Transactions of the American Fisheries Society
Publication details, including instructions for authors and subscription information:
http://www.tandfonline.com/loi/utaf20

Impacts of Exotic Rainbow Trout on Habitat Use by Native Juvenile Salmonid Species at an Early Invasive Stage

Isabel Thibault [a] [c] & Julian Dodson [b]

[a] Département de Biologie, Québec-Océan , Université Laval , Quebec City , Québec G1V 0A6 , Canada

[b] Département de Biologie, Pavillon A-Vachon, Local 3044, 1045 Avenue de la Médecine , Université Laval , Quebec City , Québec , G1V 0A6 , Canada

[c] Ministère du Développement Durable , de l'Environnement , de la Faune et des Parcs, 880 Chemin Sainte-Foy, 2e étage, Quebec City , Québec , G1S 4X4 , Canada

To cite this article: Isabel Thibault & Julian Dodson (2013) Impacts of Exotic Rainbow Trout on Habitat Use by Native Juvenile Salmonid Species at an Early Invasive Stage, Transactions of the American Fisheries Society, 142:4, 1141-1150, DOI: 10.1080/00028487.2013.799516

To link to this article: http://dx.doi.org/10.1080/00028487.2013.799516

Transactions of the American Fisheries Society 142:1141–1150, 2013

ISSN: 0002-8487 print / 1548-8659 online
DOI: 10.1080/00028487.2013.799516

ARTICLE

Impacts of Exotic Rainbow Trout on Habitat Use by Native Juvenile Salmonid Species at an Early Invasive Stage

Isabel Thibault*[1]
Département de Biologie, Québec-Océan, Université Laval, Quebec City, Québec G1V 0A6, Canada

Julian Dodson
Département de Biologie, Pavillon A-Vachon, Local 3044, 1045 Avenue de la Médecine, Université Laval, Quebec City, Québec G1V 0A6, Canada

Abstract
The detrimental impact of introduced Rainbow Trout *Oncorhynchus mykiss* on native communities has been well documented around the world. Previous studies have focused on streams where the invasion has been successful and the species is fully established. In eastern Quebec, the invasion of Rainbow Trout is an ongoing process and, for now, there are few established populations. The presence of two native salmonids in these rivers, Atlantic Salmon *Salmo salar* and Brook Trout *Salvelinus fontinalis*, implies a risk of competition for habitat, despite the relatively low density of the Rainbow Trout populations, as all three species are known to use similar resources. In order to evaluate the strength of the interaction between the invading fish and the native species, we sampled nine rivers (five with Rainbow Trout and four free of Rainbow Trout) and characterized the habitat used by the three salmonids at the juvenile stage. River-scale analysis revealed that in invaded rivers, Rainbow Trout were associated with habitats characterized by closer proximity to the shoreline and by increasing shoreline cover. Estimates of habitat niche overlap integrating depth, water velocity, and substrate size revealed that niche overlap between Brook Trout and Atlantic Salmon significantly increased in the presence of Rainbow Trout. Furthermore, the two indigenous species preferred full cover in the absence of Rainbow Trout but in the presence of Rainbow Trout, which also preferred full cover, the indigenous species moved to more open habitats. Rainbow Trout showed a high growth rate, despite a size disadvantage at the beginning of the growing season, as compared with Atlantic Salmon and Brook Trout. It thus appears that even at an early stage of invasion, when its density is still low, Rainbow Trout significantly impact native salmonids.

Ecological and evolutionary impacts of biological invasions on native fauna and ecosystems are numerous (Hutchinson 1959; MacArthur and Levins 1964; Welcomme 1984; Kohler and Courtenay 1986; Williamson 1996; Mooney and Cleland 2001), but the interspecific competition exerted by an invader is generally the most important consequence of an alien species' establishment (Williamson 1996), even sometimes leading to the competitive exclusion of native species (e.g., Waters 1983; Waters 1999; Peterson et al. 2004; Bøhn et al. 2008). As such, biological invasions constitute one of the major contemporary threats to aquatic biodiversity.

Rainbow Trout[1] *Oncorhynchus mykiss* (both freshwater resident and anadromous forms) is one of the most introduced fish species worldwide (MacCrimmon 1971; Crowl et al. 1992; Cambray 2003), and its impacts (such as competition, predation, genetic and trophic alterations, and disease and parasite introductions) on native fauna, including fish, amphibians, and invertebrates, are extensively documented (e.g.,

*Corresponding author: isabel.thibault@mrnf.gouv.qc.ca
[1]Present address: Ministère du Développement Durable, de l'Environnement, de la Faune et des Parcs, 880 Chemin Sainte-Foy, 2e étage, Quebec City, Québec G1S 4X4, Canada.
Received April 13, 2012; accepted April 18, 2013

Welcomme 1984; Larson and Moore 1985; Fausch 1988; Krueger and May 1991; Crowl et al. 1992; Cambray 2003 and references therein; Hitt et al. 2003; Hasegawa and Maekawa 2006; Baxter et al. 2007). In many cases, Rainbow Trout invasions result in the displacement, reduction, or even extinction of native fish species, especially native salmonids. Rainbow Trout is considered among the 100 most harmful invasive exotic species (Lowe et al. 2007).

In Quebec, Rainbow Trout were introduced at the end of the 19th century for angling purposes and subsequently intensively stocked in the southwestern part of the province. Since the beginning of the 1980s, several decades following the first introduction, a few small established populations were documented in eastern Quebec, well outside the stocking area (Thibault et al. 2009; Thibault 2010). Reproduction was first documented in two rivers of the Charlevoix region (Malbaie and Du Gouffre) in 1982–1984. No other self-sustaining populations in eastern Quebec were observed before 2006, when the present study documented the presence of juveniles in five rivers. It is probable that Rainbow Trout were established in these rivers several years earlier, but their low abundance and the restricted area of reproduction impeded detection.

In 2007 and 2008, electrofishing surveys of five established populations in eastern Quebec revealed that the invader is mainly restricted to tributaries, where its density remains lower than 0.05 fish/m^2 (Thibault 2010). Questions have been raised about the potential impact of the exotic species on two native salmonids, Atlantic Salmon *Salmo salar* and Brook Trout *Salvelinus fontinalis*, that are abundant and almost ubiquitous (~0.10 fish/m^2; Thibault 2010) in the rivers of eastern Quebec. Several authors have demonstrated that the habitat requirements of Rainbow Trout are similar to that of Atlantic Salmon (Gibson 1981; Hearn and Kynard 1986; Fausch 1988) and Brook Trout (Larson and Moore 1985; Rose 1986; Magoulick and Wilzbach 1998; Blanchet et al. 2007).

The most serious impacts of introduced Rainbow Trout on native fish involve other salmonid species (Crowl et al. 1992). Whereas previous studies have demonstrated the negative impacts of introduced Rainbow Trout on indigenous salmonids once the invader is fully established (when abundant and widely distributed), questions remain concerning if—and to what extent—Rainbow Trout can impact native conspecifics at an early stage of the invasion process or at low population densities. The aim of this study was thus to obtain evidence of potentially detrimental interactions between low-density Rainbow Trout populations and native salmonids in eastern Quebec rivers.

Native salmonid species that inhabit the rivers recently colonized by Rainbow Trout are known to be territorial; Atlantic Salmon being aggressive and well adapted to exploiting riffles, whereas the early emergence of Brook Trout can provide a size advantage over Rainbow Trout of the same cohort during the first year of life (Gibson 1981; Rodríguez 1995 and references therein). In this context, sympatric native salmonids might compete successfully with Rainbow Trout at the juvenile stage as long as population densities of the salmonid invader are low, thus delaying or impeding its progression and impacts and increasing the capacity of managers to restrict or eliminate the newly established populations. On the other hand, Rainbow Trout are known to demonstrate strong competitive capacities (Hearn and Kynard 1986; Volpe et al. 2001; Hasegawa et al. 2004; Blanchet et al. 2007; Seiler and Keeley 2007a; Seiler and Keeley 2007b), and young of the year have a high growth rate related to their aggressive behavior in foraging and territorial defense (Gibson 1981; Whitworth and Strange 1983; Rose 1986). We thus predicted that the invader may negatively interact with native fish to such an extent that it could force them into less preferred habitats. To test this prediction, we evaluated habitat niche overlap among species and habitat preferences and growth rates of each species.

METHODS

The approach we adopted here does not allow us to directly demonstrate the presence or intensity of interspecific competition. To do so, species presence and densities must be manipulated (Fausch 1988), involving an inacceptable level of intervention into protected Atlantic Salmon habitat. Rather, a sampling plan was designed to exploit rivers characterized by natural variations in species composition and fish densities, allowing us to demonstrate interspecific interactions suggestive of true competition.

Study area.—A total of nine rivers, distributed in eastern Quebec on both shores of the St. Lawrence Estuary (Figure 1), were sampled during the summers of 2007 and 2008. Five rivers supported self-sustaining Rainbow Trout populations (designated as “invaded rivers”: Malbaie, Du Gouffre, Matane, Mechins, Tortue rivers), and the four remaining rivers were free of the invader (designated as “noninvaded rivers”: Calway, Petit-Saguenay, Trois-Pistoles, Sud-Ouest rivers). All rivers supported Brook Trout populations, but Atlantic Salmon was present in only five, including three invaded rivers (Malbaie, Du Gouffre, Matane, Petit-Saguenay, Sud-Ouest rivers). In general, mean densities of native fish were approximately double that of Rainbow Trout (Thibault 2010). Since sampling took place exclusively during the summer season, we assumed minimal temporal variations in water temperature and in fish distribution and habitat preferences (e.g., Vondracek and Longanecker 1993; Sotiropoulos et al. 2006). Data obtained from thermographs installed by the Ministère des Ressources Naturelles et de la Faune (MRNF) in three rivers and water temperature obtained by extrapolating air temperature from nearby meteorological stations for the six other rivers (Environment Canada), showed that temperature ranges during sampling periods were not significantly different among rivers (data not shown).

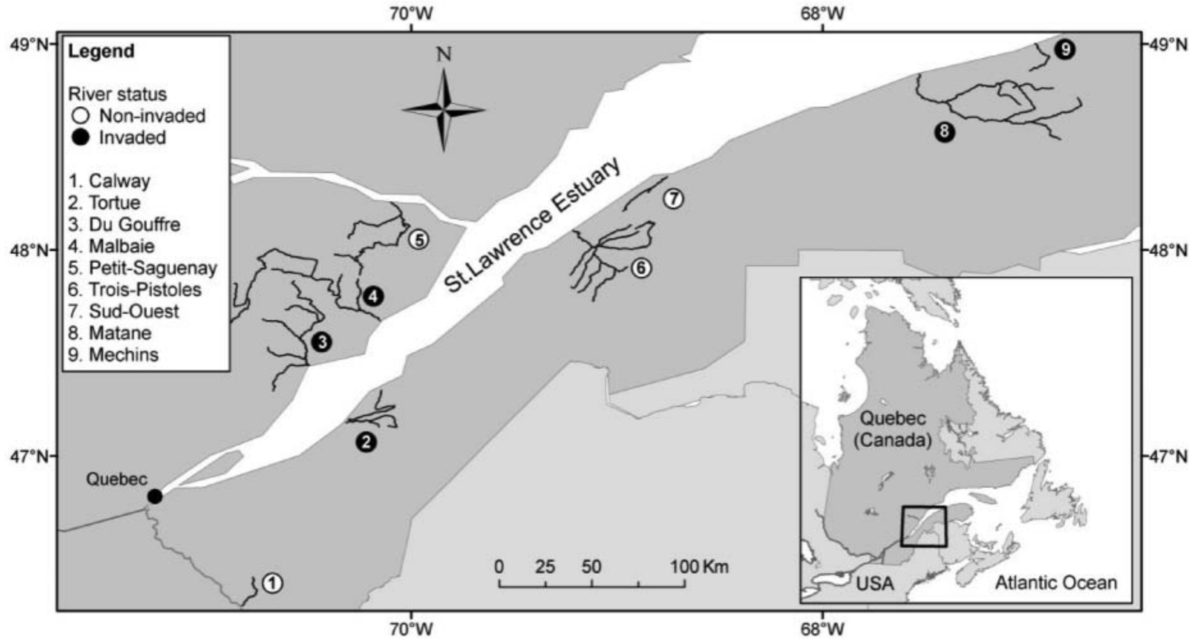

FIGURE 1. Location of the nine sampled rivers in eastern Quebec during the summers of 2007 and 2008. The four noninvaded rivers (without Rainbow Trout) are identified by open circles, whereas filled circles represent the five invaded rivers (with Rainbow Trout).

River-scale surveys.—Sampling took place between mid-June and the end of August 2007[2]. Between 9 and 24 sites of 100 m^2 were sampled at intervals of 1 km, in each river and some of their tributaries. Fishing was done during the daytime using portable electrofishers. Sites ($n_{tot} = 117$) were sampled twice, with a pause of 10–15 min between passes. At each site, we noted the following: salmonid density, velocity (qualitatively), mean depth ($\pm$1 cm, from three measurements), slope (%), flow type (channel, riffle, run), site's position (stream's center or near the shores), and substrate composition (%) estimated using the following key: sand (<5 mm), gravel (5–40 mm), pebble (40–80 mm), cobble (80–250 mm), block (>250 mm), bed rock. Proportions of each category were thereafter multiplied by the median size of their own category and summed to obtain one relative substrate size per site. We also assessed shoreline cover (total, partial, no cover). Riparian vegetation, canopy, prominent rocks on the shore or structures overhanging the river are examples of shoreline cover. A "total" cover means that the position of the sampling site was 80% or more covered. No cover means there was little or no shelter at the fish location (with the exception of riverbed substrate). A "partial" cover means an intermediate situation between the total cover and no-cover situations.

[2]The Tortue River was sampled in 2008. The river-scale survey was done by the MRNF and the protocol differed from that used for the other rivers. This river was thus excluded from these specific analyses. However, the smaller-scale sampling (see below) was done in the same way in all rivers.

Sampling and habitat characterization.—Based on the abundance and composition in salmonid species observed during river-scale surveys, three sites per river (two in Trois-Pistoles River) were selected for further sampling (Table 1). Depending on river width, two or three transects of 2 m × 30 m per site were sampled parallel to the stream banks in habitats that appeared suitable for salmonids, both near the shores and in the middle of the rivers. Each transect was separated into 15 units of 2 m × 2 m (hereafter referred to as 4-m^2 units). Two electrofishing passes, spaced approximately 0.5 m apart, were performed in each unit, from side to side. Positions of each salmonid (first sighting point) observed during each pass were identified with a weighted, color-coded flag for each species. To minimize disturbances and maximize success of capture, fishers progressed upstream, always staying just behind the anode. Although some imprecision of fish position relative to habitat characteristics may result from the disturbance of the fish by the fishers, the restricted sampling area insured that fish positions were flagged within at most 0.5 m of their original position. Beyond this, fish could not have been sampled as they would have moved out of the sampling area.

For each 4-m^2 unit, we noted shoreline cover (total, partial, no cover), mean depth ($\pm$1 cm, from three measurements), mean water velocity (m/s)[3], and substrate size using a d_{50} index (Guay et al. 2003). To calculate the index, we measured the intermediate axis (β, $\pm$ 0.5 cm) of 30 particles haphazardly

[3]As the means used to determine water current differed between the two sampling years, the velocity data from Tortue River were treated separately.

TABLE 1. Features of the nine rivers sampled in 2007 and 2008 in eastern Quebec. "Invaded" rivers supported a Rainbow Trout population, whereas no Rainbow Trout were captured in "noninvaded" rivers. For the Tortue River, density values were not determined (nd) since the area sampled was not available.

			Mean density ± SE (fish/m²)[a]			Sampling design	
River	Sampling starting date	Type	Rainbow Trout	Atlantic Salmon	Brook Trout	No. of sites	No. of transects
Calway	Jun 18, 2007	Noninvaded	0.00	0.00	0.060 ± 0.018	3	5[b]
Tortue[c]	Aug 7, 2008	Invaded	nd	0.00	nd	3	6[d]
Du Gouffre	Jul 2, 2007	Invaded	0.019 ± 0.006	0.089 ± 0.025	0.033 ± 0.009	3	9
Malbaie	Jul 9, 2007	Invaded	0.046 ± 0.023	0.061 ± 0.028	0.046 ± 0.017	3	9
Petit-Saguenay	Jul 16, 2007	Noninvaded	0.00	0.183 ± 0.054	0.040 ± 0.021	3	9
Trois-Pistoles	Jul 23, 2007	Noninvaded	0.00	0.00	0.047 ± 0.022	2[e]	6
Sud-Ouest	Jul 30, 2007	Noninvaded	0.00	0.020 ± 0.010	0.390 ± 0.000	3	9
Matane	Aug 11, 2007	Invaded	0.026 ± 0.016	0.101 ± 0.024	0.012 ± 0.003	3	9
Mechins	Aug 6, 2007	Invaded	0.083 ± 0.070	0.00	0.199 ± 0.057	3	9

[a]In sites where the species was present. Based on a preliminary sampling.
[b]In one site, we sampled a single transect of 39 units. In a second site, we sampled only two transects.
[c]Presampling was done by the MRNF and no site area was available, impeding density calculation.
[d]Only two transects by site.
[e]One site was abandoned since very few salmonids were captured in that river.

sampled across the sampling unit. A value of "0" was attributed to sand and a value of "99" to bedrock and large blocks. The d_{50} was equal to the median value of sediment size. Some sites selected for their abundance of Rainbow Trout were resampled in 2008 to capture additional specimens. These measures were used to address macrohabitat use (see Niche Overlap and Habitat Preferences sections).

All captured fish were held until sampling was completed. Salmonids were measured (± 1 mm, FL). Fish of less than 175 mm were considered as juveniles (age 0–2, young of the year being the most abundant year-class). Larger fish were assumed to be adults and thus were removed from the analysis. Some excluded fish might have been immature, but by excluding fish greater than 175 mm, we were confident that our analyses excluded smolts (for Atlantic Salmon and Rainbow Trout [Thibault et al. 2010]) and adults (mainly for Brook Trout), and thus only juveniles would be considered in the analysis.

Data analysis.—To evaluate the distribution of sampling sites relative to habitat heterogeneity within and among rivers, a principal component analysis (PCA; princomp procedure with varimax transformation [SAS 2001]) was performed using the seven habitat variables (distance from the shore, depth, flow type, velocity, slope, shoreline cover, substrate size) measured during river-scale surveys in eight rivers. Since there is no *P*-value associated with the varimax transformation, variables significantly related to the PCA axis were identified according to the magnitude of loadings: (1) between the two axes for a given variable and (2) between all the variables for a given axis. In the present analysis, a variable was considered significantly related to the PCA axis when its loading after varimax rotation was $\geq$0.6.

The Tortue River could not be included in this analysis as the large-scale sampling was conducted by the MRNF and their measured habitat variables were not the same as those measured in the other eight rivers. To evaluate the success of assigning sampling sites to their river of origin (and hence the distinctiveness of rivers), we conducted a discriminant analysis (DA; *discrim* procedure) performed on the eigenvalues of PC 1 and 2, using rivers as categories. To evaluate if the occurrence of Rainbow Trout in invaded rivers (Matane, Méchins, Du Gouffre and Malbaie) was associated with particular combinations of habitat variables, logistic regression analyses (proc logistic, binary logit model, Fisher's scoring) were conducted to relate the presence of Rainbow Trout at sampling sites quantified according to their PC1 and PC2 scores.

Estimates of habitat niche overlap, integrating three quantitative variables (depth, water velocity, and substrate size) were calculated using data obtained in the 4-m² units within the 60-m² transects. Estimates of weighted average (w) niche overlap (NO) were calculated based on a nonparametric index developed by Mouillot et al. (2005), NO_{Kwt}, that estimates the superposition strength of nonparametric kernel (K) density functions for several variables (t) between two species. A detailed description of the formula is presented in Mouillot et al. (2005). Niche overlap indices were compared (1) two by two between each pair of species (Rainbow Trout and Brook Trout, Rainbow Trout and Atlantic Salmon, and Brook Trout and Atlantic Salmon) based on samplings done in invaded rivers and (2) for native species only (Rainbow Trout and Atlantic Salmon), according to different levels of Rainbow Trout presence (Rainbow Trout present in the sample site versus Rainbow Trout absent from the sample site but present in the invaded river versus in noninvaded rivers). Nonparametric confidence intervals (CI95%) were generated for each niche overlap using the bootstrap resampling method (1,000 replicates) and the relationship between Rainbow Trout presence and the niche superposition of native fish was analyzed using a chi-square test, followed by a Z-test in R (Venables and Smith 2009).

TABLE 2. Categorization of the three quantitative variables used to calculate the preference index.

Category	Depth (cm)	Substrate size	Velocity (m/s)[3]
1	≤ 15.0	≤ 5.0	< 0.24
2	> 15.0 and ≤ 21.5	> 5.0 and ≤ 8.5	≥ 0.24 and < 0.39
3	> 21.5 and ≤ 28.0	> 8.5 and ≤ 10.0	≥ 0.39 and < 0.55
4	> 28.0 and ≤ 38.0	> 10.0 and ≤ 14.5	≥ 0.55 and < 0.78
5	> 38.0	> 14.5	≥ 0.78

Habitat preference, that is habitat use according to habitat availability (values measured in 4-m^2 units), was calculated using the method of Blanchet et al. (2007), which is based on the preference index developed by Beecher et al. (1993). The following formula was used:

$$M_i = \left(\frac{(n_i/n_t)/(p_i/p_t)}{[(n_i/n_t)/(p_i/p_t)]\,\max} \right) - 0.5 \times 2, \qquad (1)$$

where M_i is the normalized habitat index for category i, n_i is the number of samples (among all transects or sites) with fish in the considered category, n_t is the total number of specimens, p_i is the number of samples belonging to the category i, and p_t is the total number of samples. Positive values indicate preference for a habitat category, whereas negative values indicate avoidance of a given category. The three quantitative variables (depth, substrate size, and velocity) were each subdivided in five categories (Table 2).

We considered that the presence of Rainbow Trout modified the habitat preferences of native species if, for a given habitat variable, preferred habitat categories (M_i: 0.8–1.0) of Rainbow Trout and Atlantic Salmon or Brook Trout (in absence of the invader) were the same and if, in the presence of Rainbow Trout, preferred habitat categories of native fish were either actively avoided (M_i: −1.0 to −0.8) or simply occupied proportional to their availability (M_i: −0.25 to +0.25).

Growth rate was evaluated for age-0 fish captured during the entire sampling season, the most abundant year-class sampled for all species (Brook Trout: $n = 357$; Atlantic Salmon: $n = 674$; Rainbow Trout: $n = 303$). Slopes of the regressions of fish length on date of capture (35 sampling dates over a period of 66 d) were compared two-by-two using a 2-factor analysis of covariance (ANCOVA) (date, species, date•species) in SAS (SAS 2001).

RESULTS

Habitat Heterogeneity and the Occurrence of Rainbow Trout

The first principal component of the PCA conducted in eight study rivers explained 28% of the total variance in the seven habitat variables and was mainly related to the proximity of the shore and the presence of shoreline cover (Figures 2, 3A). The second principal component explained another 21% of the variation and was mainly related to flow type, water velocity, and substrate size (Figures 2, 3B). Habitat heterogeneity within rivers was so great that less than 30% of the 117 sites were correctly reassigned to their river of origin in the discriminant analysis (total rate of error count estimates for river: 0.712). Sites were considered as independent samples in further analyses as rivers could not be considered distinct based on the habitat characteristics considered here.

Sites where Rainbow Trout were present tended to cluster towards the positive end of PC1 and the negative end of PC2 (Figure 2), suggesting that well-covered habitats located near the river shore with a slower and more laminar flow were preferred by Rainbow Trout. Using only the sites located in invaded rivers (Matane, Méchins, Du Gouffre, and Malbaie), logistic regression analysis revealed that increasing scores on PC1 significantly predicted the presence of Rainbow Trout (Wald = 5.56; DDL = 1; $P = 0.018$) but not so on PC2 (Wald = 2.93; DDL = 1; $P = 0.087$). Rainbow Trout was thus significantly and positively associated with habitats characterized by closer proximity to the shoreline and by increasing shoreline cover.

Niche Overlap

Niche overlap for substrate, water velocity, and depth between native salmonids and Rainbow Trout was higher than 0.80, and tended to surpass that of the two indigenous species (Figure 4). Niche overlap between Brook Trout and Rainbow Trout was greater than that of Atlantic Salmon and Rainbow Trout. In sites where Rainbow Trout was present, native species shared approximately 80% of the habitat based on the three measured variables (Figure 4). However, in sites and rivers free of Rainbow Trout, the niche overlap between the two indigenous species decreased significantly (χ^2obs = 4.58, $Z = 2.11$, $P = 0.03$).

Habitat Preferences

Among variables analyzed for habitat preferences, we observed a major modification in the habitat selection of native species for shoreline cover in response to the presence of Rainbow Trout. In the absence of Rainbow Trout, Atlantic Salmon and Brook Trout showed a clear preference for highly covered habitats ("total" cover scored at 1), but in sympatry with Rainbow Trout, which also preferred total cover, they shifted towards more open habitats ("partial" cover scored at 1) (Figure 5).

For all the other variables tested (distance from the shore, depth, flow type, velocity, slope, and substrate size; results not shown), no clear modification of habitat selection was observed in the presence of Rainbow Trout: either native species did not show a preference for any particular habitat category, or the selection pattern did not change in the presence of Rainbow Trout, or a habitat change was observed but could not be associated with the presence of Rainbow Trout.

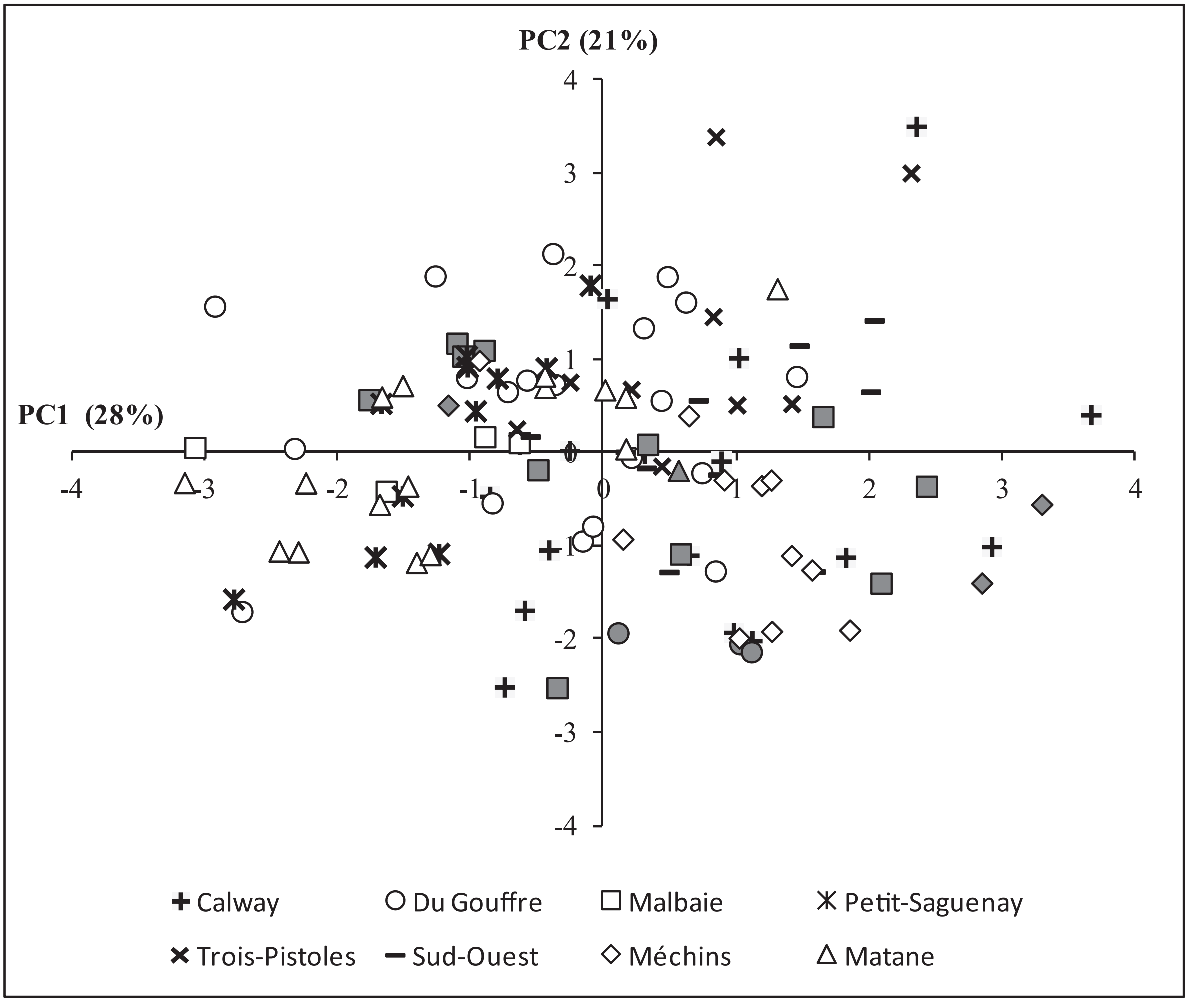

FIGURE 2. Positions of sampling sites relative to the two axes of a principal component analysis based on seven habitat variables. Each river is represented by a different symbol. Open symbols identify sites in invaded rivers where Rainbow Trout have not been captured. Filled symbols identify sites in invaded rivers where Rainbow Trout have been captured.

Growth Rates

During their first year of life (0+), growth rate was similar ($F = 1.21$, DDL = 1, $P = 0.27$) for Atlantic Salmon (0.29 mm/d [95% CI: 0.29–0.30 mm/d]) and Brook Trout (0.26 mm/d [95% CI: 0.24–0.29 mm/d]) but was significantly greater for Rainbow Trout (0.46 mm/d [95% CI: 0.44–0.47 mm/d], Atlantic Salmon: $F = 27.34$, DDL = 1; Brook Trout: $F = 15.40$, DDL = 1; $P < 0.01$). Despite a later emergence date, and assuming constant growth rates until the end of the growing season, Rainbow Trout would have almost caught up in size with both native species.

DISCUSSION

Introduced Rainbow Trout has been shown to outcompete native salmonids where populations are well established and in designed experiments (Seiler and Keeley 2007a; Seiler and Keeley 2007b). But at an early stage of establishment and dispersal, when Rainbow Trout densities are low, interaction with indigenous species might not systematically favor Rainbow Trout. In eastern Quebec, the Rainbow Trout invasion is an ongoing process, and recently established populations are still at low densities. Since two native salmonids co-occurred in the colonized rivers, these provided an ideal system to evaluate the potential impact of the exotic species at a relatively early stage of the invasion.

Impact of Rainbow Trout on Native Species

In invaded rivers, Rainbow Trout were positively associated with habitats characterized by closer proximity to the shoreline and by increasing shoreline cover. Accordingly, when considering the species' preference for three categories of shoreline cover (no cover, partial, and total), we found that preference changed for both native species according to Rainbow Trout occurrence. In the absence of Rainbow Trout, the two indigenous species preferred full cover, but in the presence of Rainbow Trout, which also preferred full cover, Atlantic Salmon and

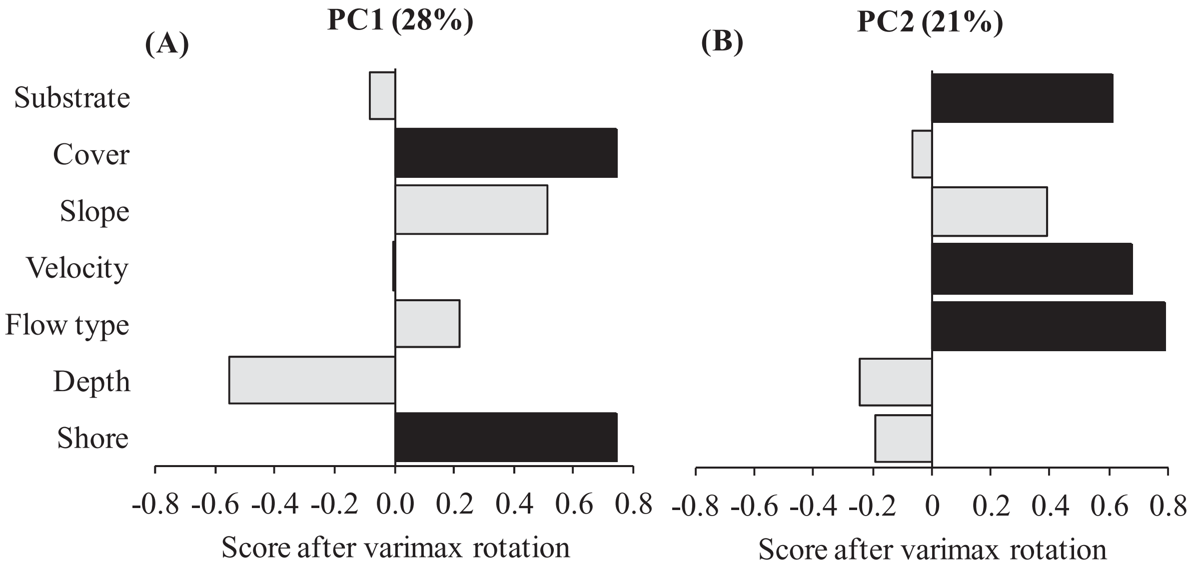

FIGURE 3. Loadings (after varimax rotation) on **(A)** PC1 and **(B)** PC2 of the principal component analysis. Significant loadings (≥0.6) are shown by black bars.

Brook Trout switched preference to partially covered habitats. Shoreline cover has been identified as an important habitat variable for salmonids, especially for Rainbow Trout (Platts 1976; Gibson 1978; Gatz et al. 1987 and references therein), and exclusion of native fish from the more shaded areas indicates that native salmonids are unable to resist displacement by the invading Rainbow Trout.

The increase in habitat niche overlap between the two indigenous salmonids in the presence of Rainbow Trout, in comparison to sites or rivers where the exotic species was not found, also suggests that Rainbow Trout is impacting native fish. Usually, in the absence of Rainbow Trout, sympatric Atlantic Salmon and Brook Trout segregate spatially, with Atlantic Salmon displacing Brook Trout to less optimal habitats (Rodríguez 1995). It appears that the presence of the invader changed the habitat uses of both species, forcing them to share more similar resources.

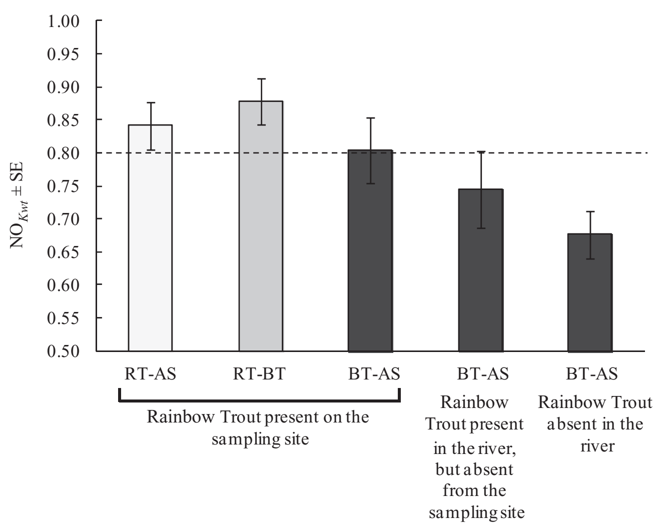

FIGURE 4. Nonparametric niche overlap indices (NO$_{Kwt}$ ± SE) for three quantitative habitat variables (substrate, depth, and velocity) between Rainbow Trout (RT), Atlantic Salmon (AS) and Brook Trout (BC), according to variable levels of Rainbow Trout presence. Eighty percent of habitat overlap is indicated by the horizontal dashed line.

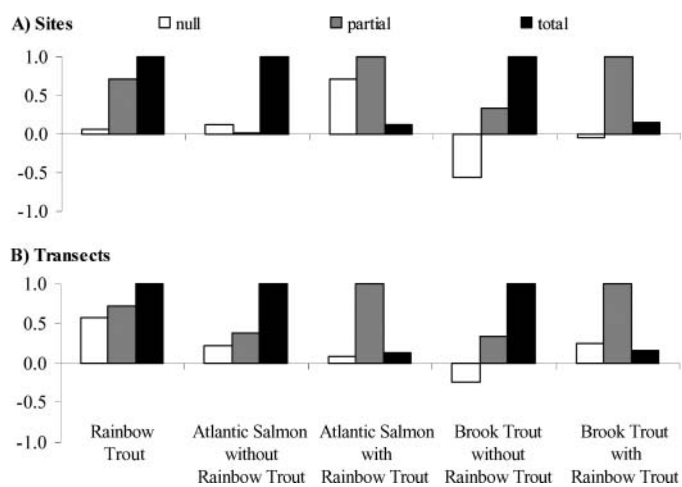

FIGURE 5. Preference of Rainbow Trout, Atlantic Salmon, and Brook Trout for shoreline cover in **(A)** sites (three transects) and **(B)** transects (60 m^2) in the presence and absence of Rainbow Trout. Riparian vegetation, canopy, prominent rocks on the shore, and bridges or other structures overhanging the river constitute examples of cover. A "total" cover means that the position of fish was more than 80% covered. A "null" cover means there was no shelter at the fish location (except the riverbed substrate). A "partial" cover means an intermediate situation between the total cover and the null cover emplacement. A value near 1 indicates an active selection for a cover category, a value near −1 indicates an active avoidance of a cover category, and a value near 0 indicates that habitat use is proportional to habitat availability.

The possibility that observed modifications in the habitat uses of Atlantic Salmon and Brook Trout is the result of ontogenetic habitat shifts cannot be totally discarded. Hasegawa et al. (2012) effectively demonstrated that the invasion of Brown Trout *Salmo trutta* in streams supporting native Masu Salmon *Oncorhynchus masou*—expected to be a greater competitor due to its size superiority related to an earlier emergence time—was facilitated by the ontogenetic niche shift of Masu Salmon, which reduced niche overlap between the two species. This phenomenon may very well contribute in part to explaining our observations. However, in the present study, habitat and niche overlap changes were revealed by comparing—almost simultaneously—sites and rivers with and without the invader. Thus, modifications in habitat use of native fish that were observed in the presence of Rainbow Trout were not observed for Atlantic Salmon and Brook Trout at the same ontogenetic development stage in noninvaded sites and rivers. This supports the contention that habitat changes were not only caused by an ontogenetic habitat switch.

Growth of Rainbow Trout

As demonstrated by the length-at-age relationships, the growth of Rainbow Trout during its first year of life was superior to that of the two native species, regardless of the delay caused by a later emergence date, which is consistent with other studies (Whitworth and Strange 1983). It appears that the foraging abilities of age-0 Rainbow Trout and their ability to displace indigenous salmonids from preferred habitat results in rapid growth despite the presence of two competitors at higher density. Rainbow Trout possessed a growth rate (0.46 mm/d) similar to that observed in long-time naturalized populations in the Great Lakes (0.32–0.42 mm/d; Johnson 1980; Rose 1986).

Management Implications

The invasion of Rainbow Trout in eastern Quebec is still ongoing: known established populations are rare and often at low density. Therefore, an absence of Rainbow Trout impact on native salmonids could have been expected. However, we found that juvenile Rainbow Trout showed a higher growth rate than its two sister species, revealing its ability to effectively exploit resources. Furthermore, this study demonstrated that introduced Rainbow Trout in eastern Quebec, despite the low densities, interact with indigenous salmonid species to such an extent that Atlantic Salmon and Brook Trout modified their habitat use. The increase in native fish niche overlap at small spatial scales is an indirect effect of the introduced salmonid, whereas the shift in preferred habitat categories of native species demonstrates a direct impact of the interactions with the invader (Hasegawa and Maekawa 2006). These results increase our concerns about the future impacts of the invader on native fish. They are consistent with the findings of Baxter et al. (2007), who demonstrated in a field experiment that the biomass of native Dolly Varden *Salvelinus malma* in the presence of the introduced Rainbow Trout, even at low density (0.2 fish/m^2), was 75% lower than at sites without Rainbow Trout. Based on a comparative experimental study, this might have been in great part caused by a usurpation of terrestrial prey subsidy by Rainbow Trout that would have forced the native fish to shift their diet. In the near future, since the interaction between native and exotic salmonids in eastern Quebec is expected to continue and even increase, it will be primordial to determine how the modification in habitat use impacts the diet composition and consumption rate of native salmonids and to what extent it affects their growth and survival.

Observations of the displacement of Brook Trout by Rainbow Trout are more numerous than for Atlantic Salmon (e.g., Larson and Moore 1985; Moore et al. 1986; Fausch 1988; Fausch 1998; Fausch 2008). However, some authors have suggested that the decline of Brook Trout populations after the introduction of Rainbow Trout was probably more the consequence of the pre-existing weakened state of the native species (Clark and Rose 1997) in combination with the impact of the invader, rather than to the Rainbow Trout invasion itself. A similar tendency has also been observed following the introduction of Brown Trout (Waters 1983). Thus, intrinsic problems in native species' populations (overexploitation, habitat degradation, etc.) may permit Rainbow Trout invasion to have a greater impact on indigenous communities. Both Brook Trout and Atlantic Salmon populations are declining in eastern Quebec because of habitat degradation and overfishing of the former (M. Arvisais, MRNF, personal communication) and a high marine mortality rate and various impediments to upstream movements for the latter (Friedland et al. 1993; Hansen and Quinn 1998; Hansen and Windsor 2006; ICES 2008). Both species may thus be less able to resist the encroachment of Rainbow Trout in their habitats.

It is often thought by anglers, and unfortunately by some wildlife managers too, that as long as an invader is not abundant and minimally dispersed, its impact on the ecosystem may be negligible, and thus management actions to eliminate or limit the potential threat are not called for. This perception is particularly true for species like Rainbow Trout, which are socially acceptable and desirable and support economic activities (such as aquaculture, angling, and tourism). However, the advantage of reacting quickly when biological invasions are discovered early in the invasion process is twofold: (1) mitigation measures are often only truly efficient when the invader is not yet abundant and is confined to a restricted area (Moore et al. 1986; Meyer et al. 2006; Peterson et al. 2008) and (2) as we demonstrated in this study for Rainbow Trout, impact on native fauna can be real and important from the start of the invasion, even when densities are low.

ACKNOWLEDGMENTS

This work was funded by grants from the Natural Sciences and Engineering Research Council of Canada (NSERC), the Réseau Aquaculture Québec, the Centre Interuniversitaire de Recherche sur le Saumon Atlantique (CIRSA) and the Fédération Québécoise de la Faune. It was supported by an Alexander Graham Bell Canada Graduate Scholarship (NSERC). We thank all the field assistants for their help with fish sampling, habitat characterization, and laboratory: François Colas, Marc-Antoine Couillard, Marie Chantal Émond, Julie Faure-Lacroix, Julien Forestier, Jessie Motard-Côté, Geneviève Ouellet-Cauchon, Rémy Pouliot, Marion Trudel, and Mélanie Trudel. We are also grateful to Jean-Guy Frenette and Pierre-Yves Collin, technicians for the Ministère des Ressources naturelles et de la Faune, for their assistance in the field and equipment loan. Finally, we thank three anonymous reviewers for their constructive comments. This is a contribution to the scientific program of CIRSA.

REFERENCES

Baxter, C. V., K. D. Fausch, M. Murakami, and P. L. Chapman. 2007. Invading Rainbow Trout usurp a terrestrial prey subsidy from native charr and reduce their growth and abundance. Oecologia 153:461–470.

Beecher, H. A., T. H. Johnson, and J. P. Carleton. 1993. Predicting microdistributions of steelhead (*Oncorhynchus mykiss*) parr from depth and velocity preference criteria: test of an assumption of the instream flow incremental methodology. Canadian Journal of Fisheries and Aquatic Sciences 50:2380–2387.

Blanchet, S., G. Loot, G. Grenouillet, and S. Brosse. 2007. Competitive interactions between native and exotic salmonids: a combined field and laboratory demonstration. Ecology of Freshwater Fish 16:133–143.

Bøhn, T., P. A. Amundsen, and A. Sparrow. 2008. Competitive exclusion after invasion? Biological Invasions 10:359–368.

Cambray, J. A. 2003. The global impact of alien trout species—a review; with reference to their impact in South Africa. African Journal of Aquatic Science 28:61–67.

Clark, M. E., and K. A. Rose. 1997. Factors affecting competitive dominance of Rainbow Trout over Brook Trout in southern Appalachian streams: implications of an individual-based model. Transactions of the American Fisheries Society 126:1–20.

Crowl, T. A., C. R. Townsend, and A. R. McIntosh. 1992. The impact of introduced Brown and Rainbow trout on native fish: the case of Australasia. Reviews in Fish Biology and Fisheries 2:217–241.

Fausch, K. D. 1988. Tests of competition between native and introduced salmonids in streams: what have we learned? Canadian Journal of Fisheries and Aquatic Sciences 45:2238–2246.

Fausch, K. D. 1998. Interspecific competition and juvenile Atlantic Salmon (*Salmo salar*): on testing effects and evaluating the evidence across scales. Canadian Journal of Fisheries and Aquatic Sciences 55(Supplement 1):218–231.

Fausch, K. D. 2008. A paradox of trout invasions in North America. Biological Invasions 10:685–701.

Friedland, K. D., D. G. Reddin, and J. F. Kocik. 1993. Marine survival of North American and European Atlantic Salmon: effects of growth and environment. ICES Journal of Marine Science 50:481–492.

Gatz, A. J., Jr., M. J. Sale, and J. M. Loar. 1987. Habitat shifts in Rainbow Trout: competitive influences of Brown Trout. Oecologia 74:7–19.

Gibson, R. J. 1978. The behavior of juvenile Atlantic Salmon (*Salmo salar*) and Brook Trout (*Salvelinus fontinalis*) with regard to temperature and to water velocity. Transactions of the American Fisheries Society 107:703–712.

Gibson, R. J. 1981. Behavioural interactions between Coho Salmon (*Oncorhynchus kisutch*), Atlantic Salmon (*Salmo salar*), Brook Trout (*Salvelinus fontinalis*), and steelhead trout (*Salmo gairdneri*) at the juvenile fluviatile stages. Canadian Technical Report of Fisheries and Aquatic Sciences 1029.

Guay, J. C., D. Boisclair, M. Leclerc, and M. Lapointe. 2003. Assessment of the transferability of biological habitat models for Atlantic Salmon parr (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences 60:1398–1408.

Hansen, L. P., and T. P. Quinn. 1998. The marine phase of the Atlantic Salmon (*Salmo salar*) life cycle, with comparisons to Pacific salmon. Canadian Journal of Fisheries and Aquatic Sciences 55(Supplement 1):104–118.

Hansen, L. P., and M. L. Windsor. 2006. Interactions between aquaculture and wild stocks of Atlantic Salmon and other diadromous fish species: science and management, challenges and solutions. ICES Journal of Marine Science 63:1159–1161.

Hasegawa, K., and K. Maekawa. 2006. The effects of introduced salmonids on two native stream-dwelling salmonids through interspecific competition. Journal of Fish Biology 68:1123–1132.

Hasegawa, K., T. Yamamoto, M. Murakami, and K. Maekawa. 2004. Comparison of competitive ability between native and introduced salmonids: evidence from pairwise contests. Ichthyological Research 51:191–194.

Hasegawa, K., C. Yamazaki, K. Ohkuma, and M. Ban. 2012. Evidence that an ontogenetic niche shift by native Masu Salmon facilitates invasion by nonnative Brown Trout. Biological Invasions 14:2049–2056.

Hearn, W. E., and B. E. Kynard. 1986. Habitat utilization and behavioral interaction of juvenile Atlantic Salmon (*Salmo salar*) and Rainbow Trout (*S. gairdneri*) in tributaries of the White River of Vermont. Canadian Journal of Fisheries and Aquatic Sciences 43:1988–1998.

Hitt, N. P., C. A. Frissell, C. C. Muhlfeld, and F. W. Allendorf. 2003. Spread of hybridization between native Westslope Cutthroat Trout, *Oncorhynchus clarki lewisi,* and nonnative Rainbow Trout, *Oncorhynchus mykiss*. Canadian Journal of Fisheries and Aquatic Sciences 60:1440–1451.

Hutchinson, G. E. 1959. Homage to Santa Rosalia or why are there so many kinds of animals? American Naturalist 93:145–159.

ICES (International Council for the Exploration of the Sea). 2008. What's happening to Atlantic Salmon? ICES, Copenhagen. Available: www.ices.dk. (April 2012).

Johnson, J. H. 1980. Production and growth of subyearling Coho Salmon, *Oncorhynchus kisutch,* Chinook Salmon, *Oncorhynchus tshawytscha,* and steelhead, *Salmo gairdneri,* in Orwell Brook, tributary of Salmon River, New York. U.S. National Marine Fisheries Service Fishery Bulletin 78:549–554.

Kohler, C. C., and W. R. Courtenay Jr. 1986. American Fisheries Society position on introductions of aquatic species. Fisheries 11(2):39–42.

Krueger, C. C., and B. May. 1991. Ecological and genetic effects of salmonid introductions in North America. Canadian Journal of Fisheries and Aquatic Sciences 48(Supplement 1):66–77.

Larson, G. L., and S. E. Moore. 1985. Encroachment of exotic Rainbow Trout into stream populations of native Brook Trout in the southern Appalachian Mountains. Transactions of the American Fisheries Society 114:195–203.

Lowe, S., M. Browne, S. Boudjelas, and M. De Poorter. 2007. 100 espèces exotiques envahissantes parmi les plus néfastes au monde: une sélection de la global invasive species database. La Commission de la Sauvegarde des Espèces (CSE), Invasive Species Specialist Group, Union Internationale pour la Conservation de la Nature (UICN), Gland, Switzerland.

MacArthur, R., and R. Levins. 1964. Competition, habitat selection, and character displacement in a patchy environment. Proceedings of the National Academy of Sciences of the USA 51:1207–1210.

MacCrimmon, H. R. 1971. World distribution of Rainbow Trout (*Salmo gairdneri*). Journal of the Fisheries Research Board of Canada 28:663–704.

Magoulick, D. D., and M. A. Wilzbach. 1998. Are native Brook Charr and introduced Rainbow Trout differentially adapted to upstream and downstream reaches? Ecology of Freshwater Fish 7:167–175.

Meyer, K. A., J. A. Lamansky Jr., and D. J. Schill. 2006. Evaluation of an unsuccessful Brook Trout electrofishing removal project in a small Rocky Mountain stream. North American Journal of Fisheries Management 26:849–860.

Mooney, H. A., and E. E. Cleland. 2001. The evolutionary impact of invasive species. Proceedings of the National Academy of Sciences of the USA 98:5446–5451.

Moore, S. E., G. L. Larson, and B. Ridley. 1986. Population control of exotic Rainbow Trout in streams of a natural area park. Environmental Management 10:215–219.

Mouillot, D., W. Stubbs, M. Faure, O. Dumay, J. A. Tomasini, J. B. Wilson, and T. D. Chi. 2005. Niche overlap estimates based on quantitative functional traits: a new family of non-parametric indices. Oecologia 145: 345–353.

Peterson, D. P., K. D. Fausch, and G. C. White. 2004. Population ecology of an invasion: effects of Brook Trout on native Cutthroat Trout. Ecological Applications 14:754–772.

Peterson, D. P., B. E. Rieman, J. B. Dunham, K. D. Fausch, and M. K. Young. 2008. Analysis of trade-offs between threats of invasion by nonnative Brook Trout (*Salvelinus fontinalis*) and intentional isolation for native Westslope Cutthroat Trout (*Oncorhynchus clarkii lewisi*). Canadian Journal of Fisheries and Aquatic Sciences 65:557–573.

Platts, W. S. 1976. Validity in the use of aquatic of methodologies to document stream environments for evaluating fishery conditions. Pages 267–284 *in* J. F. Orsborn and C. H. Allman, editors. Instream flow needs, volume 2. American Fisheries Society, Western Division, Bethesda, Maryland.

Rodríguez, M. A. 1995. Habitat-specific estimates of competition in stream salmonids: a field test of the isodar model of habitat selection. Evolutionary Ecology 9:169–184.

Rose, G. A. 1986. Growth decline in subyearling Brook Trout (*Salvelinus fontinalis*) after emergence of Rainbow Trout (*Salmo gairdneri*). Canadian Journal of Fisheries and Aquatic Sciences 43:187–193.

SAS (Statistical Analysis Systems). 2001. SAS v9 language guide, release 6.03. SAS Institute, Cary, North Carolina.

Seiler, S. M., and E. R. Keeley. 2007a. A comparison of aggressive and foraging behaviour between juvenile Cutthroat Trout, Rainbow Trout and F1 hybrids. Animal Behaviour 74:1805–1812.

Seiler, S. M., and E. R. Keeley. 2007b. Morphological and swimming stamina differences between Yellowstone Cutthroat Trout (*Oncorhynchus clarkii bouvieri*), Rainbow Trout (*Oncorhynchus mykiss*), and their hybrids. Canadian Journal of Fisheries and Aquatic Sciences 64:127–135.

Sotiropoulos, J. C., K. H. Nislow, and M. R. Ross. 2006. Brook Trout, *Salvelinus fontinalis,* microhabitat selection and diet under low summer stream flows. Fisheries Management and Ecology 13:149–155.

Thibault, I. 2010. Invasion de la Truite Arc-en-Ciel (*Oncorhynchus mykiss*) dans l'est du Québec. Doctoral dissertation. Université Laval, Quebec City, Québec.

Thibault, I., L. Bernatchez, and J. J. Dodson. 2009. The contribution of newly established populations to the dynamics of range expansion in a one-dimensional fluvial-estuarine system: Rainbow Trout (*Oncorhynchus mykiss*) in eastern Quebec. Diversity and Distributions 15:1060–1072.

Thibault, I., R. D. Hedger, J. J. Dodson, J. C. Shiao, Y. Iizuka, and W. N. Tzeng. 2010. Anadromy and the dispersal of an invasive fish species (*Oncorhynchus mykiss*) in eastern Quebec, as revealed by otolith microchemistry. Ecology of Freshwater Fish 19:348–360.

Venables, W. N., and D. M. Smith. 2009. Notes on R: a programming environment for data analysis and graphics. The R Foundation for Statistical Computing, Vienna.

Volpe, J. P., B. R. Anholt, and B. W. Glickman. 2001. Competition among juvenile Atlantic Salmon (*Salmo salar*) and steelhead (*Oncorhynchus mykiss*): relevance to invasion potential in British Colombia. Canadian Journal of Fisheries and Aquatic Sciences 58:197–207.

Vondracek, B., and D. R. Longanecker. 1993. Habitat selection by Rainbow Trout *Oncorhynchus mykiss* in a California stream: implications for the instream flow incremental methodology. Ecology of Freshwater Fish 2:173–186.

Waters, T. F. 1983. Replacement of Brook Trout by Brown Trout over 15 years in a Minnesota stream: production and abundance. Transactions of the American Fisheries Society 112:137–146.

Waters, T. F. 1999. Long-term trout production dynamics in Valley Creek, Minnesota. Transactions of the American Fisheries Society 128:1151–1162.

Welcomme, R. L. 1984. International transfers of inland fish species. Pages 22–40 *in* W. R. Courtney Jr. and J. R. Stauffer Jr., editors. Distribution, biology, and management of exotic fishes. Johns Hopkins University Press, Baltimore, Maryland.

Whitworth, W. E., and R. J. Strange. 1983. Growth and production of sympatric Brook and Rainbow trout in an Appalachian stream. Transactions of the American Fisheries Society 112:469–475.

Williamson, M. 1996. Biological invasions. Chapman and Hall, London.