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Effects of Competition with Four Nonnative Salmonid Species on Atlantic Salmon from Three Populations

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Abstract

The presence of ecologically similar nonnative species may impede recovery efforts for native species. We assessed the survival and growth of juvenile Atlantic Salmon *Salmo salar* from three populations (LaHave River, Sebago Lake, and Lac Saint-Jean) in the presence of four naturalized nonnative salmonid competitors. The three populations are being used for reintroduction efforts in Lake Ontario, where Atlantic Salmon are extirpated. Juvenile Atlantic Salmon were placed into artificial stream tanks with combinations of juvenile Brown Trout *S. trutta*, Rainbow Trout *Oncorhynchus mykiss*, Chinook Salmon *O. tshawytscha*, and Coho Salmon *O. kisutch*. Survival of all three Atlantic Salmon populations was lower in the presence of Brown Trout; growth was lower in the Brown Trout treatment and in the multispecies treatment. In contrast, Atlantic Salmon survival and growth were not negatively impacted by the presence of Chinook Salmon, Rainbow Trout, or Coho Salmon. Based on measurements of circulating hormones, Atlantic Salmon were not chronically stressed and did not show a change in social status after 10 months in the artificial stream tanks. Our results support the theory that differences in aggression and niche overlap can influence competitive outcomes and suggest that tributaries containing Brown Trout should be avoided during Atlantic Salmon reintroduction into Lake Ontario.

Efforts to reintroduce populations into systems where they have been extirpated face many challenges, particularly when the environments have changed from historical conditions. The introduction or establishment of nonnative competitors or predators can alter ecological conditions and hinder reintroduction efforts (Vitousek 1990; Olden et al. 2004; Simberloff 2011). This issue is typified by salmonids because meeting freshwater habitat and ecological requirements at the juvenile stage is made more challenging by the presence of nonnative species with similar habitat requirements (e.g., Hearn and Kynard 1986; Scott et al. 2005; Hasegawa et al. 2012). Such

niche overlap can lead to competition and predation and can impede the successful reintroduction of native populations (Vitousek 1990; Olden et al. 2004; Simberloff 2011).

In the Laurentian Great Lakes, a recent large-scale effort that typifies these challenges is the reintroduction of Atlantic Salmon *Salmo salar* into Lake Ontario. Atlantic Salmon were extirpated from Lake Ontario by 1898 (Crawford 2001; COSEWIC 2006), and the plan to restore self-sustaining populations into the lake and its tributaries explicitly recognizes several challenges (Greig et al. 2003). Specifically, within Lake Ontario and its tributaries, Atlantic Salmon may

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encounter four introduced and now-naturalized salmonid species: Brown Trout *S. trutta*, Rainbow Trout *Oncorhynchus mykiss*, Chinook Salmon *O. tshawytscha*, and Coho Salmon *O. kisutch* (Jones and Stanfield 1993; Crawford 2001; COSEWIC 2006, 2010). Atlantic Salmon juveniles have varying degrees of ecological niche overlap with these four species; the greatest overlap is with Brown Trout and Rainbow Trout juveniles, followed by Chinook Salmon and Coho Salmon juveniles (e.g., Gibson 1981; Hearn and Kynard 1986; Scott et al. 2005). Aggression can be a beneficial trait for acquiring resources in a competitive environment (Holway and Suarez 1999). Brown Trout and Rainbow Trout juveniles can be more aggressive than Atlantic Salmon juveniles, with Brown Trout in particular being highly aggressive (e.g., Gibson 1981; Vehanen 2006), whereas Chinook Salmon and Coho Salmon exhibit levels of aggression similar to that of Atlantic Salmon (e.g., Gibson 1981; Scott et al. 2005).

For Atlantic Salmon reintroduction efforts in Lake Ontario, it may be advantageous to use source populations that possess competitive traits, such as increased aggression (Holway and Suarez 1999), or that avoid agonistic interactions altogether (Metcalf 1986). Experiments are a useful way to compare the responses of several source populations to competition with nonnative salmonids, allowing the best population for reintroduction to be identified (Meffe 1995). Atlantic Salmon juveniles from three source populations are currently being stocked into tributaries of Lake Ontario. Stocking (hatchery) populations originated from Lac Saint-Jean (hereafter, Saint-Jean population) in Quebec, Sebago Lake (Sebago population) in Maine, and the LaHave River (LaHave population) in Nova Scotia. The three source populations were chosen based on their potential suitability and ecological contrasts (Dimond and Smitka 2005). The Sebago and Saint-Jean populations are native to freshwater lakes and are nonanadromous, whereas the LaHave population—the focus of previous reintroduction efforts (Jones and Stanfield 1993; Greig et al. 2003)—is anadromous (Dimond and Smitka 2005). Of the three populations, Saint-Jean Atlantic Salmon are likely the closest genetic relatives of the historical Lake Ontario population (Tessier and Bernatchez 2000). In Lake Champlain, stocked Sebago Atlantic Salmon co-occur with naturalized and stocked Brown Trout and Rainbow Trout (Marsden et al. 2010), whereas none of the four nonnative salmonid species are present in Lac Saint-Jean or the LaHave River (Dimond and Smitka 2005).

We examined the survival and body size traits of juvenile Atlantic Salmon from the three source populations in artificial stream tanks containing varied combinations of the four nonnative salmonid species (Brown Trout, Rainbow Trout, Chinook Salmon, and Coho Salmon). To assess the physiological state of Atlantic Salmon juveniles, we measured the circulating concentrations of cortisol (related to stress in fish; Wendelaar Bonga 1997; Iwama et al. 2004) and 11-ketotestosterone (11-KT; related to social status in fish; Oliveira et al. 2009) in their blood. This study builds on our

previous study (Houde et al. 2015), which was conducted the year before in the same artificial stream tanks by using age-0 Atlantic Salmon of the LaHave and Sebago populations only. The Houde et al. (2015) study indicated that Atlantic Salmon performance was reduced in the presence of Brown Trout, Rainbow Trout, or multiple nonnative species, but a change in hormone concentrations was not detected. We (Houde et al., in press) also previously examined siblings of the age-0 LaHave and Sebago Atlantic Salmon in natural streams and found suboptimal habitat use and reduced growth in the presence of Rainbow Trout. Previous studies of older (age 1) Atlantic Salmon from three source populations in the artificial stream tanks also demonstrated that Brown Trout and Rainbow Trout have the potential to negatively impact growth and increase circulating cortisol concentrations, but those studies did not assess the full suite of nonnative salmonids (Van Zwol et al. 2012a, 2012b).

Although it repeats our previous study (Houde et al. 2015), the present study is novel because it (1) includes the third source population (Saint-Jean; a natural population) to more broadly assess which nonnative salmonid species are the most problematic for the pre-smolt (freshwater) life stages of Atlantic Salmon; (2) assesses the repeatability of competitive effects with new fish in the same artificial stream tanks; and (3) examines correlations with density and differences in initial body size of the species. Moreover, the performance outcomes of these trials have important management implications for identifying Atlantic Salmon stocking locations and source populations that will facilitate reintroduction efforts in Lake Ontario.

METHODS

Study populations and nonnative salmonid species.—Juveniles of all salmonid species were provided by the Ontario Ministry of Natural Resources and Forestry (OMNRF). LaHave and Sebago Atlantic Salmon families ($n = 25$ per population) were produced in early November 2011 by using mature individuals at the OMNRF Harwood Fish Culture Station, Harwood. Families of fertilized eggs were transported the same day to the OMNRF Codrington Research Facility, Codrington. Saint-Jean Atlantic Salmon families ($n = 66$) were produced in early November 2011 at the Harwood Fish Culture Station and were transferred to the Codrington Research Facility as fry (age-0 parr; $n = 500$) in spring 2012. Rainbow Trout, Brown Trout, Chinook Salmon, and Coho Salmon fry ($n = 250$ for each species) were transferred from various OMNRF fish culture stations to the Codrington Research Facility in 2012. Details on the broodstock and breeding of the salmonid species are described in Houde et al. (2015). Stocking efforts in Lake Ontario tributaries use the same age of juveniles; thus, although the body sizes of the nonnative species differed, they mirrored the differences occurring in natural streams (see Table 1).

TABLE 1. Summary of the initial body sizes (tank means \pm SD) of fry from three populations of Atlantic Salmon and four nonnative salmonid species (Brown Trout, Rainbow Trout, Chinook Salmon, and Coho Salmon). Condition was examined as the residuals of a \log_e transformed length–mass regression using all data across species over the 10 months in artificial stream tanks (intercept = -4.681 ; slope = 3.08 ; $R^2 = 0.99$). Within a row, different letters indicate significant differences between populations or species (Tukey's post hoc multiple comparisons: $P < 0.05$). Sample sizes are 12 tanks for each Atlantic Salmon population and 12 tanks for each nonnative salmonid species.

Variable	Atlantic Salmon			Nonnative salmonids			
	LaHave	Sebago	Saint-Jean	Brown Trout	Rainbow Trout	Chinook Salmon	Coho Salmon
FL (cm)	6.5 \pm 0.1 z	6.8 \pm 0.1 y	6.8 \pm 0.1 y	6.7 \pm 0.2 x	6.0 \pm 0.1 w	9.8 \pm 0.1 v	10.6 \pm 0.1 u
Mass (g)	2.95 \pm 0.10 z	3.69 \pm 0.20 y	3.26 \pm 0.26 x	3.27 \pm 0.28 x	2.25 \pm 0.11 w	10.22 \pm 0.27 v	14.10 \pm 0.41 u
Condition ($\times 10^{-2}$)	-2.15 \pm 0.81 zy	4.82 \pm 0.73 x	-8.34 \pm 1.02 w	-0.89 \pm 0.96 y	-5.10 \pm 2.93 v	-3.08 \pm 1.98 z	5.75 \pm 1.47 x

Experimental apparatus and setup.—At the Codrington Research Facility, artificial stream tanks (width = 25 cm; length = 240 cm) were set up to contain two types of microhabitats: a 160-cm-long riffle section (velocity [mean \pm SD] = 20 ± 6 cm/s; depth = 28 ± 3 cm) followed by an 80-cm-long pool section (velocity = 7 ± 3 cm/s; depth = 68 ± 3 cm). Water velocities were measured in the center of the riffle and pool sections by using a digital flowmeter. Tank substrate was composed of two parts gravel (2–64 mm) to one part cobble (65–256 mm) river rock. The water depth, water velocity, and substrate composition were within the ranges used by juvenile Atlantic Salmon and the four nonnative salmonid species in natural streams (Johnson and Kucera 1985; Morantz et al. 1987; Bisson et al. 1988; Armstrong et al. 2003; Holecek et al. 2009).

Using a substitutive design that reduces the strength of intraspecific competition while adding interspecific competition (Fausch 1998), we filled the tanks with a total of 32 juvenile salmonids for one of six treatments: Atlantic Salmon in allopatry (32 LaHave, Sebago, or Saint-Jean individuals held alone); Atlantic Salmon in sympatry with one nonnative salmonid species (16 Atlantic Salmon held with 16 nonnative individuals); and Atlantic Salmon in sympatry with multiple nonnative species (16 Atlantic Salmon held with 4 individuals of each nonnative salmonid species). There were two replicate tanks per treatment for each Atlantic Salmon population (total = 36 tanks), and tanks were randomly assigned a treatment. Juveniles remained in the tanks from September 2012 to July 2013 (10 months). During this period, juveniles were fed a ration equal to 3% of body mass per day, which induces competition (e.g., Garner et al. 2008); this ration was reduced to 1% of body mass per day during the winter months (January–April). Because juvenile salmonids compete for upstream positions so as to obtain first access to food in natural streams (Chapman 1966; Metcalfe 1986), we delivered the daily ration to the upstream side of the tanks. The ration either was administered at a random time once per day or was divided in half and given at two random times per day to mimic the natural environment, where food availability and quantity are unknown to a juvenile (Keenleyside and Yamamoto 1962).

Additional details on the artificial stream tanks and setup are described in Houde et al. (2015).

Survival, body size, riffle use, and circulating hormone concentrations.—We measured Atlantic Salmon survival and three body size traits—specifically, body length (FL), mass, and condition. These size traits are related to survival in salmonids (Fausch 1984, 1998). We measured riffle use by Atlantic Salmon, as riffles are their preferred microhabitat (Morantz et al. 1987; Heggenes et al. 1999), and we also determined the extent of downstream displacement. Body length, mass, and condition measurements were collected on November 11 and December 17, 2012, and on May 29, June 26, and July 25, 2013; riffle use and downstream displacement measurements were collected the day before each of the above dates. For riffle use and downstream displacement, digital photographs were taken three times during the day (morning, noon, and evening) every 80 cm within the tanks using cameras (Sony HDRXR200V) supported on a rig. Photographs were analyzed using ImageJ version 1.38 (National Institutes of Health, Bethesda, Maryland; www.rsweb.nih.gov/ij/). Riffle use was measured as the proportion of Atlantic Salmon in the riffle section; downstream displacement was measured for each individual as the average of the distance downstream from the beginning of the riffle section. The day after photographs were collected, all juveniles were removed from the tanks, lightly anaesthetized using tricaine methanesulfonate (MS-222), and measured for FL, mass, and condition. Condition was examined as the residuals of a \log_e transformed length–mass regression (intercept = -4.812 ; slope = 3.14 ; $R^2 = 0.99$) using all data collected over the 10 months in the artificial stream (Cone 1989).

After 10 months (July 2013) in the artificial stream tanks, marking the termination of the experiment, blood from Atlantic Salmon individuals was collected by caudal peduncle severance using a heparin-lined tube. We collected as many Atlantic Salmon as possible within 2 min, and we aimed to process the individuals in less than 5 min/tank. For the hormone analysis, we randomly selected a median of four of the collected blood samples (range = 2–9) to be measured for concentrations of cortisol and 11-KT. Additional details on blood

collection and measurement of hormone concentrations are described in Houde et al. (2015).

Statistical analysis of traits.—Survival, FL, mass, condition, riffle use, downstream displacement, and circulating hormone concentrations were analyzed using tank means of individual Atlantic Salmon as independent observations. We calculated condition at the individual level prior to taking the tank means. Analyses were performed using R version 3.0.1 (available: www.r-project.org), and statistical significance was set at $\alpha = 0.05$. Survival was examined as a proportion relative to the initial count of individuals. Circulating hormone concentrations were $\log_e(x + 1)$ transformed to increase normality. Due to differences in the initial body length, mass, and condition of each population (Table 1), FL and mass were standardized as a proportion relative to the initial mean FL and mass for each tank, and condition was standardized by subtracting the initial mean condition for each tank in all size analyses. Juvenile densities across treatments differed from May to July because of Atlantic Salmon mortality (see Supplementary Table S.1 available in the online version of the article); thus, individual traits were statistically examined at 3 months (December 17, 2012) and at the last 10-month time point (July 25, 2013). Data from the 2-, 8-, and 9-month time points (November 11, 2012; May 29, 2013; and June 26, 2013) are presented in Figures S.1 and S.2 (see Supplement).

Binomial models (or quasi-binomial in cases of overdispersion; i.e., if residual deviance was much larger than df) were used for survival and riffle use. Poisson or quasi-Poisson models were used for downstream displacement. Linear models were used for the remaining traits. Atlantic Salmon models contained effects for population, treatment, and the population \times treatment interaction. Effects were examined using Tukey's post hoc multiple comparisons for pairwise combinations of populations and treatments.

Initial body size differences.—Tank means from the three Atlantic Salmon populations initially differed in FL, mass, and condition (Table 1). LaHave juveniles were intermediate in condition and were shorter and lighter than Sebago and Saint-Jean juveniles. Saint-Jean juveniles were also lighter and in lower condition than Sebago juveniles. Among the salmonid species, Coho Salmon were the largest in initial body size, followed by Chinook Salmon, Sebago and Saint-Jean Atlantic Salmon, Brown Trout, LaHave Atlantic Salmon, and Rainbow Trout (Table 1).

RESULTS

Survival

Differences in Atlantic Salmon survival were explained by treatment effects at 3 and 10 months and treatment \times population effects at 3 months (Table 2; Figure 1a, b). Populations did not differ in survival across all treatments at either time point. Atlantic Salmon in the presence of Brown Trout had

lower survival at 10 months (mortality [mean \pm SD] = 51.0 \pm 32.0%) relative to those in the Atlantic Salmon-only (allopatric) treatment (4.2 \pm 4.7%). LaHave juveniles in the Brown Trout, Coho Salmon, and multispecies treatments had lower survival relative to LaHave juveniles in the allopatric treatment at 3 months only. There were no significant differences in Atlantic Salmon survival between the allopatric treatment and the Rainbow Trout, Chinook Salmon, Coho Salmon, or multispecies treatment at 10 months.

Body Length, Mass, Condition, Riffle Use, and Downstream Displacement

Differences in Atlantic Salmon FL and mass at 3 and 10 months and differences in condition at 10 months were explained by population effects (Table 2; Figure 1c–h). After standardizing for differences in the initial FL, mass, and condition of the populations, Sebago Atlantic Salmon juveniles had grown more in FL and mass across treatments at 3 months than did both LaHave and Saint-Jean juveniles. At 10 months, Sebago juveniles had grown more in FL than LaHave juveniles, followed by Saint-Jean juveniles. Sebago and LaHave juveniles had gained more mass by 10 months than Saint-Jean juveniles. Furthermore, LaHave and Saint-Jean juveniles had achieved greater increases in condition relative to Sebago juveniles at 10 months but not at 3 months.

Differences in Atlantic Salmon FL and mass were also explained by treatment effects at 10 months but not at 3 months (Table 2; Figure 1c–h). A marginal treatment effect was detected for body condition at 10 months. Significant treatment effects were first detected for Atlantic Salmon juveniles at 8 months in the tanks (see Figure S.2). Relative to the allopatric treatment, Atlantic Salmon in the Brown Trout and multispecies treatments had lower body mass at 10 months, whereas those in the Chinook Salmon and Coho Salmon treatments had greater body mass at 10 months. In addition, given the 3% body mass ration based on initial tank density, the FL, mass, and condition of Atlantic Salmon were not correlated with the densities observed at 3 months or 10 months (Spearman's rank correlations: $P > 0.45$ for all). However, Atlantic Salmon FL, mass, and condition were negatively correlated with species differences in the initial values at 10 months (Pearson's product-moment correlations: $r = -0.48$ to -0.69 , $P < 0.007$ for all) but were nonsignificant when Chinook Salmon and Coho Salmon treatments were removed and were also nonsignificant at 3 months ($P > 0.05$).

Differences in Atlantic Salmon riffle use were explained by treatment effects at 10 months but not at 3 months (Table 2; Figure 1i, j). Treatment effects for downstream displacement were not detected at either time point (Table 2; Figure 1k, l). In general, few Atlantic Salmon or nonnative salmonids were observed in the riffle section. However, observations were made outside of feeding periods, and greater numbers of individuals were observed to enter the riffle section when the

TABLE 2. Summary of model results for performance traits in three populations of Atlantic Salmon that were held alone or with nonnative salmonids in artificial stream tanks. Displayed are quasi-binomial model results for survival and riffle use; quasi-Poisson model results for downstream displacement; and linear model results for body length (FL), mass, condition, circulating cortisol concentration, and circulating 11-ketotestosterone concentration (11-KT). Models used the mean values for tanks as independent observations. All of the LaHave Atlantic Salmon juveniles from one Brown Trout treatment tank died by 10 months, explaining the lower df for variables at 10 months.

Trait or effect	3 months			10 months		
	df	<i>F</i> -statistic	<i>P</i> -value	df	<i>F</i> -statistic	<i>P</i> -value
Survival						
Population	2, 18	1.15	0.338	2, 18	0.57	0.570
Treatment	5, 18	3.45	0.023	5, 18	8.08	<0.001
Population × treatment	10, 18	2.91	0.024	10, 18	1.44	0.239
Body length						
Population	2, 18	15.74	<0.001	2, 17	11.42	<0.001
Treatment	5, 18	1.27	0.318	5, 17	5.98	0.002
Population × treatment	10, 18	0.70	0.713	10, 17	0.97	0.503
Body mass						
Population	2, 18	11.05	<0.001	2, 17	6.32	0.009
Treatment	5, 18	1.06	0.412	5, 17	12.81	<0.001
Population × treatment	10, 18	0.69	0.721	10, 17	0.92	0.542
Body condition						
Population	2, 18	0.40	0.678	2, 17	32.25	<0.001
Treatment	5, 18	1.62	0.20	5, 17	2.74	0.054
Population × treatment	10, 18	0.47	0.89	10, 17	0.76	0.659
Riffle use						
Population	2, 18	2.25	0.134	2, 17	1.04	0.372
Treatment	5, 18	1.91	0.143	5, 17	7.48	<0.001
Population × treatment	10, 18	1.66	0.167	10, 17	1.99	0.098
Downstream displacement						
Population	2, 18	0.77	0.480	2, 17	1.31	0.295
Treatment	5, 18	0.70	0.631	5, 17	1.61	0.208
Population × treatment	10, 18	1.26	0.321	10, 17	0.79	0.639
Cortisol						
Population				2, 17	0.19	0.836
Treatment				5, 17	0.88	0.514
Population × treatment				10, 17	1.32	0.293
11-KT						
Population				2, 17	5.07	0.019
Treatment				5, 17	1.94	0.140
Population × treatment				10, 17	1.41	0.256

ration was administered (authors' anecdotal observation). The three Atlantic Salmon populations did not differ in their riffle use or downstream displacement across all treatments at either time point. Riffle use by Atlantic Salmon at 10 months was higher for those in the Chinook Salmon treatment relative to those in the allopatric treatment. Atlantic Salmon riffle use at 10 months did not significantly differ between the allopatric treatment and the Brown Trout, Rainbow Trout, Coho Salmon, or multispecies treatment. Riffle use and downstream displacement of Atlantic Salmon were not correlated with density at either 3 months or 10 months (Spearman's rank correlations: $P > 0.07$ for all).

Circulating Hormone Concentrations

Circulating cortisol and 11-KT concentrations in Atlantic Salmon were not influenced by treatment (Table 2; Figure 2). However, 11-KT concentrations were significantly different among Atlantic Salmon populations. LaHave juveniles had higher circulating 11-KT concentrations than Sebago and Saint-Jean juveniles. The average circulating cortisol concentration was 4.6 ng/mL, which is below the level indicating stress (10 ng/mL) in these Atlantic Salmon juveniles. There was no correlation between cortisol and 11-KT concentrations ($r = -0.121$, $df = 141$, $P = 0.149$). Circulating cortisol concentrations were correlated with the final (10 months) FL and

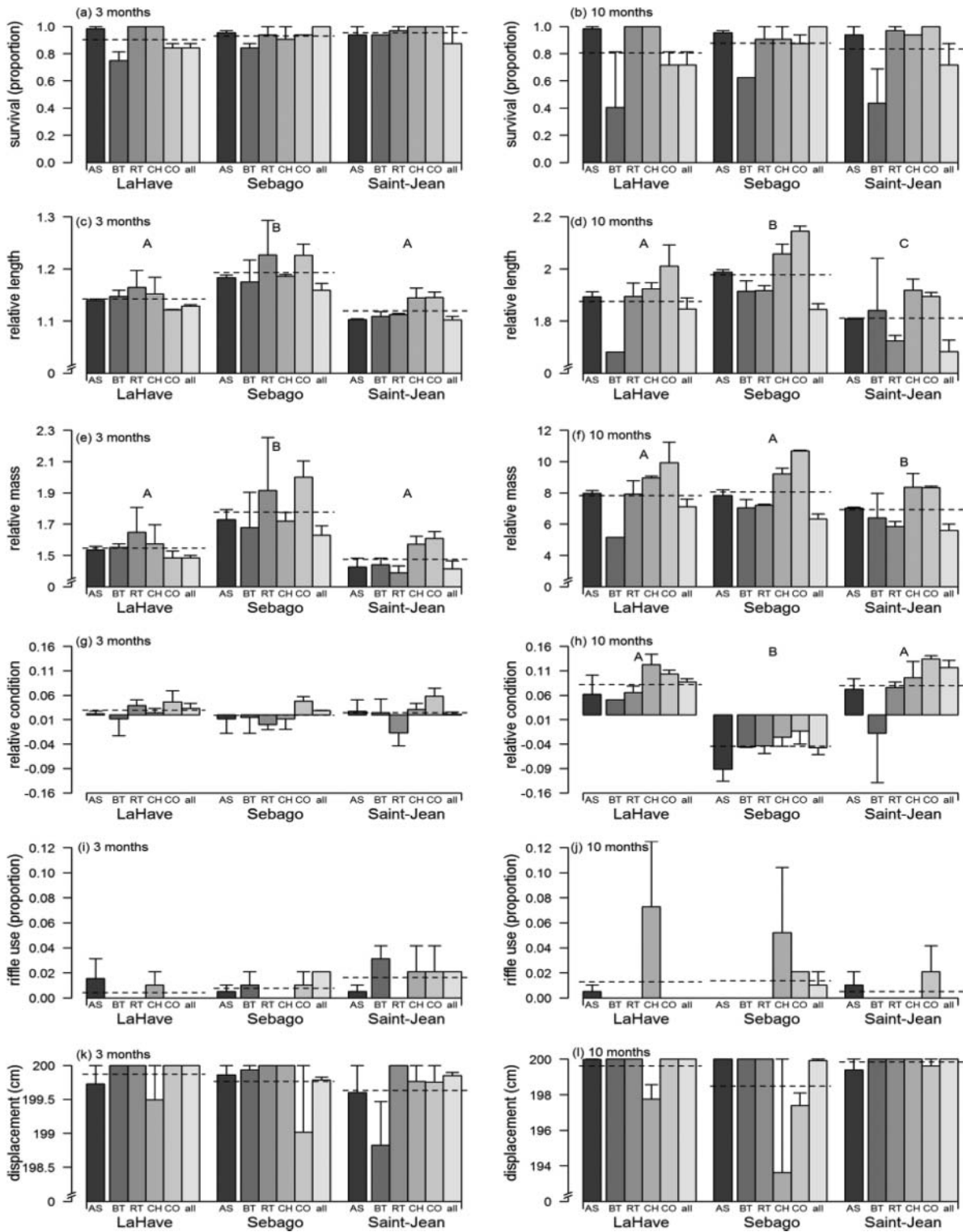


FIGURE 1. Performance traits (mean + SE) at 3 and 10 months for three populations of Atlantic Salmon held in artificial stream tanks alone (treatment = AS), with Brown Trout (BT), with Rainbow Trout (RT), with Chinook Salmon (CH), with Coho Salmon (CO), or with all four nonnative salmonid species (all). Relative length and mass are proportions relative to the initial mean FL and mass for each tank. Relative condition is the condition at 3 or 10 months minus the initial condition values for each tank. Dashed lines indicate the means for each Atlantic Salmon population across all treatments. Significant differences between populations are represented by different uppercase letters (Tukey's post hoc multiple comparisons: $P < 0.05$).

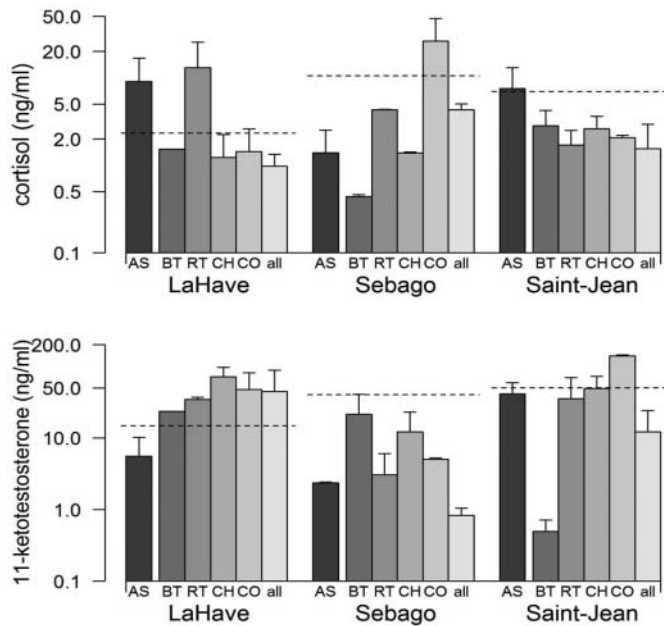


FIGURE 2. Circulating hormone concentrations (mean + SE) at 10 months for three populations of Atlantic Salmon held in artificial stream tanks (treatment symbols are defined in Figure 1). Circulating cortisol and 11-ketotestosterone concentrations were $\log_e(x + 1)$ transformed for analysis. Dashed lines indicate the means for each Atlantic Salmon population across all treatments.

condition of LaHave juveniles (FL: $r = 0.350$, $df = 49$, $P = 0.012$; condition: $r = -0.363$, $df = 49$, $P = 0.009$) and with the final FL and mass of Saint-Jean juveniles (FL: $r = 0.393$, $df = 49$, $P = 0.004$; mass: $r = 0.371$, $df = 49$, $P = 0.007$). There were no correlations between these metrics for Sebago juveniles ($P > 0.07$ for all). Circulating 11-KT concentrations were correlated with the FL and condition of LaHave juveniles (FL: $r = -0.376$, $df = 49$, $P = 0.007$; condition: $r = 0.313$, $df = 49$, $P = 0.025$) and with the body condition of Saint-Jean juveniles ($r = 0.688$, $df = 49$, $P < 0.001$). No correlations between these metrics were detected for Sebago juveniles ($P > 0.13$ for all). Atlantic Salmon circulating cortisol and 11-KT concentrations were not correlated with density (Spearman's rank correlations: $P > 0.16$ for both).

DISCUSSION

Nonnative species have the capacity to reduce the performance of native species, which could have significant consequences for reintroduction efforts. Although the width of the artificial streams was narrower than that of natural streams, the water depths, water velocities, and substrate composition in the artificial stream were within the ranges reported for juvenile Atlantic Salmon and the four nonnative salmonid species in natural streams (e.g., Morantz et al. 1987; Armstrong et al. 2003). In addition, comparison of results from the artificial streams in our previous study (Houde et al. 2015) to

results from natural stream sites (Houde et al., in press) revealed that Atlantic Salmon had similar responses to the presence of Rainbow Trout (i.e., no change in water depth use; and lower body size). One objective of this study was to examine the repeatability of our prior results (Houde et al. 2015) by using new fish in the same artificial streams. In the present study, we found that Atlantic Salmon survival was lower in the presence of Brown Trout and that body size was smaller in the Brown Trout and multispecies treatments. These effects were detected as early as 8 months in the artificial streams. In addition, Atlantic Salmon survival and body size were generally not affected by the presence of Chinook Salmon or Coho Salmon, consistent with the results from our previous study (Houde et al., in press). The effects of Brown Trout, Chinook Salmon, Coho Salmon, and the multispecies treatment were therefore repeatable across studies. On the other hand, our prior study (Houde et al. 2015) indicated that Atlantic Salmon survival and body size were negatively affected by the presence of Rainbow Trout, whereas these effects were not observed in the current study. This latter difference between the studies highlights the need for the repeatability of experiments to make robust conclusions about competition, such as the possibility of stochastic influences on the outcome of competition between Atlantic Salmon and Rainbow Trout.

Ecological niche overlap and differences in aggression may be primary determinants of the outcome of competition between salmonid species. Although initial size differences between salmonids can influence competitive outcomes, with larger individuals generally outcompeting smaller individuals (Huntingford et al. 1990), we did not detect this relationship among species in our study. For example, the Brown Trout used here were about the same size as the Atlantic Salmon, yet the Brown Trout negatively impacted the growth of Atlantic Salmon. Similarly, although differences in density can also influence the outcomes of competition for salmonids (Fausch 1998), there was no relationship between competition effects and density in the artificial streams. Atlantic Salmon performance may have been reduced when in sympatry with Brown Trout and Rainbow Trout due to niche overlap in the stream environment and because these species are generally more aggressive than Atlantic Salmon (Gibson 1981; Hearn and Kynard 1986; Volpe et al. 2001; Scott et al. 2005; Vehanen 2006). On the other hand, Chinook Salmon and Coho Salmon have little ecological niche overlap with Atlantic Salmon in streams, and their levels of aggression are generally similar to that of Atlantic Salmon (Gibson 1981; Beall et al. 1989; Heland and Beall 1997; Scott et al. 2005; Holecek et al. 2009). In addition, Atlantic Salmon may be an ecological equivalent to Rainbow Trout, which are sympatric with Chinook Salmon and Coho Salmon in their native environment (Quinn 2005). Nonnative salmonids that are more aggressive and that possess niches similar to those of native salmonids may be particularly problematic for fish management due to their competitive exclusion of the native salmonids.

Older life stages (e.g., age 1 and spawning adult) of nonnative salmonids may have greater competitive impacts on Atlantic Salmon. Although we found only small effects of competition using age-0 Atlantic Salmon in the present study, with age-1 Brown Trout, age-1 Atlantic Salmon had reduced growth (but not reduced survival) after just 7 d of competition in artificial streams (Van Zwol et al. 2012a). When in sympatry with age-1 Rainbow Trout in Lake Ontario tributaries, age-0 Atlantic Salmon showed reductions in survival and growth (Jones and Stanfield 1993; Stanfield and Jones 2003; Coghlan et al. 2007). Age-0 Atlantic Salmon in the presence of 3-month-old Coho Salmon also exhibited reduced survival and growth (Beall et al. 1989; Heland and Beall 1997). Although competition between juvenile Atlantic Salmon and Chinook Salmon has not been examined beyond the age-0 stage (e.g., Scott et al. 2005), adult Atlantic Salmon exhibited greater aggressive behavior, lower survival, lower mating success, and delayed nesting when in the presence of spawning adult Chinook Salmon (Scott et al. 2003). The larger negative impact on juvenile Atlantic Salmon in the presence of older nonnative salmonids may be attributable to predation by older life stages on younger fish (Gibson 1981), an increased number of competitive interactions (Scott et al. 2003, 2005), increased ecological niche overlap (i.e., Atlantic Salmon have a stronger preference for deeper microhabitats with increasing body size; Fausch 1988), or a combination of such factors.

Stress level and social status in fish can be evaluated by using measures of circulating hormone concentrations (Wendelaar Bonga 1997; Iwama et al. 2004; Oliveira et al. 2009). Similar to our previous study (Houde et al. 2015) that measured circulating cortisol concentrations in Atlantic Salmon, we found that competition with nonnative species did not appear to induce chronic stress. Chronic stress for salmonids is indicated at cortisol concentrations above 10 ng/mL (Maule et al. 1987; Pickering and Pottinger 1989), and the concentrations we measured in Atlantic Salmon juveniles were below this value in all but two treatments during the present study. Our results differ from those of a previous study (Van Zwol et al. 2012b), in which Brown Trout and Rainbow Trout were observed to induce chronic stress in Atlantic Salmon. However, those authors examined older fish (age 1) and measured the hormone concentrations only after a 7-d treatment. It is possible that competition and aggression increase with age or that the fish habituate to the competition sometime after 7 d. Additionally, similar to the previous studies (Van Zwol et al. 2012b; Houde et al. 2015) that evaluated circulating 11-KT concentrations, we found that competition with nonnative species did not appear to change the social status of Atlantic Salmon juveniles. However, we did detect differences in survival and body size of Atlantic Salmon when in competition with nonnative salmonids, despite the lack of change in hormone concentrations. These results could indicate that social status and stress level in juvenile salmonids are mediated by other hormones that were not examined here (e.g., growth hormone: Jonsson et al. 1998;

testosterone: Desjardins et al. 2006; arginine vasotocin: Dewan and Tricas 2011); alternatively, it is possible that 11-KT and cortisol are not sensitive indicators of performance at this life stage in Atlantic Salmon. More research is needed on the changes in circulating hormones of juvenile salmonids when exposed to competition with nonnative salmonids, particularly over different life stages.

Competitive outcomes among salmonid species may be influenced by rearing differences. Hatchery-reared salmonids can be more aggressive than their wild conspecifics, and the differences may be developmental as well as genetic (reviewed by Weber and Fausch 2003; Huntingford 2004). The hatchery rearing histories of the LaHave Atlantic Salmon, Brown Trout, and Rainbow Trout used in our study are longer than those of the Sebago Atlantic Salmon, Saint-Jean Atlantic Salmon, Chinook Salmon, and Coho Salmon, whose parents or grandparents were wild adults (OMNR 2005). The three Atlantic Salmon populations, however, had similar responses to the presence of nonnative salmonids. In addition, LaHave and Sebago Atlantic Salmon displayed similar responses to wild Rainbow Trout in natural streams (Houde et al. 2015). These results suggest that (1) even short periods of development in the hatchery environment can mask differences in the long-term culture history or (2) the effects of culture history are small in comparison with the effects of differences in aggression and competitiveness across species.

Our results have implications for efforts to reintroduce an extirpated species. Although it is still premature to comment on the relative suitability of different Atlantic Salmon source populations for whole-lake restoration, our findings suggest that the three populations may exhibit differential performance during the early life stage. Juvenile Atlantic Salmon from the Sebago population generally fared better than juveniles of the other two populations, but there were exceptions. In the present study, Sebago juveniles grew more than both LaHave and Saint-Jean juveniles (after standardizing for differences in initial body size). In a previous study (Houde et al. 2015), the presence of Rainbow Trout reduced the survival of LaHave juveniles but not Sebago juveniles, although LaHave juveniles had better survival in the multispecies treatment than Sebago juveniles. In addition, the present study and previous studies (Van Zwol et al. 2012a, 2012b; Houde et al. 2015) indicate that Brown Trout and Rainbow Trout can negatively affect the performance of Atlantic Salmon over the entire 2-year stream residency period, with Brown Trout having a particularly strong impact on survival and growth. Adjustment of stocking efforts to avoid tributaries that contain established Brown Trout populations may therefore increase the effectiveness of Atlantic Salmon reintroduction.

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