 3 = 12.7%	PC 4 = 9.2%
Distance to nearest population (km)	15.2	18.2	12.4	68.3	71.7	24.4	**<0.001**	**0.6**	0.1	0.4	−0.4
Watershed area (km²)	37.3	54.5	35.5	31.8	39.0	39.3	0.160	−0.2	−0.2	−0.2	0.8
Mean slope (°)	3.94	4.19	1.02	3.37	3.25	1.34	**0.022**	**−0.6**	−0.2	−0.7	0.1
Agriculture (%)	42.58	46.25	18.32	24.56	29.52	21.17	**0.012**	**−0.8**	0.0	0.5	0.2
Forest (%)	48.25	43.28	18.09	62.23	57.72	21.11	0.072	**0.7**	0.1	−0.6	−0.1
Residential (%)	1.56	1.73	0.95	1.01	1.20	1.03	0.105	**−0.8**	−0.2	0.3	−0.1
Transportation (%)	2.01	2.02	0.40	1.95	1.93	0.43	0.566	−0.5	−0.4	0.1	−0.3
Wetland (%)	2.39	3.18	2.49	6.31	6.58	4.41	**0.045**	**0.9**	0.0	0.2	0.0
Degree-days (°D)	2801	2843	266	2760	2889	394	0.792	0.0	**−0.9**	0.0	−0.1
Winter degree-days	168	191	5	74	135	104	0.095	**−0.6**	0.2	−0.2	−0.4
Effective growing degree-days	1364	1380	266	1484	1547	435	0.329	0.2	**−0.9**	0.2	0.0
Incubation degree-days	810	820	74	809	853	131	0.496	0.1	**−1.0**	0.1	0.0
Discharge (m³·ha⁻¹·year⁻¹)	7842	801	1396	7660	7498	1465	0.359	−0.5	−0.1	−0.2	−0.4
Mean conductivity (μS/cm)	199	207	43.93	224	221	45.91	0.492	−0.2	0.5	0.6	0.0
Mean pH	7.89	7.90	0.10	7.95	7.94	0.16	0.367	0.3	−0.4	0.3	0.0

Note: p values in bold indicate significant differences between rivers with and without rainbow trout (*Oncorhynchus mykiss*). Pearson correlation values (r) are presented from principal components analysis of all landscape variables.

downstream at the counting fence at the head of tide on North Lake Creek on 29 May 2016; the fish was sacrificed for evaluation of reproductive status. Considering that all three of these watersheds are along the north shore, it appears that rainbow trout are actively dispersing into new areas along the north shore of the province.

Landscape-scale survey

Landscape-scale differences in watershed attributes showed that certain factors influenced the likelihood of rainbow trout establishment. The mean distance to source for watersheds with rainbow trout was 18.2 ± 12.4 km, while those without rainbow trout had a mean distance of 71.7 ± 24.4 km (Table 1).

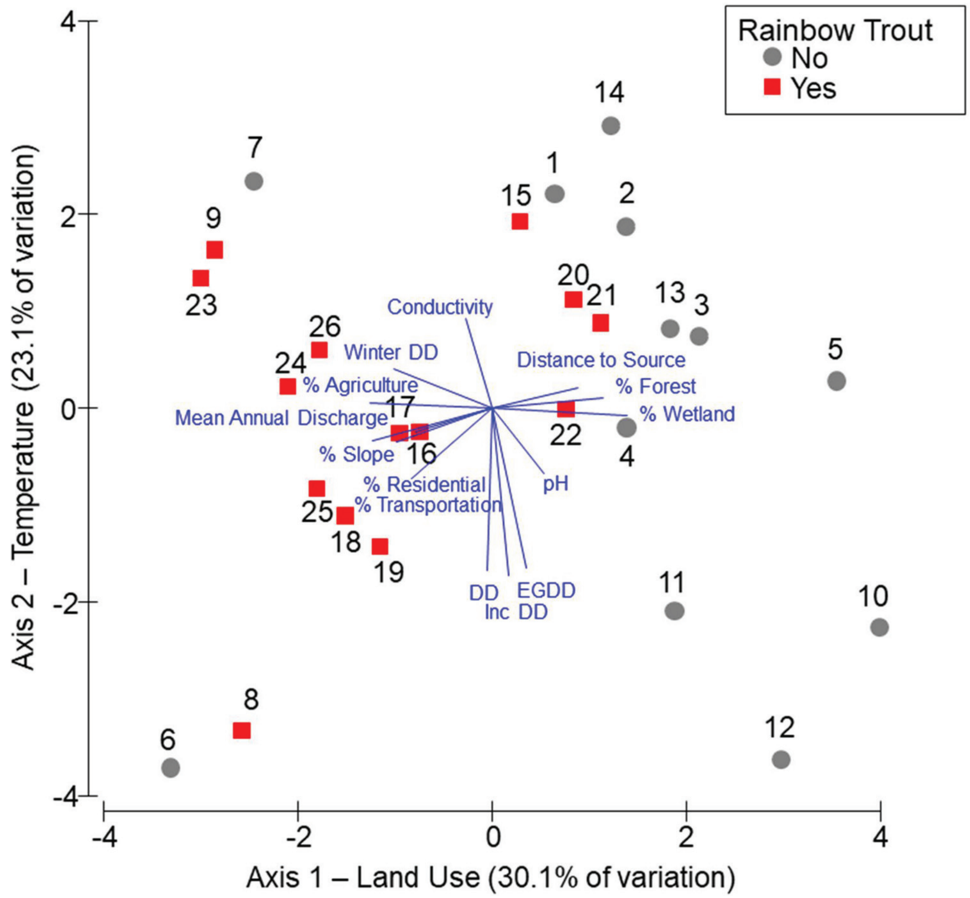
Including distance to source, there were statistically significant differences between invaded and noninvaded rivers for four of the 15 watershed parameters. Watersheds with established rainbow trout also had higher slope, a greater proportion of agriculture, and a lower proportion of wetland than systems without. Temperature metrics were not significantly different between invaded and uninvaded watersheds. A PCA was conducted to visualize the landscape variables in the context of the presence and absence of rainbow trout (Fig. 3). PC axis 1 represented 30.1% of the variation and was primarily driven by the land-use gradient. Variables related to human land use (percent agriculture and percent residential area) were inversely related to percent forest and wetland area, meaning that areas with more human development had less forest and wetland. Additionally, the farther a watershed was from a source population, the more forest cover and wetland area it was likely to have. Other variables associated with the land-use axis were mean slope and winter DD. Watersheds with higher agriculture tended to have higher slope. The second PC axis was governed by the degree-day metrics (EGDD, incubation DD, and DD) and conductivity, which explained 23.1% of the variation in the data set. Warmer streams tended to have lower conductivity. The third PC axis was related to mean watershed slope and explained 12.7% of the variability in the data. Watershed area came out as the primary factor in PC axis 4, which explained 9.2% of the variability. In total, the first four principal components explained 75.1% of the variation in the landscape and hydrological data set. There was a general grouping of watersheds with and without rainbow trout along PC axis 1, although two watersheds without rainbow trout (6 and 7) more closely resembled invaded watersheds than noninvaded watersheds. Consistent with the univariate statistics, this suggests that the presence and absence of rainbow trout are primarily related to proximity to source populations and watershed attributes (high agriculture, residential area, and mean slope).

Reach-scale surveys

In the watershed-scale study (2001–2002), rainbow trout were found in four of 13 watersheds (nine of 32 reaches), Atlantic salmon were found in eight watersheds (14 of 32 reaches), and brook trout were found in all study reaches. Atlantic salmon were the most abundant species in four reaches and brook trout dominated the remaining sites. Rainbow trout were not the most abundant salmonid at any of the sites in the survey. Overall, bankfull bed in motion, agriculture area, and depth were all significant factors in the outcome of the DistLM. The DistLM determined to be most predictive of the salmonid community (ordination overlaid in red in Fig. 4) retained nine of the original 13 habitat variables (adjusted R^2 = 0.56). dbRDA axis 1 represented 50.3% of the total variation and was associated with bankfull bed in motion (r = 0.54) and wetland area (r = −0.45). The second axis described 14.9% of total variation and was associated with agriculture area (r = 0.66) and forest area (r = −0.34) (Fig. 4*a*). Rainbow trout density was most clearly related to slope and land use, and Atlantic salmon density was related to stream width and wetland but negatively correlated with bed in motion. Brook trout were not as clearly aligned with habitat variables, although density tended to be higher in reaches with less forested land, smaller substrate, and greater bed in motion.

Of the 43 reach sites in the 2014 reach-scale survey on three rivers, rainbow trout were present at 33 sites, Atlantic salmon at 29 sites, and brook trout at all 43 reaches. The ordination of the fish community (Fig. 4*b*) shows that Atlantic salmon were most predominant in the mainstem of the rivers and brook trout dominated the community in the headwaters. Rainbow trout were typically abundant in high-slope tributary habitats. In Cross River, where rainbow trout are not present, Atlantic salmon were found in the two tributary sites, one of which had very similar habitat to what rainbow trout occupy in other rivers (see sites 4 and 5, Fig. 4*b*). In the reach-scale survey, the habitat variable model determined to be most predictive of the salmonid community retained eight of the original 15 habitat variables (adjusted R^2 = 0.47). Mean width, bankfull bed in motion, percent cobble, and upstream distance were all significant contributors to the DistLM. The first dbRDA axis represented 39.6% of the total variation and was associated with stream width (r = 0.48) and percent cobble

Fig. 3. Groupings of watersheds with rainbow trout (*Oncorhynchus mykiss*) (red squares) and without (grey circles) separated by measured stream variables and land-use characteristics at each site using principal components analysis (axes 1 and 2). Numbers on the graph refer to individual rivers reported in Table S2. [Color online.]



(r = 0.45) that were negatively correlated with upstream distance of site (r = −0.46). The second dbRDA axis accounted for 39.6% of total variation and was associated with bankfull bed in motion and bankfull width (r = −0.58, −0.59) and fine pebble (r = 0.50). Atlantic salmon were most clearly associated with cobble substrate and with river width, as indicated by their predominance in the mainstem. Rainbow trout were most abundant in reaches with higher slope and greater bed in motion and brook trout were most associated with smaller order streams with fine pebble.

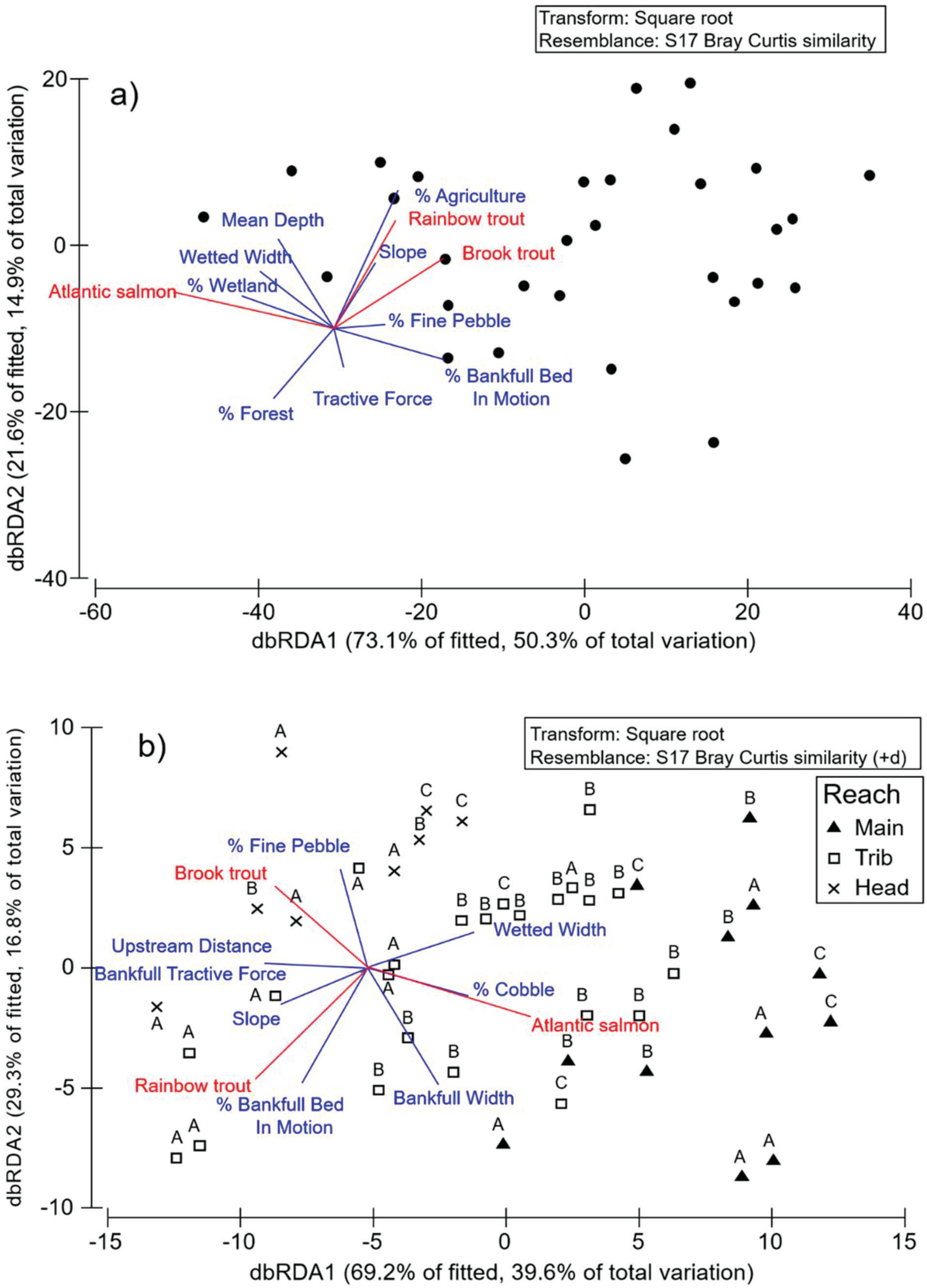
Discussion

This study confirmed an increase in the known distribution of rainbow trout to 32 watersheds on PEI and this information can be used as baseline data to monitor subsequent invasions across the province. Watersheds with new records of rainbow trout tended to be nearby to established populations, suggesting that these areas act as a source for dispersal. The landscape-scale study (of established and nonestablished rivers) confirmed that a lower distance to the nearest source population was associated with rainbow trout presence. Other variables associated with the presence of rainbow trout were high agricultural land use and watershed slope. Variables associated with water chemistry and temperature were not correlated with rainbow trout distribution. In the first reach survey with 13 watersheds, rainbow trout presence correlated with higher upstream agricultural land use and higher stream slope. When salmonid communities were examined along the length of the three rivers, rainbow trout presence was associated with higher stream slope and its correlate bed in motion. The reach surveys provide evidence that wide stream channels with abundant cobble are the primary habitats of Atlantic salmon juveniles. Brook trout were the most widespread (found in all study reaches) and tended to be the dominant species in headwater reaches with fine substrate.

With adjacent rivers interconnected by dispersing individuals, it is possible that populations on PEI function as metapopulations, discrete populations linked by dispersal (Schtickzelle and Quinn 2007; Thibault et al. 2010*b*). In coastal ecosystems, anadromy is required for metapopulations, and PEI remains one of the few known places where non-native rainbow trout have established an anadromous life cycle outside of Chile, Argentina, and other parts of the Gulf of St. Lawrence (see Pascual et al. 2001; Thibault et al. 2009; Arismendi et al. 2014). Companion tracking studies have shown that PEI adult rainbow trout enter saltwater and stray out of the system in which they are resident occasionally (authors' unpublished data). Fausch (2007) speculated that the risk of subsequent invasion would be high if coastal populations of non-native rainbow trout were to establish an anadromous life cycle phase. Anadromy may have other, less obvious consequences that promote establishment. It has been demonstrated that rainbow trout juveniles with anadromous mothers grow faster and larger than resident counterparts (Liberoff et al. 2014) and anadromous individuals are certainly more fecund. Thus, it is plausible that anadromy imparts other fitness advantages in these coastal systems (Thibault et al. 2009, 2010*b*).

Most studies of competitive interactions between juvenile rainbow trout and Atlantic salmon have been conducted in the laboratory or confined stream reaches (Blanchet et al. 2007, 2008; Van Zwol et al. 2012; Houde et al. 2015). Extrapolating from

Fig. 4. Distance-based redundancy analysis (dbRDA) for the reach-scale watershed surveys for (*a*) 13 watersheds across a gradient of land-use intensity and (*b*) three watersheds across a longitudinal gradient. Letters in Fig. 4*b*) correspond to the respective watersheds (A, West River; B, Pisquid River; C, Cross River). Reach summary data are presented in Table S3. [Color online.]



manipulative interaction studies to the natural environment represents a key challenge in the effort to determine potential threats to native species. Additionally, the common practice of using hatchery stocks to compare inter- and intraspecific competition may further confound the ability to draw ecologically relevant conclusions (Weber and Fausch 2003; Buoro et al. 2016). Rainbow trout have been shown to dominate direct competitive interactions with Atlantic salmon (Blanchet et al. 2008; Van Zwol et al. 2012), but in the native range of rainbow trout, competitive interactions with invading Atlantic salmon favored the resident over the challenger. Studies have shown that salmonid species other than rainbow trout pose a greater risk of competition with Atlantic salmon (Volpe et al. 2001; Johnson and Chalupnicki 2014). In a natural stream setting, Johnson and McKenna (2015) concluded that inherent variability between streams, diel activity differences, and differences in competition between individuals and species are a major limitation for drawing general management applications from habitat-use studies. However, one study of Atlantic salmon rivers that were newly invaded by rainbow trout found that Atlantic salmon changed habitat use in the presence of rainbow trout (Thibault and Dodson 2013).

Determining if these competitive interactions and habitat shifts result in tracible changes in survival or fitness of wild Atlantic salmon populations continues to be a major challenge in prioritizing the threat posed by rainbow trout. Stanfield and Jones (2003) found that the presence of high-quality habitat (large substrate) enabled both rainbow trout and Atlantic salmon to coexist in high densities. Both reach-scale surveys in this study suggest that Atlantic salmon in PEI streams require suitable substrate to carry out freshwater life cycle phases. In this study, rainbow trout tended to use tributary habitats for spawning and rearing, while Atlantic salmon used mainstem habitats. However, in Cross River, where no rainbow trout occur, Atlantic salmon were found in the two tributary habitat sites, suggesting that tributary habitats can support Atlantic salmon. This leads to further research questions. Are rainbow trout outcompeting Atlantic salmon in tributary habitat? Or alternatively, are habitat degradations in highly agricultural watersheds driving salmon declines? Additionally, the recent documentation of rainbow trout on two highly forested Atlantic salmon rivers (Cow River and North Lake Creek) could grant an opportunity to study the invasion of rainbow trout in salmon rivers with high-quality salmon habitat. North Lake Creek was a "rainbow trout absent" site in the landscape analysis (site 14, Fig. 3), but the species has recently been found in the system. Future research in these watersheds could further the understanding of these interactions and help prioritize limited management resources.

While interspecific interactions between juvenile salmonids have been well studied, other potential interactions such reproductive habitat overlap have received less attention. As spring spawners, the shorter time in the redd and high spring flows could impart other advantages over the native species whose eggs incubate overwinter. Rainbow trout spawning starts just before spring freshets turn over the substrate and clean gravel (Muhlfeld et al. 2009). Spring-spawning rainbow trout could superimpose redds over Atlantic salmon and brook trout redds and compromise hatching success. Taniguchi et al. (2000) showed that introduced rainbow trout superimpose redds over native charrs in Japan. In New Zealand, rainbow trout redd superimposition over brown trout (*Salmo trutta*) reduced brown trout spawning success by 94% in an experimental stream section (Hayes 1987). In PEI rivers, brook trout often chose spawning sites nearby to groundwater upwelling, which may make reproductive overlap less likely (Curry and Noakes 1995; Alberto et al. 2017). However, in high-gradient tributaries, where rainbow trout are particularly successful, reproductive superimposition over Atlantic salmon redds could have serious consequences for Atlantic salmon spawning success. A study of wild rainbow trout in Alaska found substrate (15–25 mm) to be an important determinant of spawning site selection, and other studies have reported that rainbow trout select stream velocities between 60 and 80 cm/s for spawning (Workman et al. 2004; Marchildon et al. 2011; Fraley et al. 2016). In a review of Atlantic salmon habitat requirements, Armstrong et al. (2003 and references within) reported spawning preferences between 30 and 85 cm/s and substrate sizes between 5.4 and 78 mm. Studies investigating spatial reproductive overlap between rainbow trout and native salmonids are needed to fill this current knowledge gap. This study, conducted at multiple ecological scales, showed that higher sloped areas in tributaries were favored by rainbow trout. However, the slopes encountered in PEI rivers can be relatively low when compared with rivers across the region; similar studies in other regions could validate the broader applicability of these findings.

Anthropogenic disturbance can also play a role in invasion dynamics, as invasive species may opportunistically capitalize on disturbed habitats, where native species have already declined (Didham et al. 2005). It has been shown that riparian areas with high anthropogenic disturbance are subject to higher levels of plant invasion (Liendo et al. 2013). Watersheds with high agricultural intensity, an indicator of anthropogenic disturbance, were more likely to have rainbow trout in this study. Additionally, rivers that were successfully established had higher mean slope and a lower proportion of wetland. While it is understandable that the proportion of wetland and agriculture in a watershed would be inversely proportional, it was not anticipated that agriculture and watershed slope would be positively correlated. It could be that these areas are located nearby to areas of original settlements or that higher sloped areas naturally provide better soil drainage for agriculture. It is more likely that this association between agriculture and slope is coincidental, as higher slope areas of the island are centrally located and nearby to higher human densities. Nonetheless, this relationship makes it difficult to discern if the ecological perturbation associated with agriculture (deforestation, siltation, etc.) has reduced biological resistance and enabled establishment or alternatively if higher sloped areas make better rainbow trout rearing habitat. It does appear that rainbow trout prosper in watersheds with higher disturbance. One study on PEI provided evidence that rainbow trout are more tolerant to disturbance; rainbow trout exhibited lower mortality than native salmonids following an agricultural chemical runoff event (Gormley et al. 2005). Sedimentation is another type of anthropogenically induced habitat degradation with the potential to affect all salmonid species, some perhaps more than others. Due to the longer incubation time of native salmonids, sedimentation may affect native species more adversely than rainbow trout.

Other abiotic attributes such as discharge patterns and temperature patterns had less influence on rainbow trout success across the province. Across broader geographical scales, flow regime can be a major predictor of rainbow trout invasion success (Fausch et al. 2001). The limited geographical scale of this study meant that hydrographic differences between watersheds were not likely to drive differential invasion success. Temperature was also considered in several metrics; however, there were no statistical differences between successfully invaded rivers and those that had not been invaded. Fausch (2007) suggested that 900–1000 EGDD (degree-days above 5 °C) was necessary for successful recruitment in rainbow trout. On PEI, both invaded and uninvaded rivers exceeded this temperature threshold.

While the ecological scales in this study cannot preclude the occurrence of direct competitive interactions, they suggest that habitat preferences on PEI may limit the opportunity for interspecific competition of Atlantic salmon and rainbow trout. Our findings coincide with those of Stanfield and Jones (2003) who found that competitive interactions with rainbow trout did not overwhelm Atlantic salmon in preferable salmon habitat. The findings of this research have implications for the management of the invading rainbow trout and the conservation of Atlantic salmon. Given limited resources for fisheries managers, Atlantic salmon spawning and rearing habitat is paramount to their restoration. The findings of this research suggest that rainbow trout thrive in higher gradient tributaries and subsequent research efforts could focus on interspecific interactions with Atlantic salmon in tributary habitats.

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