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The Effect of Nonnative Salmonids on Social Dominance and Growth of Juvenile Atlantic Salmon

Jessica A. Van Zwol and Bryan D. Neff*

Department of Biology, University of Western Ontario, 1151 Richmond Street, London, Ontario N6A 5B7, Canada

Chris C. Wilson

Aquatic Research and Development Section, Ontario Ministry of Natural Resources, Trent University, 2140 East Bank Drive, Peterborough, Ontario K9J 7B8, Canada

Abstract

Nonnative species have been shown to negatively impact the native community in which they are introduced. In the Great Lakes, competition with nonnative salmonids may be hindering the restoration efforts of Atlantic salmon *Salmo salar*, a once-native top predator in Lake Ontario. We examined the effects of brown trout *S. trutta* and rainbow trout *Oncorhynchus mykiss*, two nonnative fishes in Lake Ontario, on the social dominance and growth rate of juvenile Atlantic salmon from three strains being used for reintroduction efforts in Lake Ontario. Using seminatural stream channels, we found that the presence of either rainbow trout or brown trout reduced aggression, dominance, and food consumption of the Atlantic salmon. Brown trout had the strongest effect, increasing aggression levels in the channels by a factor of two and sharply reducing the dominance of Atlantic salmon. When both nonnatives were present, initiated aggression by Atlantic salmon decreased by a factor of three and food consumption halved as compared with when the salmon were alone. Consequently, over a 7-d time period, standard growth rate of the Atlantic salmon dropped from no change in mass when alone to a value of –0.3% per day when with the nonnative species. Of the three strains tested, one strain was least affected by the nonnative trouts, implicating genetic differences among the strains and suggesting that one strain may have greater poststocking success in Lake Ontario tributaries with naturalized populations of brown trout and rainbow trout.

The introduction of nonnative species can negatively affect individuals through competition and displacement (Hamilton et al. 1999), as well as entire communities or ecosystems by altering productivity and nutrient cycling (D'Antonio and Vitousek 1992). Reductions in biodiversity and abundance of biota within the ecosystem typically follow (D'Antonio and Vitousek 1992; Olden et al. 2004). For example, establishment of nonnative species like the zebra mussel *Dreissena polymorpha* and Eurasian water milfoil *Myriophyllum spicatum* have sharply decreased species diversity in impacted native communities with dramatic species loss (Madsen et al. 1991; Ricciardi et al. 1998). Nonnative species often overwhelm ecosystems leaving native species to cope or risk extirpation (Ricciardi et al. 1998).

Among fishes, salmonids are among the most widely introduced species around the world (Crawford and Muir 2008). Indeed, Edge et al. (1993) and Dewald and Wilzbach (1992) showed that native fishes fed less in the presence of brown trout *Salmo trutta*, while Nakano et al. (1998) found that introduced brook trout *Salvelinus fontinalis* shifted foraging frequency, microhabitat selection, and reaction distances of native bull trout *Salvelinus confluentus*. Similarly, Kitano (2004) found that rainbow trout *Oncorhynchus mykiss*, brown trout, and brook trout have reduced native populations of whitespotted

char *Salvelinus leucomaenis*, Dolly Varden *Salvelinus malma*, masu salmon (also known as cherry salmon) *Oncorhynchus masou*, and Sakhalin taimen (also known as Japanese huchen) *Hucho perryi*, either directly by predation, or indirectly by competition for resources. In fact, rainbow trout and brown trout have had such widespread negative effects on native ecosystems that they have been listed among the top 100 of the world's worst invasive alien species (Lowe et al. 2000).

In the Great Lakes, nonnative salmonids may also be impacting the restoration efforts of native fishes (Crawford 2001). Specifically, Atlantic salmon *Salmo salar* was once a native top predator in Lake Ontario but was extirpated at the end of the 19th century through a combination of habitat loss and exploitation (MacCrimmon 1977). During the past century, there have been numerous attempts to restore this species, but a naturally reproducing population has yet to be established (Stanfield and Jones 2003). Conversely, nonnative rainbow trout, brown trout, chinook salmon *O. tshawytscha*, coho salmon *O. kisutch*, and sockeye salmon *O. nerka*, have been routinely stocked in Lake Ontario tributaries to enhance recreational fisheries (Crawford 2001; Stewart and Schaner 2002). Rainbow trout and brown trout were both introduced starting in the early 1900s from different populations across North America and developed naturalized populations (MacCrimmon 1977; Crawford 2001; Kerr 2006). The presence of these nonnative salmonid species could be adversely affecting Atlantic salmon restoration efforts (Grieg et al. 2003). Indeed, Scott et al. (2005) examined brief interactions (<1 d) between some of these nonnative salmonids and Atlantic salmon and noted adverse impacts on social behavior of juvenile Atlantic salmon (also see Scott et al. 2003). Other research revealed that interactions with rainbow trout may heighten aggression, territoriality, and competition for resources in stream because of niche overlap with Atlantic salmon and, in some cases, these two species have been considered ecological equivalents (Gibson 1981; Hearn and Kynard 1986). In Europe, brown trout coexist with Atlantic salmon (Armstrong et al. 2003) and are the more aggressive and socially dominant of the two species (Stradmeyer et al. 2008). Dominant individuals typically have preferential access to resources, which can lead to increased growth and survivorship (e.g., Ens and Goss-Custard 1984). In addition, in Lake Ontario the presence of rainbow trout, brown trout, and other nonnative salmonids increases species richness in the streams and lake which can increase competition for the same resources and likely alters the carrying capacity for Atlantic salmon simply through density effects (Crawford 2001).

Understanding variation in behavior within a species is crucial for determining the role phenotypic differences play in restoration efforts and for understanding the impact of nonnative species (Curio 1996; Caro 1999). Knowledge derived from such behavioral studies can aid in creating effective management strategies for the establishment of a species. As such, we examined the potential effect that nonnative and ecologically similar salmonids have on Atlantic salmon during the juvenile life stage. Using seminatural stream environments, we observed agonistic and feeding behaviors of juvenile Atlantic salmon in the presence of juvenile brown trout and rainbow trout to determine if their presence hindered Atlantic salmon aggression, food consumption, or growth. Although rainbow trout and brown trout represent taxa that are subdivided into major lineages (e.g., Bernatchez 2001; Blankenship et al. 2011), our study focuses on the impact of the naturalized populations of these species in the Laurentian Great Lakes watershed. We examined the comparative performance of three different strains of Atlantic salmon, (LaHave River, Rivière aux Saumons [Lac Saint-Jean], and Sebago Lake) that are being used as part of a large-scale effort to reestablish Atlantic salmon in Lake Ontario (Grieg et al. 2003). Thus, we were able to look at population-specific genetic differences in Atlantic salmon behavior and performance when in competition with the nonnative salmonids and assess the potential importance of performance differences within and among strains for reestablishing this formerly native species in Lake Ontario.

METHODS

Study species.—In this study, brood stocks were used from three Atlantic salmon populations. Past restoration efforts have focused on stocking only one Atlantic salmon strain originating from the LaHave River in Nova Scotia (Stanfield and Jones 2003; Dietrich et al. 2008). This strain was chosen primarily because of its availability as a broodstock, rather than specific ecological considerations (Grieg et al. 2003). The LaHave strain of Atlantic salmon is anadromous, a life cycle thought to be different from the original strain that inhabited Lake Ontario, which may have spent its entire life cycle in freshwater (Blair 1938; Parsons 1973). The freshwater Sebago Lake strain from Maine is both physiologically and (now) physically landlocked (Ward 1932; Watts 1999). Finally, the Lac Saint-Jean strain from Quebec lives entirely in freshwater much like the original extirpated strain of Lake Ontario was believed to have been (Blair 1938; Gage 1963).

As juvenile mortality among salmonids is high (Elliott 1990; Good et al. 2001), restoration efforts in Lake Ontario stock various age-groups of Atlantic salmon including 1.5-year-old individuals. Our behavioral trials involved 1.5-year-old Atlantic salmon ($N = 504$), brown trout ($N = 180$), and rainbow trout ($N = 180$). All fish were reared from brood stocks established by the Ontario Ministry of Natural Resources (OMNR). LaHave Atlantic salmon ($N = 168$) and brown trout were obtained from the OMNR Harwood Fish Culture Station (Harwood, Ontario), while Lac Saint-Jean ($N = 168$) and Sebago Lake ($N = 168$) Atlantic salmon and rainbow trout came from the OMNR Normandale Fish Culture Station (Normandale, Ontario). Fish were of the same age and culture history as those routinely stocked in streams feeding Lake Ontario. As such, the yearlings of the three species differed in size (see below) as they do under local natural conditions. Prior to the start of the experiment, fish were held for

one month at the OMNR Codrington Fisheries Research Facility (Codrington, Ontario) in flow-through tanks with an average density of 0.6 fish/L, exposed to a natural light cycle, and fed trout chow (Corey Aquafeeds, Fredericton, New Brunswick).

Experimental setup.—Seminatural streams were used to perform six behavioral trials in blocks between May and July 2009 at the Codrington hatchery. The streams were designed to provide substrate and flow conditions similar to those used by Atlantic salmon and trout found in southern Ontario and area streams (Gibson 1973; Hearn and Kynard 1986). Each stream channel had an overall length of 2.4 m with a riffle and pool section. The upstream riffle section was 1.6 m long, 0.4 m high, and 0.5 m wide with a water depth of approximately 0.2 m and flow velocity of 0.18 ± 0.05 m/s. Substrate in the riffle consisted of 7–10 cm river rock and two 15–18 cm rocks to provide potential cover. The riffle section was followed by a pool section measuring 0.8 m long, 0.8 m high, and 0.5 m wide. The pool water depth was 0.6 m with a surface current of 0.027 ± 0.025 cm/s. Pool substrate consisted of river rock ranging in size from 2 to 10 cm.

Water from the hatchery's surface water head pond (gravity-fed system) was piped to the stream channels through a headbox inside the hatchery, which ensured equal flow to all stream channels. Water temperature was $9.8 \pm 1.4°C$ (mean $\pm$ SD). Stream channels were set up in two parallel series of six channels each. Water flowed from the headbox through the first two channels and then into subsequent channels in both series. Channels were connected using two 10-cm PVC pipes, which were covered with wire mesh on one end to prevent the movement of fish between channels.

Each trial block was composed of 12 treatments, with 12 fish per treatment. Each Atlantic salmon strain underwent four treatments: Atlantic salmon alone (12 fish), Atlantic salmon with brown trout (+BT; 6 salmon, 6 trout), Atlantic salmon with rainbow trout (+RT; 6 salmon, 6 trout), and finally, Atlantic salmon with both brown trout and rainbow trout (+BTRT; 4 salmon, 4 of each trout species). Density in the stream channels was 10 fish/m², which is the upper end of densities found in the field (Fransen et al. 1993), but by holding density constant, we were still able to determine the relative strengths of intraspecific and interspecific competition among ecologically similar species (Fausch 1998). The three Atlantic salmon strains were considered separately in all trials (not mixed) in order to independently evaluate their comparative performance. There were seven trial start dates (one trial block had a pair of dates, due to logistical constraints at the onset of the experiment, with the commencement of four treatments followed by eight treatments).

At the beginning of each trial, fish were randomly selected with similar catch effort and anesthetized with MS-222 (tricaine methanesulfonate). Once sedated, the initial mass and total length of each fish were recorded. In order to observe and record individual behavior and feeding, each fish was tagged with a colored 2-cm vinyl anchor tag (Floy Tag & Mfg., Seattle, Washington). Tags were applied using a fine fabric gun (Avery Mark II Fine Fabric Pistol Grip) with a maximum insertion depth

of 0.95 cm. Tags were applied to either the left or right side of the fish just below the dorsal fin to ensure all the fish within each channel could be uniquely identified. Between fish, the needle was disinfected with hydrogen peroxide and rinsed with water. The fish were released into a flow-through holding tank to recuperate before being placed in the appropriate stream channel. A random number generator was used to determine the placement of each treatment in the 12 channels for each trial block.

Behavioral observations began the day after the fish were tagged (day 1) and continued for 7 d. Behaviors were monitored each day in both a morning and afternoon session using a rig made up of three high definition camcorders (Sony HDR-XR200V) set up above a stream channel: one camera above the pool and two equally spaced out above the riffle section. The camcorder rig could easily be moved from channel to channel and was situated approximately 1 m above the water. Two rigs were constructed (six cameras total), which enabled two stream channels to be simultaneously recorded before moving the rigs to the next pair of channels. The fish were given 15 min to acclimate to the presence of the camcorder rig before recording began. Aggressive and feeding behaviors were then recorded for 30 min.

In the morning session (0800–1230 hours), each day for 7 days, fish were fed trout chow (Corey Aquafeeds) and frozen bloodworms (Chironomidae; Hikari, Japan). Specifically, every minute for the first 10 min of a recording session, either 50–100 bloodworms or 1 g of trout chow were alternately released at the top and middle of the stream channel, with the current carrying food items through the channel to simulate natural invertebrate drift (∼2% of biomass in each stream channel). Care was taken to avoid being seen by the fish. The afternoon recordings (1400–1830 hours) did not involve food. The order that channels were filmed was randomized using a random number generator for each day.

On day 8 of each trial, fish were collected from the stream channels for final mass and length measurements. Collection of fish began at the channels farthest from the headbox to prevent disturbance. Netted fish were sedated with MS-222 before final masses and lengths were recorded. The initial and final mass measurements were used to calculate standard growth rate (%/d) using the following equation (Bernier et al. 2004):

$$\text{Standard growth rate} = 100 \times [\log_e(\text{final mass}) - \log_e(\text{initial mass})]/\text{d fed}.$$

Video analysis.—Analysis of the videos focused on aggressive and feeding behaviors. Aggressive behaviors monitored comprised chasing, charging, and nipping (see Keenleyside and Yamamoto 1962 for definitions of behaviors). Feeding observations were of the number of items consumed. Aggressive and feeding behavior data from 4 days of each trial were analyzed, comprising day 1, 3, 5, and 7. Approximately 864 h of video

were observed in real time and paused every time an action occurred, with actor, act, and recipient recorded.

Statistical analysis.—Agonistic and feeding behaviors across the 4 days were summed and converted to a rate by dividing by the total time of observation. Dominance was calculated using David's score, which creates an index for individuals within a social hierarchy based on an individual's initiated and received aggressive acts, while accounting for repeated interactions among group members (David 1988; see Gammell et al. 2003 for details of the calculation).

Differences in initial mass and total length of the Atlantic salmon strains were analyzed using one-way analysis of variance (ANOVA) models, with strain as the main effect. Student's *t*-tests were used post hoc to determine differences between pairs of strains. Data of initiated aggression, received aggression, and food consumption were normalized using logarithmic $(x + 1)$ transformation. Next, we conducted linear mixed models to test the effects of strain and treatment on initiated and received aggression, David's scores, food consumption, and standard growth rate. The interaction between strain and treatment was included while initial mass was entered as a covariate in the models. Trial block and channel number were entered as random effects. We used a variance components covariance structure and denominator degrees of freedom were calculated using a Satterthwaite approximation (Satterthwaite 1946). When main effects were significant or a significant interaction existed between strain and treatment, Student's *t*-tests were used post hoc to determine differences in variables. To test the effect of dominance on growth parameters, linear regression analysis was used to compare David's score and food consumption or standard growth rate.

To examine the effect of nonnative trout species on each Atlantic salmon strain in multivariate space, we used direct discriminant function analysis (DFA; Dunteman 1984). The DFA examined the variation in the five aggression and growth variables (initiated and received aggression, David's score, food consumption, and standard growth rate) to assess how the three Atlantic salmon strains clustered when alone or with nonnative trout species by grouping each strain by the presence or absence of nonnative trout species (e.g., LaHave individuals alone or LaHave individuals with nonnatives). All nonnative treatments were grouped together for this analysis. All five dependent variables were included in the analysis as predictors and the pooled within-group structure matrix was analyzed to determine which variables most strongly correlated with the discriminant functions. A two-way ANOVA was then used to examine the effects of treatment (alone versus nonnative) and strain on the first two DFA axes. All statistics were performed using JMP 4 (version 4.0.2, SAS Institute Inc., Cary, North Carolina), SPSS 16.0 (SPSS Inc., Chicago), or Microsoft Office Excel 2003 (Microsoft Corporation, Redmond, Washington). Presented *P*-values are two-tailed probabilities.

RESULTS

The strains of Atlantic salmon differed significantly from one another in initial mass and total length (mass: $F_{2, 297} = 71.5$, $P < 0.001$; total length: $F_{2, 297} = 37.8$, $P < 0.001$, Table 1). Atlantic salmon from the Sebago Lake strain were the largest, followed by Lac Saint-Jean fish, while those from the LaHave strain were the smallest. Overall, the average mass of Atlantic salmon was 40 ± 16 g (mean $\pm$ SD), while the average length was 164 ± 22 mm. Brown trout had an average mass of 39 ± 14 g and length of 151 ± 18 mm, while rainbow trout were on average 21 ± 10 g and 126 ± 19 mm in length. Both mass and length differed among the three species (initial mass: $F_{2,861} = 130.7$, $P < 0.001$; length: $F_{2,861} = 212.5$, $P < 0.001$), with Atlantic salmon being longer but not heavier than brown trout (length: $t_{401} = 7.85$, $P < 0.001$; mass: $t_{365} = 0.72$, $P = 0.47$), while both species were longer and heavier than rainbow trout (Atlantic salmon length: $t_{370} = 21.9$, Atlantic salmon mass: $t_{520} = 19.5$, brown trout length: $t_{358} = 13.0$, brown trout mass: $t_{322} = 15.1$; $P < 0.001$ for all comparisons).

TABLE 1. Summary of phenotypic and behavioral characteristics of three strains of juvenile Atlantic salmon in four treatments in seminatural stream behavioral trials. Means $\pm$ SDs across all four treatments to which the strains were exposed ($N = 168$ in each strain) are shown. Different lowercase letters indicate significant differences among strains (Student's *t*-test; $P < 0.05$).

Characteristic	Atlantic salmon strains		
	LaHave	Lac Saint-Jean	Sebago Lake
Initial mass (g)	30.9 ± 11.7 x	36.6 ± 9.7 y	53.2 ± 16.1 z
Total length (mm)	150 ± 22 x	162 ± 15 y	181 ± 18 z
Initiated aggression/h	2.8 ± 4.3 z	3.6 ± 4.4 z	1.3 ± 2.8 y
Received aggression/h	6.8 ± 6.2 z	6.6 ± 5.6 z	3.1 ± 3.2 y
David's score	-4.7 ± 13.5	-3.7 ± 14.8	-1.5 ± 7.8
Food consumption (items/h)	10.7 ± 10.5 z	8.8 ± 7.0 zy	7.4 ± 7.3 y
Standard growth rate (%/d)	-0.12 ± 0.99	-0.06 ± 0.85	-0.15 ± 0.64

TABLE 2. Summary of linear mixed model results for the frequency of agonistic, foraging, and growth characteristics of three strains of juvenile Atlantic salmon in four treatments in seminatural stream behavioral trials. Strain and treatment were coded as main factors; initial mass was treated as a covariate.

Dependent variable	Independent	Degrees of freedom	F-statistic	P-value
Initiated aggression/h	Treatment	3,380.0	8.60	<0.001
	Strain	2,355.1	28.1	<0.001
	Initial mass	1,482.7	7.41	0.007
	Strain × treatment	6,168.4	6.89	<0.001
Received aggression/h	Treatment	3,474.3	27.6	<0.001
	Strain	2,462.9	26.0	<0.001
	Initial mass	1,488.8	9.90	0.002
	Strain × treatment	6,366.9	6.67	<0.001
David's score	Treatment	3,491.0	26.0	<0.001
	Strain	2,491.0	2.61	0.07
	Initial mass	1,491.0	0.63	0.43
	Strain × treatment	6,491.0	2.22	0.04
Food consumption (items/h)	Treatment	3,466.7	13.29	<0.001
	Strain	2,451.7	6.76	0.001
	Initial mass	1,489.8	0.61	0.43
	Strain × treatment	6,334.7	3.64	0.002
Standard growth rate (%/d)	Treatment	3,472.7	5.16	0.002
	Strain	2,472.8	0.21	0.81
	Initial mass	1,486.6	18.6	<0.001
	Strain × treatment	6,368.4	1.94	0.07

Agonistic Interactions and David's Score

Treatment significantly influenced initiated and received aggression and David's score of Atlantic salmon (Table 2). Across all strains, Atlantic salmon juveniles initiated more aggression when alone than in either +BT and +BTRT treatments (+BT, Student's t-test, $t_{258} = 2.28$, $P = 0.02$; +BTRT, Student's t-test, $t_{284} = 5.40$, $P < 0.001$) and were significantly more aggressive in the +RT treatment than in the +BTRT treatment (Figure 1a). Initiated aggression by Atlantic salmon varied between the +BT and +BTRT treatment with aggression observed to be higher in the +BT treatment (Figure 1a). Atlantic salmon also received much less aggression when alone or in the +RT treatment compared with either +BT (alone, Student's t-test, $t_{132} = 5.51$; +RT, Student's t-test, $t_{165} = 4.37$, $P < 0.001$ for both comparisons) or +BTRT treatments (alone, Student's t-test, $t_{106} = 5.48$; +RT, Student's t-test, $t_{178} = 3.90$, $P < 0.001$ for both comparisons; Figure 1b). When Atlantic salmon were alone or in the +RT treatment, they scored higher David's scores than in the +BT and +BTRT treatments; David's scores in the +BT treatment were lower than the +BTRT treatment (Table 2; Figure 1c).

The strain of Atlantic salmon also influenced initiated and received aggression (Tables 1, 2). The LaHave and Lac Saint-Jean strains both initiated significantly more aggression than Sebago Lake, whereas there was no difference in aggression between Lac Saint-Jean and LaHave strains (Table 1). Analogously, Sebago Lake received significantly less aggression than both LaHave and Lac Saint-Jean, which did not differ from one another (Table 1). An interaction between strain and treatment was also found for both initiated and received aggression and David's score (Table 2, Table A.1 in the appendix). Sebago Lake initiated and received the least aggression when alone or with brown trout, whereas in the +RT treatment, Lac Saint-Jean initiated significantly more aggression than either LaHave or Sebago Lake (Figure 1). There was no difference among the strains in either initiated or received aggression when they were with both brown trout and rainbow trout (Figure 1). Sebago Lake individuals scored significantly higher David's scores than either of the two other strains in the +BT treatment and in the +BTRT treatment, this strain scored significantly higher than LaHave individuals (Figure 1c).

As a covariate, initial mass of Atlantic salmon influenced agonistic interactions: heavier individuals both initiated more, and received fewer, aggressive acts (Table 2). However, initial mass did not influence David's score (Table 2).

Food Consumption and Standard Growth Rate

Food consumption and standard growth rate of Atlantic salmon individuals were significantly influenced by treatment (Table 2). Food consumption was highest when Atlantic salmon individuals were with conspecifics, followed by consumption in the +RT treatment, and was lowest in the two treatments containing brown trout (+BT and +BTRT; Table 2; Figure 2a). Standard growth rate largely mirrored the food consumption data: it was highest in the alone and +RT treatments and was the lowest in the +BT and +BTRT treatments (Figure 2b).
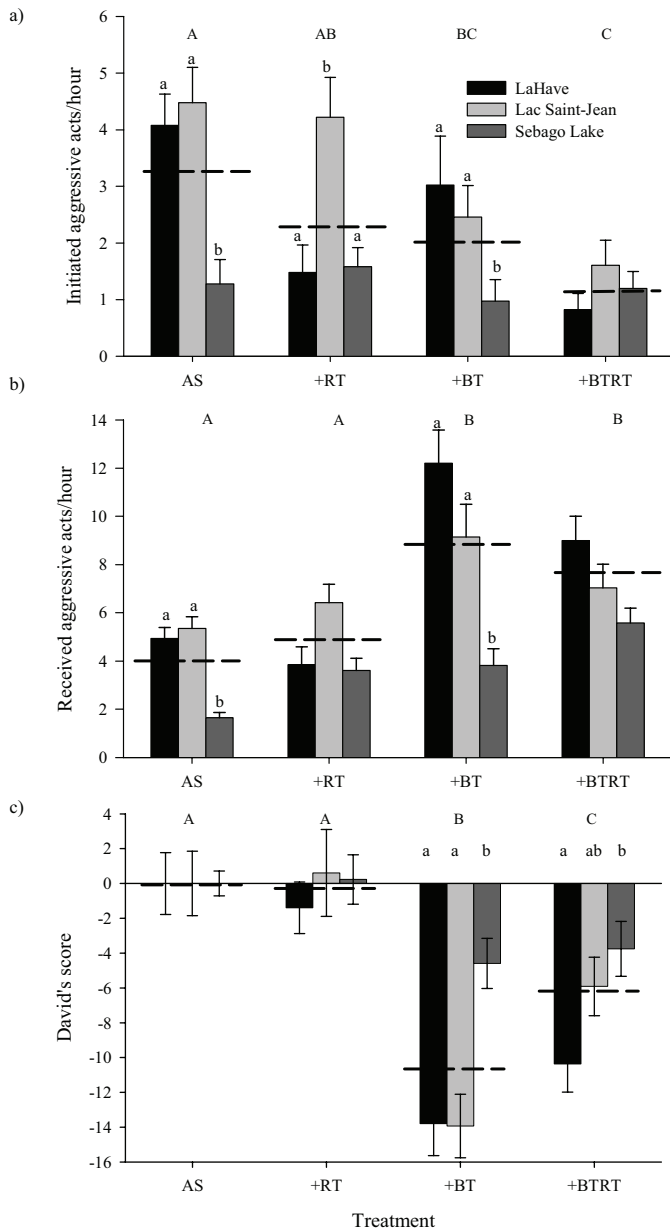
FIGURE 1. Agonistic interactions and dominance of three strains of juvenile Atlantic salmon (LaHave, Lac Saint-Jean, and Sebago Lake) in four treatments in seminatural stream behavioral trials showing (a) the number of initiated aggressive acts per hour, (b) the number of received aggressive acts per hour, and (c) David's score. The four experimental treatments include Atlantic salmon alone (AS), Atlantic salmon with rainbow trout (+RT), Atlantic salmon with brown trout (+BT), and Atlantic salmon with both brown trout and rainbow trout (+BTRT). Behavioral observations were summed for individual fish and then converted to a rate by dividing by the total observation time for a given channel. Bars denote mean ± SE for each of the three strains, while dashed lines indicate the mean of the three strains for each treatment. Different uppercase letters indicate significant differences between treatments, while different lowercase letters indicate significant differences among Atlantic salmon strains within a specific treatment (at $P < 0.05$).
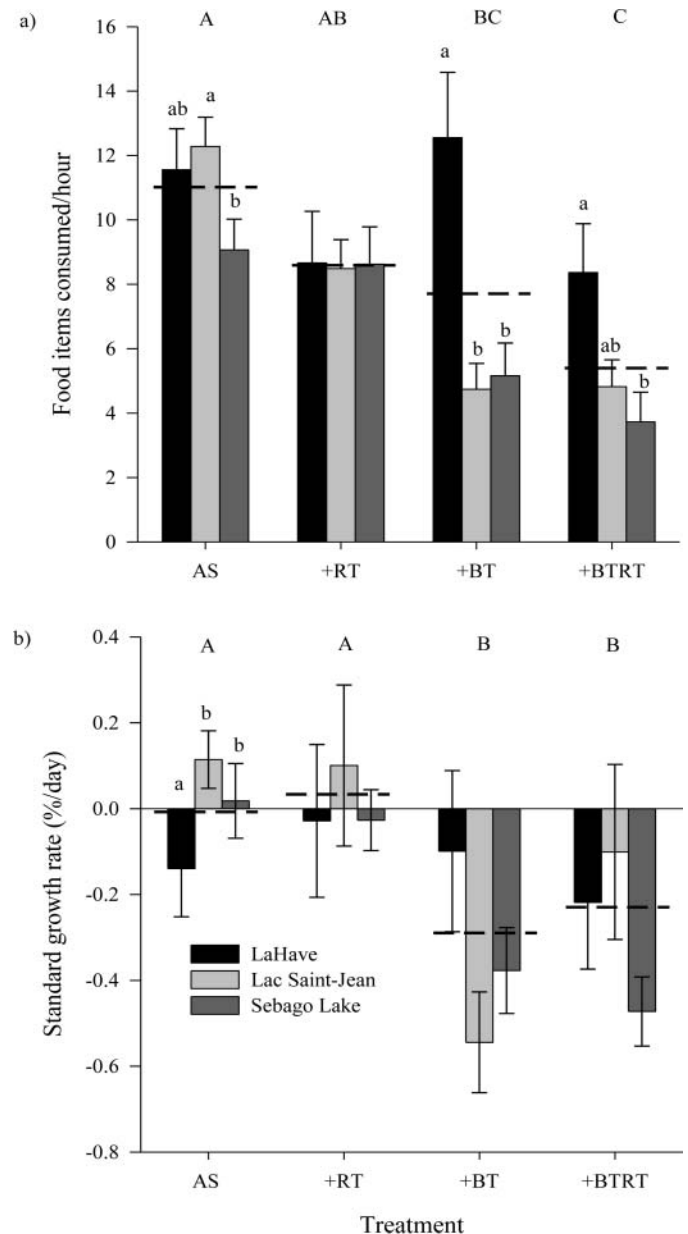
FIGURE 2. Feeding behaviors and growth of three strains of juvenile Atlantic salmon (LaHave, Lac Saint-Jean, and Sebago Lake) in four treatments in seminatural stream behavioral trials showing (a) the number of food items consumed per hour and (b) the standard growth rate. The four experimental treatments include Atlantic salmon alone (AS), Atlantic salmon with rainbow trout (+RT), Atlantic salmon with brown trout (+BT), and Atlantic salmon with both brown trout and rainbow trout (+BTRT; $N = 6$). Behavioral observations were summed for individual fish and then converted to a rate by dividing by the total observation time for a given channel. Bars denote mean ± SE for each of the three strains, while dashed lines indicate the mean of the three strains for each treatment. Different uppercase letters indicate significant differences between treatments, while different lowercase letters indicate significant differences among Atlantic salmon strains within a specific treatment (at $P < 0.05$).

The three strains also differed significantly in food consumption but not standard growth rate (Tables 1, 2). LaHave consumed significantly more food than Sebago Lake and more than Lac Saint-Jean, albeit the latter effect was marginally nonsignificant (post hoc t-test: $t_{292} = 1.96$, $P = 0.052$). An interaction between strain and treatment revealed that Sebago Lake consumed significantly fewer food items than either Lac Saint-Jean or LaHave in all but the $+$RT treatment (Figure 2a, Table A.1 in the appendix). Conversely, the LaHave strain consumed more food or equivalent amounts of food as compared to the other two strains across the four treatments (Figure 2a). Despite these differences in food consumption, however, there was no observed difference in standard growth rate among the strains in any of the treatments during the 7-d trials (Figure 2b).

David's score was positively related to both food consumption and standard growth rate of the Atlantic salmon (food consumption, linear regression: $R^2 = 0.008$, $\beta = 0.09$, $N = 504$, $P = 0.05$; standard growth rate, linear regression: $R^2 = 0.01$, $\beta = 0.11$, $N = 504$, $P = 0.01$).

Discriminant Function Analysis

Differences in aggression and growth predictors among Atlantic salmon strain groupings were detected by the DFA ($\chi^2_{(25)} = 267.7$, $P < 0.001$, Figure 3). The second function was also significant ($\chi^2_{(16)} = 109.1$, $P < 0.001$), as were the third ($\chi^2_{(9)} = 30.1$, $P < 0.001$) and fourth functions ($\chi^2_{(4)} = 12.1$, $P = 0.02$). The first and second discriminant functions of the analysis accounted for 62% and 28% of the variation, respectively, and were the focus of our analysis. The first discriminant function (DFA 1) was positively correlated with initiated and received aggression and negatively with, to a lesser extent, David's score (Table 3; Figure 3).

The two-way ANOVA revealed that for DFA 1, all three strains differed significantly from one another ($F_{2,498} = 82.8$, $P < 0.001$) with the Lac Saint-Jean strain scoring the highest, followed by LaHave and then Sebago Lake individuals (Figure 3). Treatment also influenced DFA 1 ($F_{1,498} = 7.30$, $P = 0.007$), with higher scores generally observed in the nonnative treatments. There was also, however, an interaction between strain and presence of nonnatives ($F_{2,498} = 11.6$, $P < 0.001$): Sebago Lake and Lac Saint-Jean, but not LaHave individuals had higher DFA 1 values in the nonnative versus alone treatments (Figure 3).

The second discriminant function (DFA 2) was positively correlated with initiated aggression, food consumption, growth rate, and David's score and negatively with received aggression (Table 3). For this function, a two-way ANOVA found that while the strains did not vary ($F_{2,498} = 2.08$, $P = 0.12$), the presence of nonnative trout species significantly influenced canonical scores ($F_{1,498} = 80.6$, $P < 0.001$), with strains initiating less aggression, consuming less food, growing less and having lower dominance scores, but receiving more aggression in the presence rather than absence of the nonnative trout species. The interaction between strain and the presence of nonnatives was not significant ($F_{1,498} = 0.39$, $P = 0.68$).

DISCUSSION

Although we cannot fully rule out the effects of body size among species, our data suggest that the presence of nonnative salmonids affects the aggressive and foraging behavior of juvenile Atlantic salmon. When juvenile Atlantic salmon were with conspecifics only, the level of aggression received by individual fish was lowest and the level of food consumption was highest. Additionally, Atlantic salmon were most aggressive in the conspecific treatment, as the presence of nonnative trout suppressed the amount of aggression Atlantic salmon initiated. Specifically, brown trout exerted a stronger influence on Atlantic salmon than rainbow trout. These data mirror those of other researchers including Stradmeyer et al. (2008), who found that juvenile brown trout were always dominant to Atlantic salmon. Using both stream channels and field surveys, Hearn and Kynard (1986) found that wild rainbow trout and juvenile Atlantic salmon compete and Blanchet et al. (2009) found that food consumption of juvenile Atlantic salmon was lowered in the presence of rainbow trout. Collective evidence now suggests that nonnative salmonids, particularly brown trout, can have strong behavioral effects on Atlantic salmon.

Body size is an important factor in determining the outcome of contests among conspecifics. Many studies have shown that dominance in fish is directly linked to larger body size (e.g., Abbott et al. 1985; Beaugrand et al. 1996). However, this relationship between body size and dominance did not exist for Atlantic salmon in our study. Consistent with our data, Huntingford et al. (1990) examined dominance competitions between pairs of juvenile Atlantic salmon in spring and summer (when we conducted our trials) and found no evidence that dominance tests were won by larger fish, regardless of the size difference between a pair. Interestingly, when the experiment was conducted in September, the relationship did exist with 72% of the dominance tests being won by the larger fish of a pair (Huntingford et al. 1990). The study found, however, that aggression levels strongly influenced the social dominance of an individual. These data suggest that dominance is a function of behavior and that large body size may be a consequence, not a cause, of dominance, at least in some salmonids.

It is well known that subordinate fish exhibit less growth as a result of the behaviors of dominant fish. This pattern has been shown in a number of salmonids (e.g., Atlantic salmon and brook trout; Gibson 1973). Consistent with these studies, we found that the presence of brown trout suppressed the growth rate of Atlantic salmon, which were typically subordinate to the brown trout. We also found that in the brown trout and Atlantic salmon treatment, subordinate fish grew at rates much lower than dominant fish, and food consumption of Atlantic salmon significantly declined as compared with when Atlantic salmon were alone. While dominant brown trout are known to
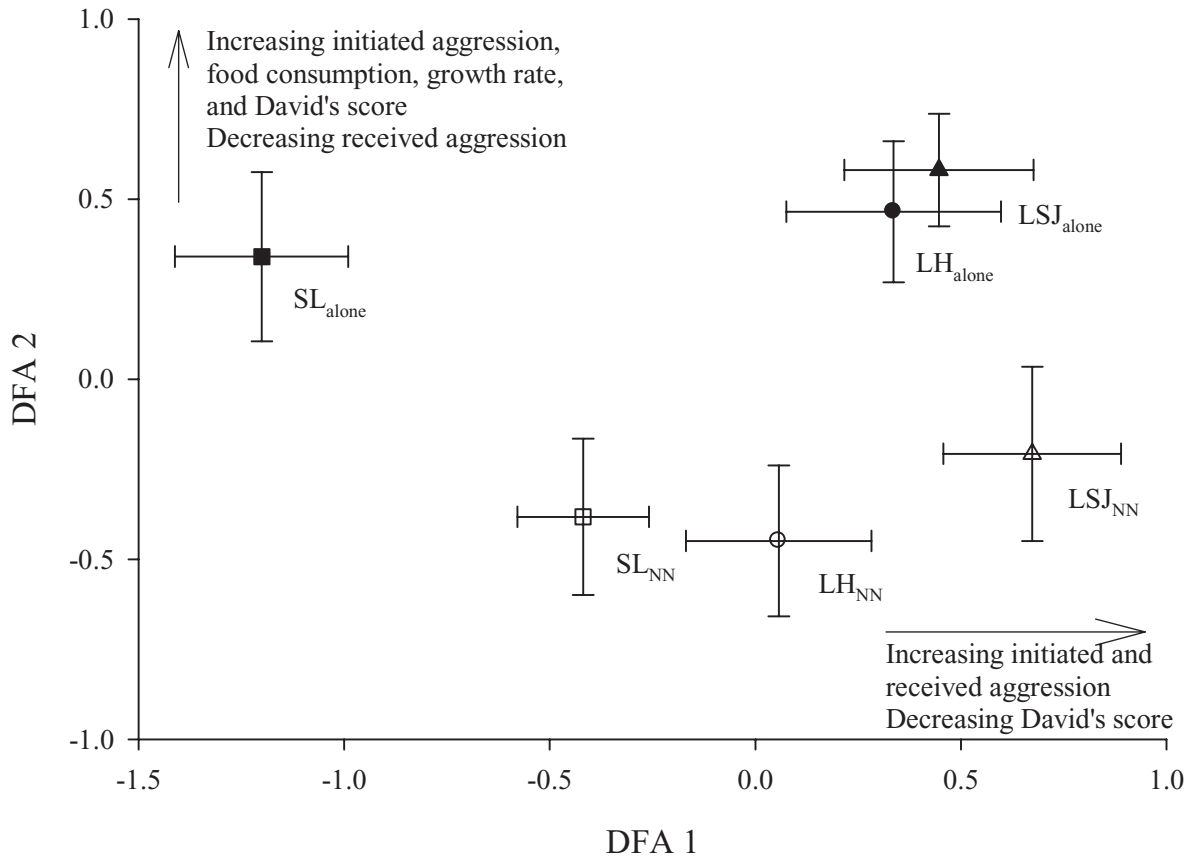
FIGURE 3. Canonical plot of the first two functions of the discriminant function analysis (DFA 1, DFA 2) examining the variation of aggression and growth measurements among three strains of juvenile Atlantic salmon in four treatments in seminatural stream behavioral trials. Treatments with nonnative species present (NN) were grouped together and compared with the Atlantic salmon alone treatment for the LaHave (LH), Lac Saint-Jean (LSJ), and Sebago Lake (SL) strains. The symbols represent strain centroids (with 95% confidence intervals).

monopolize feeding areas, reducing feeding opportunities of subordinates (Höjesjö et al. 2005), Metcalfe (1986) has postulated that regardless of the actions of the dominant fish, it is better for subordinate fish to minimize energetic costs, rather than maximize food intake. Although we did not directly quan-

tify the behavioral tactics used to acquire food, our results are consistent with Metcalfe (1986). For example, Sebago Lake salmon appeared to choose a growth strategy that minimized energy expenditure, opting out of the competition and consequently consuming the least amount of food and losing the most

TABLE 3. Summary of discriminant function analysis (DFA) of agonistic and growth measurements of three strains of juvenile Atlantic salmon in four treatments in seminatural stream behavioral trials. The DFA was performed on five agonistic and growth measurements of the LaHave, Lac Saint-Jean, and Sebago Lake strains. Treatments with nonnative species present were grouped together and compared with the Atlantic salmon alone treatment for each strain. Values represent pooled within-group correlations of canonical roots and standardized canonical discriminant function coefficients.

Variable	Correlation of variables with discriminant functions				Standardized canonical discriminant function coefficients			
	DFA 1	DFA 2	DFA 3	DFA 4	DFA 1	DFA 2	DFA 3	DFA 4
Initiated aggression/h	0.641	0.632	−0.05	0.395	1.26	0.706	−0.460	−0.679
David's score	−0.161	0.564	−0.463	0.587	−0.797	−0.81	−0.169	1.26
Received aggression/h	0.640	−0.397	0.462	0.461	0.157	−0.792	0.344	0.962
Food consumption (items/h)	0.067	0.580	0.786	0.198	−0.493	0.565	0.788	0.271
Standard growth rate (%/d)	−0.022	0.263	0.490	−0.137	0.16	−0.164	0.247	−0.220

mass of the three strains in the treatments with nonnative trout. Regardless of the actual feeding tactics used by Atlantic salmon, our data clearly show that Atlantic salmon feed less in the presence of dominant brown trout and consequently display reduced growth.

Community ecology studies have long shown that competition among ecologically similar species can lead to spatial separation or shifts in resource use if the species continue to live in sympatry (e.g., Werner and Hall 1977; Langeland et al. 1991). Brown trout and Atlantic salmon have historically coexisted in rivers in Europe (Höjesjö et al. 2005) but tend to spatially separate in streams, largely driven by the aggressive behavior of brown trout (Armstrong et al. 2003). Our study confirmed the dominance of brown trout over Atlantic salmon as has been shown by Stradmeyer et al. (2008). Additionally, we found that the food consumption and growth of Atlantic salmon declined in the presence of brown trout. Rainbow trout and Atlantic salmon, however, have not historically coexisted, yet studies have shown there is a degree of niche overlap (Gibson 1981; Hearn and Kynard 1986), which we expected would influence the agonistic interactions and growth of Atlantic salmon in our study. Similar to research by Blanchet et al. (2008), the presence of rainbow trout did not affect the food consumption or growth rate of Atlantic salmon. Atlantic salmon received no more aggression in the presence of rainbow trout than they did in the conspecifics treatment. These data support a study by Volpe et al. (2001) that found that although rainbow trout were much more aggressive than Atlantic salmon, agonistic interactions were largely between rainbow trout conspecifics and not Atlantic salmon. Hence, it is conceivable that although there is niche overlap between these two species, rainbow trout largely ignore Atlantic salmon, at least during agonistic interactions. Thus, density issues aside, these data suggest that brown trout, more than rainbow trout, influence Atlantic salmon agonistic and feeding behaviors, and unless spatial separation is possible for brown trout and Atlantic salmon, competition between these two species poses a threat to Atlantic salmon establishment in Lake Ontario streams.

Behavioral differences among populations or strains within a species have been observed across many taxa (e.g., Jones 1977; Rex et al. 1996; Moretz et al. 2007), and comparing these differences can provide an understanding of phenotypic attributes that will strengthen efforts of native species reintroduction (Curio 1996). One important attribute for successful establishment and persistence is aggression (as reviewed by Holway and Suarez 1999). We have shown differences among Atlantic salmon strains in both aggressive and feeding behaviors. Indeed, the Lac Saint-Jean strain initiated the most aggression and lost the least mass of the three strains, suggesting they are better competitors against brown trout and rainbow trout, two nonnative species prevalent in Lake Ontario tributaries. The DFA confirmed these strain differences by showing that the presence of nonnative trout species influenced the LaHave and Sebago Lake strains the most but had less of an impact on the

Lac Saint-Jean strain. Differences observed here suggest that stocking the Lac Saint-Jean strain, the strain believed to be the closest geographically and genetically of the three strains to the original Lake Ontario population (Dimond and Smitka 2005), will achieve greater restoration success as they are better competitors against brown trout and rainbow trout. Indeed, the fact that LaHave strain was the most significantly affected by the presence of the nonnative trout may explain the previous failed attempts of restoring Atlantic salmon with this strain.

High species richness can lead to competition for resources, resulting in declines in growth rates of the competing species. This effect has been shown in, for example, sunfish (Centrarchidae; Mittelbach 1988), *Daphnia* spp. (Bengtsson 1993), and desert annuals, where competition among the plants leads to decreases in growth, biomass, and fecundity (Inouye et al. 1980). We found that the presence of multiple salmonid species led to increases in aggression received and, in the case of Atlantic salmon, reductions in food consumption and growth. Such interactions often lead to partitioning of habitat and resources among the competing species allowing the individuals to coexist (e.g., Robertson and Gaines 1986; Young 2001). Because of our experimental setup, we could not easily assess potential habitat or resource partitioning. Nevertheless, we found no evidence that Atlantic salmon shifted habitat use across the pool and riffle sections when alone versus with either or both of the nonnative species. Regardless, our data suggest that high salmonid species richness could be detrimental for Atlantic salmon during the stream stage of life. Assessing the species community of targeted streams and rivers for Atlantic salmon restoration may also help to alleviate competition for Atlantic salmon.

In conclusion, our data point to some considerations that may help to direct restoration of Atlantic salmon among the naturalized populations of brown trout and rainbow trout in the Laurentian Great Lakes watershed. First, the three strains are predicted to have differential poststocking ecological success in tributary environments, with Atlantic salmon originating from Lac Saint-Jean outperforming the LaHave and Sebago Lake strains. Whether these differences would similarly extend to increased performance in Lake Ontario in terms of growth, survival, and adult returns still needs to be determined. Second, the successful establishment of juvenile Atlantic salmon may be greatly impeded by the presence of brown trout. Lake Ontario rainbow trout appear to have less of an influence on Atlantic salmon, albeit high species richness did impede the performance of Atlantic salmon. As such, we suggest avoiding stocking juvenile Atlantic salmon in Lake Ontario streams with high densities of brown trout or in streams with multiple established salmonid species.

REFERENCES

Abbott, J. C., R. L. Dunbrack, and C. D. Orr. 1985. The interaction of size and experience in dominance relationships of juvenile steelhead trout (*Salmo gairdneri*). Behaviour 92:241–253.

Armstrong, J. D., P. S. Kemp, G. J. A. Kennedy, M. Ladle, and N. J. Milner. 2003. Habitat requirements of Atlantic salmon and brown trout in rivers and streams. Fisheries Research 62:143–170.

Beaugrand, J. P., D. Payette, and C. Goulet. 1996. Conflict outcome in male green swordtail fish dyads (*Xiphophorus helleri*): interaction of body size, prior dominance/subordination experience and prior residency. Behaviour 133:303–319.

Bengtsson, J. 1993. Interspecific competition and determinants of extinction in experimental populations of three rockpool *Daphnia* species. Oikos 67:451–464.

Bernatchez, L. 2001. The evolutionary history of brown trout (*Salmo trutta* L.) inferred from phylogeographic, nested clade, and mismatch analyses of mitochondrial DNA variation. Evolution 55:351–379.

Bernier, N. J., N. Bedard, and R. E. Peter. 2004. Effects of cortisol on food intake, growth, and forebrain neuropeptide Y and corticotropin-releasing factor gene expression in goldfish. General and Comparative Endocrinology 135:230–240.

Blair, A. A. 1938. Scales of Lake Ontario salmon indicate a land-locked form. Copeia 1938:206.

Blanchet, S., L. Bernatchez, and J. J. Dodson. 2009. Does interspecific competition influence relationships between heterozygosity and fitness-related behaviors in juvenile Atlantic salmon (*Salmo salar*)? Behavioral Ecology and Sociobiology 63:605–615.

Blanchet, S., G. Loot, L. Bernatchez, and J. J. Dodson. 2008. The effects of abiotic factors and intraspecific versus interspecific competition on the diel activity patterns of Atlantic salmon (*Salmo salar*) fry. Canadian Journal of Fisheries and Aquatic Sciences 65:1545–1553.

Blankenship, S. M., M. R. Campbell, J. E. Hess, M. A. Hess, T. W. Kassler, C. C. Kozfkay, A. P. Matala, S. R. Narum, M. M. Paquin, M. P. Small, J. J. Stephenson, K. I. Warheit, and P. Moran. 2011. Major lineages and metapopulations in Columbia River *Oncorhynchus mykiss* are structured by dynamic landscape features and environments. Transactions of the American Fisheries Society 140:665–684.

Caro, T. 1999. The behaviour–conservation interface. Trends in Ecology and Evolution 14:366–369.

Crawford, S. S. 2001. Salmonine introductions to the Laurentian Great Lakes: an historical review and evaluation of ecological effects. Canadian Special Publication of Fisheries and Aquatic Sciences 132.

Crawford, S. S., and A. M. Muir. 2008. Global introductions of salmon and trout in the genus *Oncorhynchus:* 1870–2007. Reviews in Fish Biology and Fisheries 18:313–344.

Curio, E. 1996. Conservation needs ethology. Trends in Ecology and Evolution 11:260–263.

D'Antonio, C. M., and P. M. Vitousek. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. Annual Review of Ecology and Systematics 23:63–87.

David, H. A. 1988. The method of paired comparisons. Oxford University Press, New York.

Dewald, L., and M. A. Wilzbach. 1992. Interactions between native brook trout and hatchery brown trout: effects on habitat use, feeding, and growth. Transactions of the American Fisheries Society 121:287–296.

Dietrich, J. P., J. N. Bowlby, B. J. Morrison, and N. E. Jones. 2008. The impacts of Atlantic salmon stocking on rainbow trout in Barnum House Creek, Lake Ontario. Journal of Great Lakes Research 34:495–505.

Dimond, P., and J. Smitka. 2005. Evaluation of selected strains of Atlantic salmon as potential candidates for the restoration of Lake Ontario. Trout Unlimited Canada, Technical Report ON-12, Guelph, Ontario.

Dunteman, G. H. 1984. Introduction to multivariate analysis. Sage Publications, Thousand Oaks, California.

Edge, K. A., C. R. Townsend, and T. A. Crowl. 1993. Investigating anti-predator behaviour in three genetically differentiated populations of non-migratory galaxiid fishes in a New Zealand river. New Zealand Journal of Marine and Freshwater Research 27:357–363.

Elliott, J. M. 1990. Mechanisms responsible for population regulation in young migratory trout, *Salmo trutta:* III. the role of territorial behaviour. Journal of Animal Ecology 59:803–818.

Ens, B. J., and J. D. Goss-Custard. 1984. Interference among oystercatchers, *Haematopus ostralegus,* feeding on mussels, *Mytilus edulis*, on the Exe estuary. Journal of Animal Ecology 53:217–231.

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.

Fransen, B. R., P. A. Bisson, J. W. Ward, and R. E. Bilby. 1993. Physical and biological constraints on summer rearing of juvenile coho salmon (*Oncorhynchus kisutch*) in small western Washington streams. Pages 271–288 *in* L. Berg and P. W. Delaney, editors. Proceedings of the coho salmon workshop. Canadian Department of Fisheries and Oceans, Vancouver.

Gage, J. F. 1963. The landlocked salmon or ouananiche in Ontario. Ontario Fish and Wildlife Review 2(2):2–7.

Gammell, M. P., H. De Vries, D. J. Jennings, C. M. Carlin, and T. J. Hayden. 2003. David's score: a more appropriate dominance ranking method than Clutton-Brock et al.'s index. Animal Behaviour 66:601–605.

Gibson, R. J. 1973. Interactions of juvenile Atlantic salmon (*Salmo salar*) and brook trout (*Salvelinus fontinalis*). International Atlantic Salmon Foundation Special Publication Series 4:181–202.

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.

Good, S. P., J. J. Dodson, M. G. Meekan, and D. A. J. Ryan. 2001. Annual variation in size-selective mortality of Atlantic salmon (*Salmo salar*) fry. Canadian Journal of Fisheries and Aquatic Sciences 58:1187–1195.

Grieg, L., B. Ritchie, L. Carl, and C. A. Lewis. 2003. Potential and strategy for restoration of Atlantic salmon in Lake Ontario: a workshop report. Ontario Ministry of Natural Resources, Lake Ontario Management Unit, Peterborough, Ontario.

Hamilton, J. G., C. Holzapfel, and B. E. Mahall. 1999. Coexistence and interference between a native perennial grass and non-native annual grasses in California. Oecologia 121:518–526.

Hearn, W. E., and B. E. Kynard. 1986. Habitat utilization and behavioural interaction of juvenile Atlantic salmon (*Salmo salar*) and rainbow trout (*Oncorhynchus mykiss*) in tributaries of the White River of Vermont. Canadian Journal of Fisheries and Aquatic Sciences 43:1988–1998.

Höjesjö, J., J. D. Armstrong, and S. W. Griffiths. 2005. Sneaky feeding by salmon in sympatry with dominant brown trout. Animal Behaviour 69:1037–1041.

Holway, D. A., and A. V. Suarez. 1999. Animal behaviour: an essential component of invasion biology. Trends in Ecology and Evolution 14:328–330.

Huntingford, F. A., J. B. Metcalfe, J. E. Thorpe, W. D. Graham, and C. E. Adams. 1990. Social dominance and body size in Atlantic salmon parr, *Salmo salar* L. Journal of Fish Biology 36:877–881.

Inouye, R. S., G. S. Byers, and J. H. Brown. 1980. Effects of predation and competition on survivorship, fecundity, and community structure of desert animals. Ecology 61:1344–1351.

Jones, R. B. 1977. Sex and strain differences in the open-field responses of the domestic chick. Applied Animal Ethology 3:255–261.

Keenleyside, M. H. A., and F. T. Yamamoto. 1962. Territorial behaviour of juvenile Atlantic salmon (*Salmo salar* L.). Behaviour 19:139–169.

Kerr, S. J. 2006. An historical review of fish culture, stocking and fish transfers in Ontario, 1865–2004. Ontario Ministry of Natural Resources, Fish and Wildlife Branch, Peterborough, Ontario.

Kitano, S. 2004. Ecological impacts of rainbow, brown and brook trout in Japanese inland waters. Global Environmental Research 8:41–50.

Langeland, A., J. H. L'Abée-Lund, B. Jonsson, and N. Jonsson. 1991. Resource partitioning and niche shift in Arctic charr *Salvelinus alpinus* and brown trout *Salmo trutta*. Journal of Animal Ecology 60:895–912.

Lowe, S., M. Browne, S. Boudjelas, and M. De Poorter. 2000. 100 of the world's worst invasive alien species: a selection from the global invasive species database. Invasive Species Specialist Group of the World Conservation Union, Auckland, New Zealand. Available: interface.creative.auckland.ac.nz/ database/species/reference_files/100English.pdf. (December 2010).

MacCrimmon, H. R. 1977. Animals, man and change: alien and extinct wildlife of Ontario. McClelland and Stewart, Toronto.

Madsen, J. D., J. W. Sutherland, J. A. Bloomfield, L. W. Eichler, and C. W. Boylen. 1991. The decline of native vegetation under dense Eurasian water-milfoil canopies. Journal of Aquatic Plant Management 29:94–99.

Metcalfe, N. B. 1986. Intraspecific variation in competitive ability and food intake in salmonids: consequences for energy budgets and growth rates. Journal of Fish Biology 28:525–553.

Mittelbach, G. G. 1988. Competition among refuging sunfishes and effects of fish density on littoral zone invertebrates. Ecology 69:614–623.

Moretz, J. A., E. P. Martins, and B. D. Robison. 2007. Behavioral syndromes and the evolution of correlated behavior in zebrafish. Behavioral Ecology 18:556–562.

Nakano, S., S. Kitano, K. Nakai, and K. D. Fausch. 1998. Competitive interactions for foraging microhabitat among introduced brook charr, *Salvelinus fontinalis,* and native bull charr, *S. confluentus*, and westslope cutthroat trout, *Oncorhynchus clarki lewisi*, in a Montana stream. Environmental Biology of Fishes 52:345–355.

Olden, J. D., N. L. R. Poff, M. R. Douglas, M. E. Douglas, and K. D. Fausch. 2004. Ecological and evolutionary consequences of biotic homogenization. Trends in Ecology and Evolution 19:18–24.

Parsons, J. W. 1973. History of salmon in the Great Lakes, 1850–1970. U.S. Fish and Wildlife Service Bureau of Sport Fisheries and Wildlife Technical Paper 68.

Rex, A., U. Sondern, J. P. Voigt, S. Franck, and H. Fink. 1996. Strain differences in fear-motivated behavior in rats. Pharmacology Biochemistry and Behavior 54:107–111.

Ricciardi, A., R. J. Neves, and J. B. Rasmussen. 1998. Impending extinctions of North American freshwater mussels (*Unionoida*) following the zebra mussel (*Dreissena polymorpha*) invasion. Journal of Animal Ecology 67:613–619.

Robertson, D. R., and S. D. Gaines. 1986. Interference competition structures habitat use in a local assemblage of coral reef surgeonfishes. Ecology 67:1372–1383.

Satterthwaite, F. E. 1946. An approximate distribution of estimates of variance components. Biometrics Bulletin 2:110–114.

Scott, R. J., D. L. G. Noakes, F. W. H. Beamish, and L. M. Carl. 2003. Chinook salmon impede Atlantic salmon conservation in Lake Ontario. Ecology of Freshwater Fish 12:66–73.

Scott, R. J., M. S. Poos, D. L. G. Noakes, and F. W. H. Beamish. 2005. Effects of exotic salmonids on juvenile Atlantic salmon behaviour. Ecology of Freshwater Fish 14:283–288.

Stanfield, L., and M. L. Jones. 2003. Factors influencing rearing success of Atlantic salmon stocked as fry and parr in Lake Ontario tributaries. North American Journal of Fisheries Management 23:1175–1183.

Stewart, T. J., and T. Schaner. 2002. Lake Ontario salmonid introductions 1970 to 1999: stocking, fishery and fish community influences. Pages 12.1–12.10 *in* Lake Ontario fish communities and fisheries: 2001 annual report of the Lake Ontario management unit. Queen's Printer for Ontario, Picton, Ontario.

Stradmeyer, L., J. Höjesjö, S. W. Griffiths, J. D. Gilvear, and J. D. Armstrong. 2008. Competition between brown trout and Atlantic salmon parr over pool refuges during rapid dewatering. Journal of Fish Biology 72:848–860.

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 Columbia. Canadian Journal of Fisheries and Aquatic Sciences 58:197–207.

Ward, H. B. 1932. The origin of the landlocked habit in salmon. Proceedings of the National Academy of Sciences of the USA 18:569–580.

Watts, D. 1999. The Presumpscot gets a chance at life. Maine Sportsman (July). Available: friendsofsebago.org/mspresumpnew.html. (December 2010).

Werner, E. E., and D. J. Hall. 1977. Competition and habitat shift in two sunfishes (Centrarchidae). Ecology 58:869–876.

Young, K. A. 2001. Habitat diversity and species diversity: testing the competition hypothesis with juvenile salmonids. Oikos 95:87–93.

APPENDIX: SUPPLEMENTAL DATA FOR ATLANTIC SALMON

TABLE A.1. Agonistic interactions, growth, and physical measurements (means ± SDs) of three strains of juvenile Atlantic salmon in four treatments in seminatural stream behavioral trials. The four experimental treatments were Atlantic salmon alone ($N = 72$ for each strain), Atlantic salmon with rainbow trout ($N = 36$ for each strain), Atlantic salmon with brown trout ($N = 36$ for each strain), and Atlantic salmon with both brown trout and rainbow trout ($N = 24$ for each strain). Physical measurements of the trout species are included with sample sizes in parentheses under the treatment column.

Treatment	Initial mass (g)	Total length (mm)	Initiated aggression/ h	Received aggression/ h	David's score	Food consumption (items/h)	Standard growth rate (%/d)
Alone							
LaHave	30.0 ± 11.0	146 ± 20	4.1 ± 4.7	4.9 ± 3.8	0.0 ± 15.1	11.6 ± 10.8	–0.1 ± 0.9
Lac Saint-Jean	35.3 ± 8.8	160 ± 14	4.5 ± 5.3	5.4 ± 4.1	0.0 ± 15.8	12.3 ± 7.7	0.1 ± 0.6
Sebago Lake	55.2 ± 17.9	183 ± 19	1.3 ± 3.6	1.6 ± 1.9	0.0 ± 6.0	9.1 ± 8.1	0.0 ± 0.7
+ Rainbow trout							
LaHave	31.5 ± 13.9	152 ± 24	1.5 ± 2.9	3.8 ± 4.5	–1.4 ± 8.9	8.7 ± 9.6	0.0 ± 1.1
Lac Saint-Jean	37.1 ± 8.9	162 ± 13	4.2 ± 4.2	6.4 ± 4.6	0.6 ± 15.0	8.5 ± 5.4	0.1 ± 1.1
Sebago Lake	48.9 ± 10.9	176 ± 14	1.6 ± 2.0	3.6 ± 3.0	0.2 ± 8.5	8.6 ± 7.0	0.0 ± 0.4
Rainbow trout (108)	21.1 ± 10.2	127 ± 20					
+Brown trout							
LaHave	31.3 ± 11.0	152 ± 23	3.0 ± 5.2	12.2 ± 8.2	–13.8 ± 11.1	12.6 ± 12.2	–0.1 ± 1.1
Lac Saint- Jean	35.9 ± 12.2	159 ± 20	2.5 ± 3.3	9.1 ± 8.2	–13.9 ± 10.9	4.7 ± 4.8	–0.5 ± 0.7
Sebago Lake	53.1 ± 17.5	181 ± 18	1.0 ± 2.3	3.8 ± 4.1	–4.6 ± 8.7	5.2 ± 6.1	–0.4 ± 0.6
Brown trout (108)	39.5 ± 13.2	151 ± 17					
+Brown trout and rainbow trout							
LaHave	32.6 ± 11.7	156 ± 24	0.8 ± 1.4	9.0 ± 4.9	–10.4 ± 7.9	8.4 ± 7.4	–0.2 ± 0.8
Lac Saint-Jean	40.7 ± 8.6	167 ± 13	1.6 ± 2.2	7.0 ± 4.8	–5.9 ± 8.2	4.8 ± 4.1	–0.1 ± 1.0
Sebago Lake	54.2 ± 14.3	180 ± 17	1.2 ± 1.5	5.6 ± 3.0	–3.8 ± 7.7	3.7 ± 4.5	–0.5 ± 0.4
Brown trout (72)	39. 1 ± 14.3	150 ± 18					
Rainbow trout (72)	20.0 ± 8.5	126 ± 19					