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Competitive effects between rainbow trout and Atlantic salmon in natural and artificial streams

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Abstract – Competition with non-native species may impede the restoration of native species, but differences in competitive abilities among intraspecific native populations may make some populations more suitable for reintroduction than others. Here, juvenile Atlantic salmon (*Salmo salar*) from two allopatric populations (LaHave and Sebago) being used for reintroduction into Lake Ontario were placed into two natural stream sites differing in the presence of ecologically similar rainbow trout (*Oncorhynchus mykiss*). We assessed the effects of competition in the natural streams on fitness-related traits and habitat use of the Atlantic salmon. We then compared these effects to those observed in artificial streams from a previous study. Atlantic salmon in natural streams had reduced fitness-related traits that were associated with suboptimal microhabitats in the presence of rainbow trout, but utilised optimal microhabitats in their absence. In the presence of rainbow trout, the two Atlantic salmon populations exhibited comparable recapture proportions to each other, but the individuals from the Sebago population had better performance (body size and condition) than those from the LaHave population. Responses of both Atlantic salmon populations to competition with rainbow trout were generally similar in both direction and magnitude when compared to results from the artificial stream study. The combined results suggest that native species restoration efforts should be focused on candidate populations that are ecologically suitable to reintroduction environments, as well as on suitable habitats that do not contain exotic competitors. Moreover, this study highlights the value of controlled experiments in artificial environments for predicting fitness-related performance in natural environments.

Key words: ecological niche overlap; aggression; survival; growth; reintroduction; restoration; lake ontario

Introduction

Non-native species are recognised as one of the top threats to preserving native species (Clavero & García-Berthou 2005) in part because competition by ecologically similar non-native species may reduce the ecological performance of native species (Hamilton et al. 1999; Maskell et al. 2006). Non-native species that are more aggressive than native species also tend to be better at acquiring resources which can cause native species to shift their ecological niche to suboptimal habitats and conditions (Holway & Suarez 1999), further reducing population growth and performance (Hearn 1987; Fausch 1988). Such competition with non-native species may also impede the restoration of native species (Simberloff 1990; Vitousek 1990).

Established populations of non-native salmonids have been identified as a potential concern for the re-establishment of formerly native Atlantic salmon into Lake Ontario (Jones & Stanfield 1993; Crawford 2001; COSEWIC 2006, 2010). Atlantic salmon were extirpated from Lake Ontario by 1900 (Crawford 2001) and decades of Atlantic salmon reintroduction attempts have yet to establish a self-sustaining population (COSEWIC 2006, 2010). Currently, Atlantic salmon in Lake Ontario streams may be competing with up to four species of non-native salmonids: brown trout (*S. trutta*), rainbow trout (*Oncorhynchus mykiss*), Chinook salmon (*O. tshawytscha*), and coho salmon (*O. kisutch*) (Parsons 1973; Crawford 2001). Of these, rainbow trout and brown trout are the most abundant (Stanfield et al. 2006) and have similar

microhabitat associations to, and are generally more aggressive than, Atlantic salmon (Gibson 1981; Hearn & Kynard 1986; Armstrong et al. 2003; Scott et al. 2005). Therefore, rainbow trout and brown trout have the potential to competitively displace Atlantic salmon to suboptimal conditions in streams, such as a higher percentage of rocks and lower water depth microhabitats (Gibson 1981; Hearn & Kynard 1986; Volpe et al. 2001).

In the case of the restoration of Atlantic salmon into Lake Ontario, three candidate populations are being considered for reintroduction: LaHave River (here after referred to as LaHave) from Nova Scotia, Sebago Lake (Sebago) from Maine, and Lac Saint-Jean (Saint-Jean) from Québec. The Sebago and Saint-Jean populations are native to freshwater lakes (Dimond & Smitka 2005), and the Saint-Jean population may be a close genetic relative of the historical Lake Ontario population (Tessier & Bernatchez 2000). Stocked Sebago-origin Atlantic salmon appear to be doing well in Lake Champlain where there are stocked and naturalised brown trout and rainbow trout (Marsden et al. 2010), whereas non-native salmonids are not present in Lac Saint-Jean (Dimond & Smitka 2005). Conversely, the LaHave population, which has been the focus of previous restoration efforts (Jones & Stanfield 1993; Greig et al. 2003), is anadromous and does not have to contend with introduced salmonids in its native habitat (Dimond & Smitka 2005). Populations of salmonid species can have genetic differences in behaviours important to competition, such as aggression (Rosenau & McPhail 1987; Swain & Holtby 1989; Houde et al. 2010; Van Zwol et al. 2012b). Therefore, candidate populations may differ in their competitive abilities when exposed to non-native salmonids.

The performance of LaHave and Sebago Atlantic salmon in competition with non-native salmonid species in Lake Ontario has been recently examined in artificial streams (see Van Zwol et al. 2012b,c; Houde et al. 2014). Artificial streams can provide important insights as they allow the manipulation of a number of conditions (e.g. combination of competitors, competitive levels, sediment types) in a controlled environment as well as for increased experimental replication in contrast to natural environments. The effectiveness of artificial environments for simulating natural environments may vary, however, and examining interspecific competition effects in natural streams can place the results into a larger management context (Fausch 1988, 1998). Relatively, few studies have contrasted interspecific competition effects between artificial and natural environments (e.g. Blanchet et al. 2007); a recent meta-analysis examining interspecific competition effects suggests that the direction of effects are similar, but that the magnitude of effects can differ across the two types of experiments (Korsu et al. 2010). A comparison between artificial and natural streams may therefore help to identify similarities and differences in the responses of Atlantic salmon to competition with non-native salmonids and allow improved application of the findings from controlled, artificial environments to natural environments.

Here, we examine LaHave and Sebago Atlantic salmon juveniles in two natural stream sites of Lake Ontario that differed in the presence and absence of non-native salmonids, mainly rainbow trout. We also compare the performance of Atlantic salmon in the natural streams to artificial streams. The Saint-Jean population was not included in these experiments, as it was not possible to obtain sufficient numbers of juveniles. Our objective was to test three hypotheses: (i) juvenile Atlantic salmon in competition with rainbow trout in streams will have suboptimal microhabitat associations and have reduced survival and fitness-related traits; (ii) juveniles from the two populations will differ in their competitive abilities and performance with rainbow trout; and (iii) that results from competition with rainbow trout in artificial streams are similar in direction, but not in magnitude to results in natural streams.

Materials and methods

Study populations

LaHave and Sebago Atlantic salmon families were produced in early November 2010 at the Ontario Ministry of Natural Resources and Forestry (OMNRF) Harwood Fish Culture Station (Harwood, ON, Canada). Five females and five males within each population were mated in all possible combinations to produce a 5×5 full factorial breeding design (Lynch & Walsh 1998) for each population. Offspring were then transported the same day as fertilisation to the OMNRF Codrington Facility (Codrington, ON, Canada) where they were exposed to natural photoperiods and local stream temperatures (mean $\pm$ SD: 8.4 ± 2.6 °C). The offspring of one Sebago female had very low survival; therefore, five of the 25 Sebago families were removed from the study. Greater details on the broodstock and rearing of families are described in Houde et al. (2013).

Study sites

Two sites within Duffins Creek, Ontario, were used to compare the performance of Atlantic salmon juveniles exposed to competition with non-native salmonids in natural conditions (Appendix S1). We were only able to use two sites because of the

challenges in getting landowner access to sites, appropriate permits to release fish in multiple locations, and minimise the overlap in sites used for our experiment and the other stocking efforts of the OMNRF. Our study nevertheless represents a rare opportunity to assess how generalisable the knowledge gained regarding the effects of competition in artificial streams is to natural systems. Because environment features may influence the outcomes of competition (Jones & Stanfield 1993; Fausch 1998; Stanfield & Jones 2003), the two sites were as similar as possible in temperature, productivity and microhabitat, but differed in the presence of rainbow trout (Stanfield et al. 2006 and confirmed by our microhabitat surveys). The first site (Upper Duffins) did not contain rainbow trout and the second site (Lower Duffins) contained juvenile rainbow trout (*Salvelinus fontinalis*), but also low numbers of brown trout. Both sites contain native brook trout and also have been used previously by the OMNRF for Atlantic salmon juvenile stocking.

Atlantic salmon fry were measured for body length (fork length) and mass, and families were pooled together by site (see Table 1 and Appendix S2). Fry were released at the sites on 24 May 2011 using plastic bags filled with oxygen saturated water. At the sites, bags were held within the stream water until the temperature was similar between the water inside the bag and the stream. Fry were then gently dispersed into riffle habitats within a 200 m section of stream using plastic watering cans (stocking area was 1066 m^2 for Upper Duffins and 1341 m^2 for Lower Duffins). Sebago salmon fry were initially larger in body length, mass, and Fulton's condition (Fulton 1904) than LaHave salmon fry (Student's *t*-tests, $P < 0.001$): Sebago salmon fry ($n = 540$) were 3.0 ± 0.2 cm (mean $\pm$ SD), 0.26 ± 0.06 g, and had a condition of 1.00 ± 0.12, and LaHave salmon fry ($n = 1125$) were 2.9 ± 0.2 cm, 0.23 ± 0.07 g, and had a condition of 0.93 ± 0.15.

Capturing juveniles and population assignments

Atlantic salmon juveniles were captured from the two sites using a backpack electrofisher (Halltech Aquatic Research, Guelph, ON, Canada) and a lip-seine net at 5 months (Fall: 7–10 November 2011) and 11 months after release (Spring: 10–11 April 2012). Electrofishing started 500 m downstream of the fry release point and moved upstream until about 50 m upstream of the fry release point following a single pass zigzag pattern to ensure the greatest sampling coverage. The entire stream area, including all habitats, was sampled. There was greater coverage sampling downstream than upstream because the majority of fry disperse downstream, usually within 500 m of the release point, within the first year (Webb et al. 2001; Einum et al. 2011). In addition, size-dependent dispersal should be captured within the first 150 m of the release point (Einum et al. 2011). Captured individuals were held in large buckets (10 l) filled with stream water until a predetermined stream section sample was completed. Stream sections were defined as areas roughly 30 m in length that contained homogenous habitat (riffle, runs or pools). These stream section boundaries were confirmed by the microhabitat survey described below. Upper Duffins had 9 stream sections, and Lower Duffins had 12 stream sections. Atlantic salmon juveniles from each section were lightly anaesthetised using food-safe clove oil (Hilltech Canada, Vankleek Hill, ON, Canada, 100 ppm) and measured for body length, mass, and Fulton's condition (Fulton 1904), traits which are considered relevant for future survival (Metcalfe & Thorpe 1992; Koskinen et al. 2002). A small fin clip (<0.15 cm^2) was then collected from one of the caudal fin lobes and stored in 95% ethanol for later genetic assignment to family and population (see Appendix S3). Juveniles were allowed to recover and were then returned to the section from where they were originally captured.

Table 1. Summary of fry releases and captured juveniles at two natural stream sites for LaHave and Sebago Atlantic salmon (*Salmo salar*).

Site	Population	Number of fry released	Area sampled (m^2)	Fall number of juveniles		Spring number of juveniles	
				Age 0+	Older	Age 1+	Older
Upper Duffins	LaHave	1444	–	18 (22)	12	5 (14)	1
	Sebago	446	–	11 (13)	0	1 (1)	1
	Total	1890	1967	29 (35)	12	6 (15)	2
Lower Duffins	LaHave	1469	–	8 (41)	10	2 (13)	5
	Sebago	457	–	3 (18)	7	0 (11)	0
	Total	1926	3436	11 (59)	17	2 (24)	5

Area sampled is the stream area sampled by electrofishing. The age 0+ and 1+ are the counts of juveniles that assigned to the families and in brackets are the counts of juveniles that assigned to a population (including other OMNRF-stocked juveniles of the target age classes). 'Older' indicates the number of juveniles that were larger than the individuals that assigned to the families and were excluded from analyses.

Nontarget species from each section were identified to species, counted and immediately returned to the site downstream of electrofishing.

Microhabitat variables

Microhabitat variables were measured once in the fall and used for both fall and spring analyses. Microhabitat measurement were collected at 10 m intervals throughout the study sites (see Peres-Neto 2004 for additional details): (i) average cross-sectional stream water depth from measurements every 50 cm along the entire cross section; (ii) cross-sectional stream width from bank to bank along the entire cross section; (iii) average cross-sectional stream water velocity from measurements at 2–3 points along the cross section using a 10 second average measurement for each point using a digital flowmeter (Höntszsch, Germany); (iv) stream substrate coarseness estimated visually from the centre of the cross section in the area bounded 1 m upstream and 1 m downstream along the cross section by percentage composition of clay (<0.002 mm), silt (0.002–0.05 mm), sand (0.05–2 mm), gravel (2–60 mm), pebbles (60–150 mm), and rocks (>150 mm). Visual classification of substrate coarseness was based off of a modified Wentworth scale (Heggenes & Saltveit 1990) and was recorded by the same individual for all sites to ensure the consistency of measurements.

Statistical analysis of microhabitat associations

Cumulative distribution functions described by Perry & Smith (1994) were used to describe the associations between each salmonid species (i.e. Atlantic salmon, brook trout, and rainbow trout) and the microhabitat variables for both fall and spring. Principal component analysis with the correlation matrix was used to simplify substrate composition variables into a smaller number of variables (Coghlan et al. 2007). The availability of each microhabitat variable at each site was quantified using the following cumulative distribution function:

$$f(t) = 100 \sum_{i=1}^{n} I \text{ where } I = \begin{cases} 1 \text{ if } x_i \leq t \\ 0 \text{ otherwise,} \end{cases} \quad (1)$$

where t was a level of the microhabitat variable and x_i was the microhabitat variable measurement for stream measurement i (i.e. taken every 10 m). Similar cumulative distribution functions were calculated for each salmonid species counts in relation to each microhabitat variable at each site for the fall and spring:

$$g(t) = 100 \sum_{i=1}^{n} \frac{y_i}{\bar{Y}} I \text{ where } I = \begin{cases} 1 \text{ if } x_i \leq t \\ 0 \text{ otherwise,} \end{cases} \quad (2)$$

where y_i was the salmonid species counts in stream section i and $\bar{Y}$ was the mean counts of the species in a given sampling site and season. Significance of the microhabitat association was determined using a randomisation procedure. The test statistic D was the maximum absolute vertical difference between $g(t)$ and $f(t)$ (Perry & Smith 1994). This observed D was compared to the distribution values of D produced by 999 random permutations of the microhabitat data (a total of 1000 permutations including the observed data). That is, under the null hypothesis of random association, we randomly paired salmonid species counts and microhabitat variables to create the distribution values of D.

Statistical analysis of recapture proportion, size, and condition

Atlantic salmon recapture proportion (number recaptured divided by the number released) between sites and populations was examined using relative fitness analyses described by Kalinowski & Taper (2005; available at http://www.montana.edu/kalinowski/RFA/RFA_Home.htm). One-way ANOVAs compared the body length, mass, and condition of recaptured Atlantic salmon between sites, seasons, and populations in R 2.15.3 (available at http://www.r-project.org/). Binomial generalised linear ordinary least squares regressions were used to test for relationships between Atlantic salmon recapture proportion with body length, mass, or condition. The binomial regressions were weighted by the number of fry released. Poisson (or quasi-Poisson in cases of overdispersion, that is if residual deviance was much larger than the degrees of freedom) generalised linear ordinary least squares regressions were used to test for relationships between Atlantic salmon counts with the average microhabitat variables of each stream section. Linear models tested for relationships between Atlantic salmon body length, mass, and condition with average microhabitat variables of each stream section. Statistical significance was set at $\alpha = 0.05$.

Statistical comparison between natural and artificial streams

Atlantic salmon water depth, body length, mass, and condition values from the natural stream sites were compared against those from artificial stream environments (Houde et al. 2014). For Atlantic salmon water depth in the natural streams, we used the average water depth of the section where individuals were

captured. The artificial streams contained siblings from eight of the families per population that were released into the two Duffins Creek sites (Houde et al. 2014). Artificial stream treatments that were used in the comparisons were (i) Atlantic salmon alone and (ii) Atlantic salmon with rainbow trout. To compare the two different environments (natural *versus* artificial), data from both environments were combined and standardised prior to analysis (mean = 0 and variance = 1 for each variable). Standardised data were analysed using two-way ANOVAS that contained treatment (rainbow trout absent or present) and source (natural streams or artificial streams).

Results

Juvenile captures and assignments

About 50% more Atlantic salmon juveniles were captured in Lower Duffins than Upper Duffins (Table 1). Because the sites potentially contained older Atlantic salmon (i.e. fall age 1+ and spring age 2+) from prior OMNRF Atlantic salmon fry releases, bimodal histograms of Atlantic salmon length were used to separate different age classes. Atlantic salmon that were in the larger mode were considered older Atlantic salmon age classes and were excluded from our analyses. This consideration was further supported based on genetic analysis of samples from the older Atlantic salmon age classes, which confirmed their exclusion from the experimental released families (data not shown). The proportions of older Atlantic salmon were not significantly different between sites ($X^2 = 0$, d.f. = 1, $P = 0.99$).

All Atlantic salmon of the target age classes (i.e. fall age 0+ and spring age 1+), except for two individuals, were assigned to the families or to the LaHave and Sebago populations (including other OMNRF-stocked juveniles of the target age classes) based on genetic analyses (see Appendix S3) and were included in our analyses. OMNRF-stocked juveniles in our sample were a small proportion of what was stocked; OMNRF-stocked juveniles in Upper Duffins originated from fry stockings at a site 500 m downstream in May 2011 ($n = 21,730$) and 2010 ($n = 19,990$) and OMNRF-stocked juveniles in Lower Duffins originated from two fry stocking sites 1.7–4 km upstream in May 2011 ($n = 36,140$) and 2010 ($n = 30,575$). In addition, Upper Duffins contained 108 and 55 brook trout in the fall and spring sampling periods, respectively, but did not contain rainbow trout. By contrast, the Lower Duffins site contained 16 and 6 brook trout, 560 and 199 rainbow trout, and 9 and 1 brown trout in the fall and spring sampling periods, respectively.

Microhabitat associations

While efforts were made to select sites that were as similar in microhabitat as possible, there were significant differences in the microhabitat variables between the Upper and Lower Duffins sites (MANOVA, $P < 0.001$). The sites were significantly different in water velocity (mean ± 1SD, Upper Duffins: $68 ± 12$ cm·s^{-1} and Lower Duffins: $81 ± 12$ cm·s^{-1}, Student's *t*-test, $P < 0.001$) and the percentages of pebbles ($19 ± 10\%$ and $37 + 22\%$, $P < 0.001$) and sand ($20 ± 14\%$ and $12 ± 13\%$, $P = 0.005$) (principal component 2, Table 2), but the sites were not significantly different in water depth ($23 ± 10$ cm and $25 ± 8$ cm, $P = 0.51$) and the percentages of gravel ($18 ± 12$ and $14 ± 13\%$, $P = 0.097$) and rocks ($29 ± 23$ and $26 ± 24\%$, $P = 0.62$) (principal component 1, Table 2). Upper Duffins had a lower water velocity, a lower percentage of pebbles, and a higher percentage of sand than Lower Duffins.

Salmonid species were significantly associated with microhabitat variables (Fig. 1). In the absence of rainbow trout (Upper Duffins), Atlantic salmon were found in habitats with a higher percentage of gravel in the fall and with a lower water depth in the spring. On the other hand, in the presence of rainbow trout (Lower Duffins), Atlantic salmon were found in habitats with a higher percentage of pebbles in the fall and with higher percentages of rocks and sand in the spring (Fig. 1). Similarly, in the absence of rainbow trout, brook trout were found in habitats with a higher percentage of gravel in the fall, but had no microhabitat associations in the spring (Fig. 1). In the absence of rainbow trout, brook trout had no microhabitat associations in the fall, but were found in habitats with a higher percentage of rocks in the spring. Rainbow trout were found in habitats with a higher percentage of rocks in the spring, but had no specific microhabitat associations in the fall.

Between sites, Atlantic salmon associated with different microhabitat variables (Fig. 1). Atlantic salmon were found in habitats with a lower water depth in the fall (one-way ANOVA, $P = 0.007$) (opposite in the

Table 2. Summary of relationships between substrate composition and the first two principal components based on two sites in a natural stream.

Variable	PC 1	PC 2
Clay	0.376	0.148
Silt	0.430	−0.415
Sand	0.122	**−0.590**
Gravel	**0.494**	0.237
Pebbles	0.147	**0.600**
Rocks	**−0.638**	−0.205
Proportion of variance explained, %	29.3	25.5

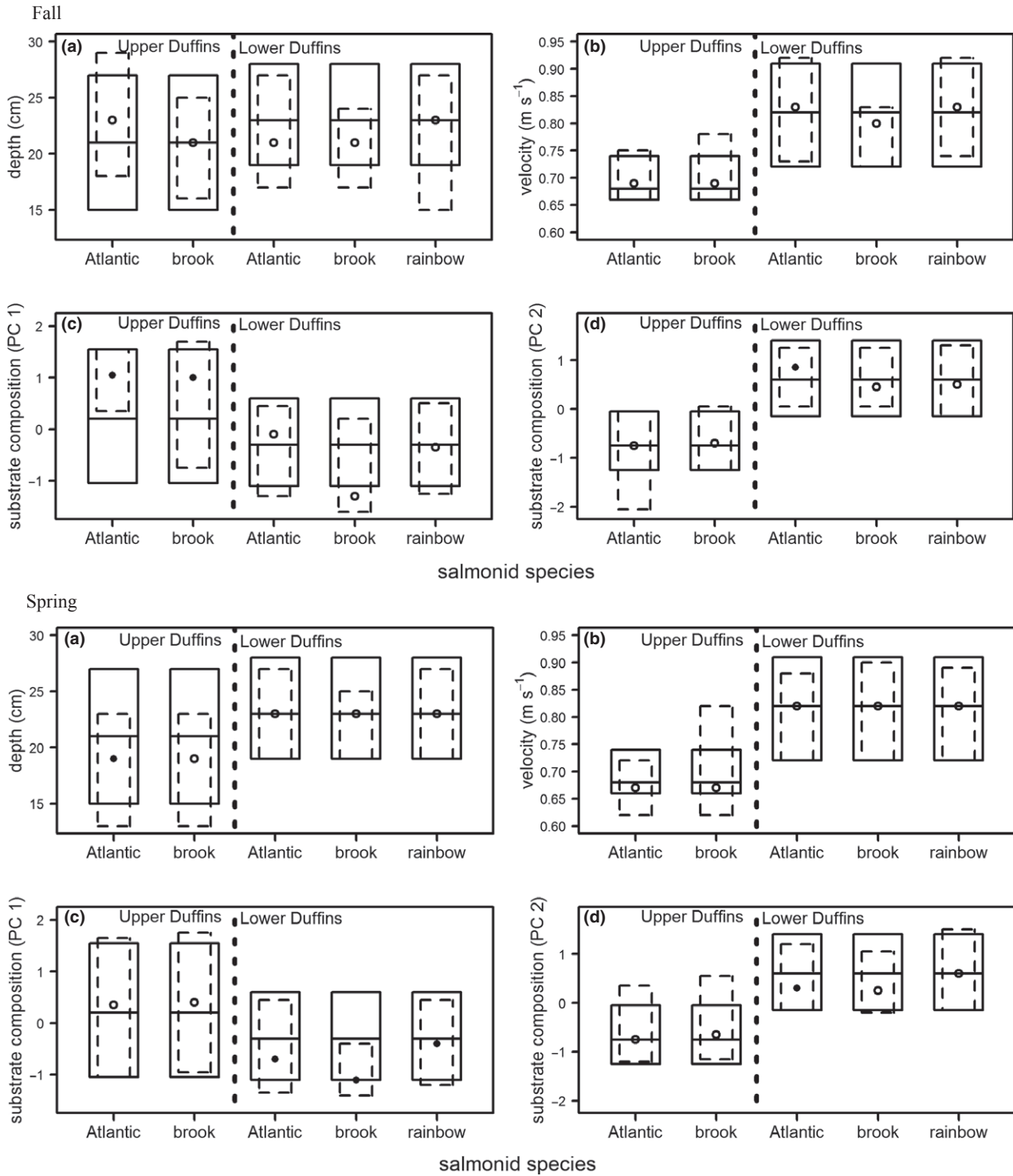Relationships >0.45 and <−0.45 are displayed in bold.

Fig. 1. Microhabitat associations of three species of salmonid (Atlantic salmon – *Salmo salar*, brook trout – *Salvelinus fontinalis* and rainbow trout – *Oncorhynchus mykiss*) at two natural stream sites. Shown are data for four microhabitat variables: (a) water depth, (b) water velocity, (c) principal component 1 of substrate composition (PC 1) and (d) principal component 2 of substrate composition (PC 2). Solid lines and boxes display the median and 25–75th percentiles of available microhabitat; dots and dashed boxes display the median and 25–75th percentiles of associated (utilised) microhabitat. Filled dots indicate significant microhabitat associations ($P < 0.05$). The principal component loadings are presented in Table 2.

spring, $P = 0.001$), and in both seasons were found in habitats with a higher water velocity (both $P < 0.001$) and higher percentages of rocks (fall, $P < 0.001$ and spring, $P = 0.026$) and pebbles (both $P < 0.001$) in the presence than in the absence of rainbow trout. Within sites, Atlantic salmon associated

with different microhabitat variables in comparison to the other salmonid species that were present. In the absence of rainbow trout, Atlantic salmon were found in habitats with a higher water depth (one-way ANOVA, $P < 0.001$) and a higher percentage of sand ($P = 0.006$) than brook trout in the fall, and there were no significant differences in microhabitat associations in the spring ($P > 0.14$ for all). Conversely, in the presence of rainbow trout, Atlantic salmon were found in habitats with similar microhabitat variables as brook trout and rainbow trout for both seasons ($P > 0.13$ for all), with exception of water depth and the percentage of sand compared to brook trout (both $P < 0.001$) and water depth compared to rainbow trout ($P = 0.047$) in the fall. Atlantic salmon populations were not significantly different in microhabitat associations in both seasons ($P > 0.08$ for all; Fig. 2), with exception that Sebago juveniles associated with a higher percentage of rocks than LaHave juveniles in the presence of rainbow trout ($P = 0.01$).

Recapture proportion, size, and condition

Over the winter, the relative recapture proportion of Atlantic salmon was not significantly different between the two sites (0.95 [95% CI = [0.50, 1.85]); therefore, fall and spring Atlantic salmon counts were combined. Although one purpose of the stocking experiment was to assess fitness variation within as well as between the two source populations, the counts of juvenile Atlantic salmon were insufficient to assess family-level differences in recapture proportions (Table 1). Using the counts from Atlantic salmon that were assigned to specific families, the relative recapture proportion of Atlantic salmon was significantly different between sites (0.36 [0.19, 0.67]), which cannot be explained by the difference in sampling area (Table 1). On the other hand, using the counts of all Atlantic salmon (our experimental fish plus the OMNRF-stocked fish), the density was similar between the sites (0.017 Atlantic salmon·m^{-2} for both sites). Also, the relative recapture proportion of the two Atlantic salmon source populations was not significantly different in both sites (Upper Duffins: 1.69 [0.81, 3.33] and Lower Duffins: 0.97 [0.22, 3.17]). There were no significant relationships between Atlantic salmon recapture proportion and initial release body length (binomial model, $P > 0.30$), mass ($P > 0.14$), and condition ($P > 0.26$) within sites (data not shown). Also, there were no significant relationships between Atlantic salmon recapture proportion and the microhabitat variables (quasi-Poisson models, $P > 0.12$ for all; data not shown) or the counts of older Atlantic salmon within sites ($P > 0.81$).

Body length, mass, and condition of Atlantic salmon were significantly different between sites and populations (Fig. 2). Atlantic salmon were shorter (one-way ANOVA, $P = 0.005$), had lower mass ($P = 0.001$), and were in lower condition ($P = 0.007$) in the presence than in the absence of rainbow trout. Sebago juveniles were longer ($P = 0.040$) and had higher mass ($P = 0.026$) than LaHave salmon in the presence of rainbow trout, whereas LaHave and Sebago juveniles were not significantly different in body length ($P = 0.12$) and mass ($P = 0.36$) in the absence of rainbow trout. Also, Sebago juveniles were in higher condition than LaHave juveniles in both sites ($P = 0.014$). For Upper Duffins, there was a significant correlation between these Atlantic salmon varia,bles (i.e. body length, mass, and condition) and substrate composition (principal component 1) ($P < 0.04$); Atlantic salmon were larger in habitats with a higher percentage of rocks and in higher condition in habitats with a higher percentage of gravel. For Lower Duffins, there was a significant correlation between body condition and substrate composition (principal component 1 and 2) ($P < 0.03$); Atlantic salmon were in higher condition in habitats with higher percentages of rocks and sand. There were no significant relationships between the Atlantic salmon variables and the remaining microhabitat variables (linear models, $P > 0.09$ for all; data not shown) or the counts of older Atlantic salmon within sites ($P > 0.81$). There also were no significant relationships between body length (linear model, $P > 0.11$), mass ($P > 0.28$), or condition ($P > 0.27$) within sites at the time of release versus the time of recapture, based Atlantic salmon family means (data not shown).

Comparisons to artificial streams

The direction and magnitude of the response of the water depth that Atlantic salmon occupied as well as their body length and mass to the presence of rainbow trout did not significantly different between natural and artificial streams (Table 3; Fig. 3). On the other hand, the body condition response to the presence of rainbow trout was significantly different between natural and artificial streams; there was a greater reduction in condition in the natural streams than in the artificial streams. In both artificial and natural streams, Atlantic salmon were not associated with different depths in the presence of rainbow trout. In addition, in both environments, there was a reduction in Atlantic salmon length, mass, and condition in the presence of rainbow trout.

Discussion

Ecological niche overlap among species has long been considered to lead to increased competition for similar
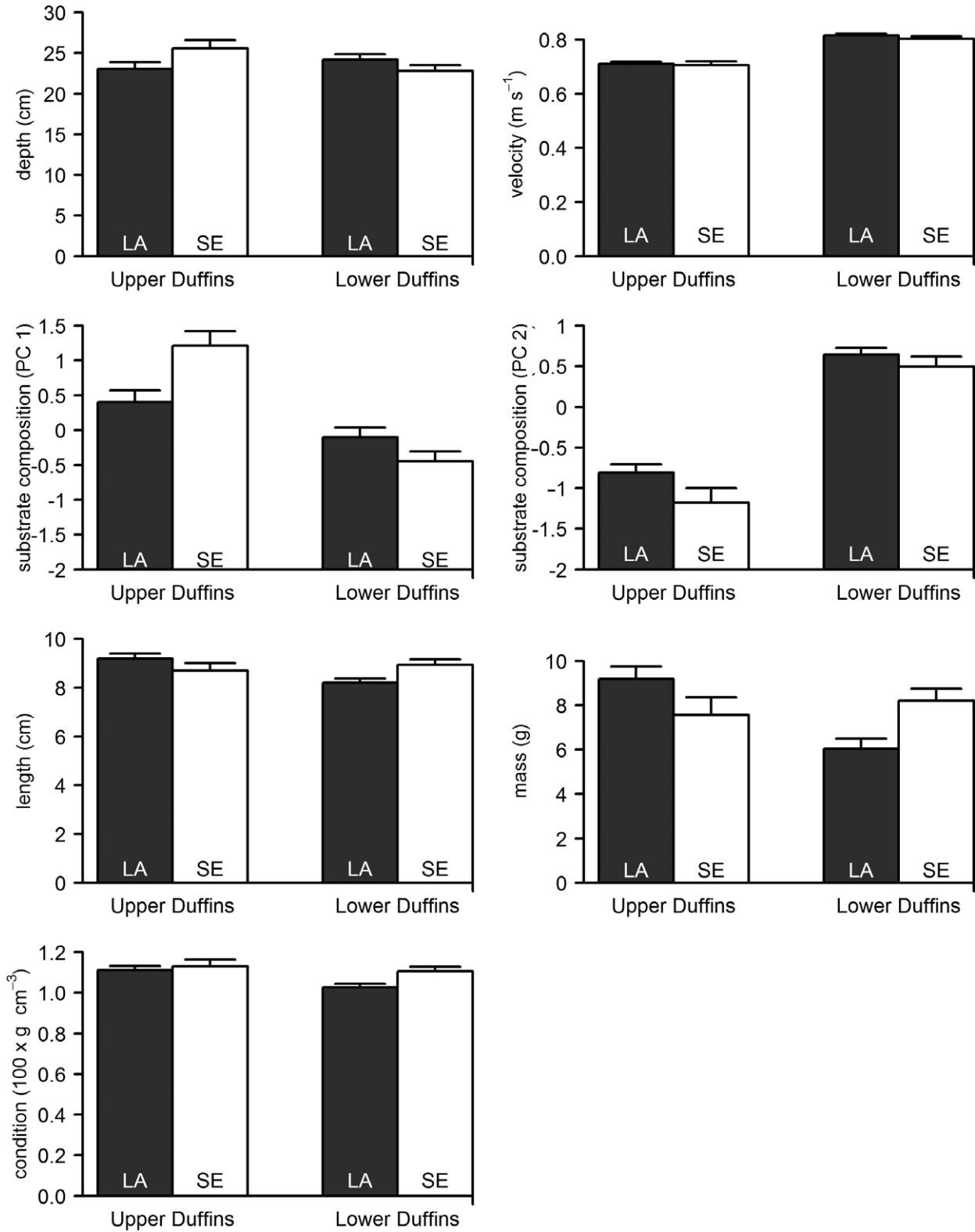
Fig. 2. Microhabitat associations, body length, mass, and condition for LaHave and Sebago Atlantic salmon (*Salmo salar*) in two natural stream sites. Displayed are means ± SE.

resources (Hutchinson 1957). We found that Atlantic salmon and rainbow trout had similar microhabitat associations in a stream during the juvenile stage. We also found that the presence of rainbow trout led to reductions in Atlantic salmon body length, mass, and condition, but not the relative recapture proportion at

Table 3. Two-way ANOVA results comparing habitat and body measurements of juvenile Atlantic salmon (*Salmo salar*) in natural and artificial streams.

Variable	d.f.	Sum sq.	Mean sq.	F	P
Water depth					
Treatment	1	2.83	2.83	86.95	<0.001
Source	1	196.56	196.56	6036.91	<0.001
Treatment × source	1	0.00	0.00	0.05	0.827
Residuals	203	6.61	0.03		
Body length					
Treatment	1	5.6	5.59	5.85	0.016
Source	1	35.2	35.19	36.85	<0.001
Treatment × source	1	0.0	0.02	0.02	0.899
Residuals	842	804.2	0.96		
Body mass					
Treatment	1	14.9	14.85	15.13	<0.001
Source	1	3.7	3.73	3.80	0.052
Treatment × source	1	0.1	0.11	0.11	0.743
Residuals	842	826.3	0.98		
Body condition					
Treatment	1	26.0	26.04	27.56	<0.001
Source	1	17.8	17.80	18.83	<0.001
Treatment × source	1	5.6	5.61	5.94	0.015
Residuals	842	795.6	0.95		

Variables tested were treatment (rainbow trout absent or present) and source (natural streams or artificial streams). Samples sizes for the natural stream experiment were $n = 51$ individuals for the rainbow trout absent and $n = 83$ individuals for the rainbow trout present treatments. Sample sizes for the artificial stream experiment were $n = 32$ average values of individuals within streams in both the rainbow trout absent and present treatments for water depth, and were $n = 486$ individuals for the rainbow trout absent and $n = 225$ individuals for the rainbow trout present treatments for the body size variables.

this juvenile stage. Our release sites were originally selected because they were similar in microhabitat composition, productivity, and temperature. Indeed, the sites were similar in water depth, and the percentages of gravel and rocks, but the sites differed in water velocity and the percentages of pebbles and sand. Nevertheless, the mean values for water velocity and the percentages of pebbles were within the optimal range for Atlantic salmon juveniles in both sites (Morantz et al. 1987; Guay et al. 2000; Beland et al. 2004; Hedger et al. 2005). Although, Atlantic salmon juveniles tend to avoid microhabitats with a high percentage of sand (e.g. Morantz et al. 1987), the difference in the percentage of sand between the two sites was small at 8%. Similarly, the sites both contained older Atlantic salmon, but the proportions were similar and the counts were not related to the changes in our focal Atlantic salmon numbers or sizes. Thus, the changes we observed in Atlantic salmon microhabitat association and size do not appear to be due to intraspecific competition with older Atlantic salmon. Instead, our results suggest that the changes in Atlantic salmon microhabitat association and size at this site are due to competition with rainbow trout, as has been documented in other studies (Jones & Stanfield 1993; Stanfield & Jones 2003; Coghlan et al. 2007; Thibault & Dodson 2013).

Competition among ecologically similar species may decrease by reducing the ecological niche overlap (Hutchinson 1957). We found that Atlantic salmon had optimal microhabitat associations in a natural stream site without rainbow trout but suboptimal microhabitat associations in a site where rainbow trout were present. Specifically, Atlantic salmon were found in habitats with a higher percentage of gravel and lower water velocity, their optimal physical microhabitats (Morantz et al. 1987), when rainbow trout were absent, but were found in habitats with a lower water depth, lower percentages of pebbles, rocks, sand and a higher water velocity in the presence of rainbow trout. Other studies have also found that Atlantic salmon shift to habitats with lower water depth and higher water velocity in the presence of rainbow trout, possibly because Atlantic salmon pectoral fins are better suited to holding position in faster water than rainbow trout (Gibson 1981; Hearn & Kynard 1986; Volpe et al. 2001). A shift in Atlantic salmon microhabitat associations may also be due to competitive displacement by the generally more aggressive rainbow trout (Gibson 1981; Hearn & Kynard 1986; but see Van Zwol et al. 2012a). The displacement could explain the reductions in Atlantic salmon body length, mass, and condition that we observed because of the increased energy expenditure or perhaps fewer available resources in the suboptimal microhabitat (Hearn 1987; Fausch 1988). Native species that are displaced by ecologically similar species may consequently have decreased fitness because of associations with suboptimal microhabitats.

Salmonid populations may differ in their ability to cope with the competition imposed by non-native species. Examining our experimental families, we found no difference in the relative recapture proportion of the populations, but this result may reflect the small sample size (driven partly by the high juvenile mortality in Lake Ontario tributaries; COSEWIC 2006, 2010). Indeed, we did detect differences between populations when examining all the Atlantic salmon caught. We found that Sebago salmon were longer, heavier, and had greater body condition than LaHave salmon in the natural stream site containing rainbow trout. Although Sebago salmon were initially larger at release, the difference was negligible and not likely to have driven the differences at recapture. For example, the body length difference was 3% (0.1 mm) whereas at recapture, the difference was 8% (7 mm). In addition, the LaHave and Sebago populations were similar in size in the natural stream site that did not contain rainbow trout. Similar results were reported for Atlantic salmon juveniles that were examined in artificial streams (Van Zwol et al. 2012b; Houde et al. 2014). Van Zwol et al. (2012b)
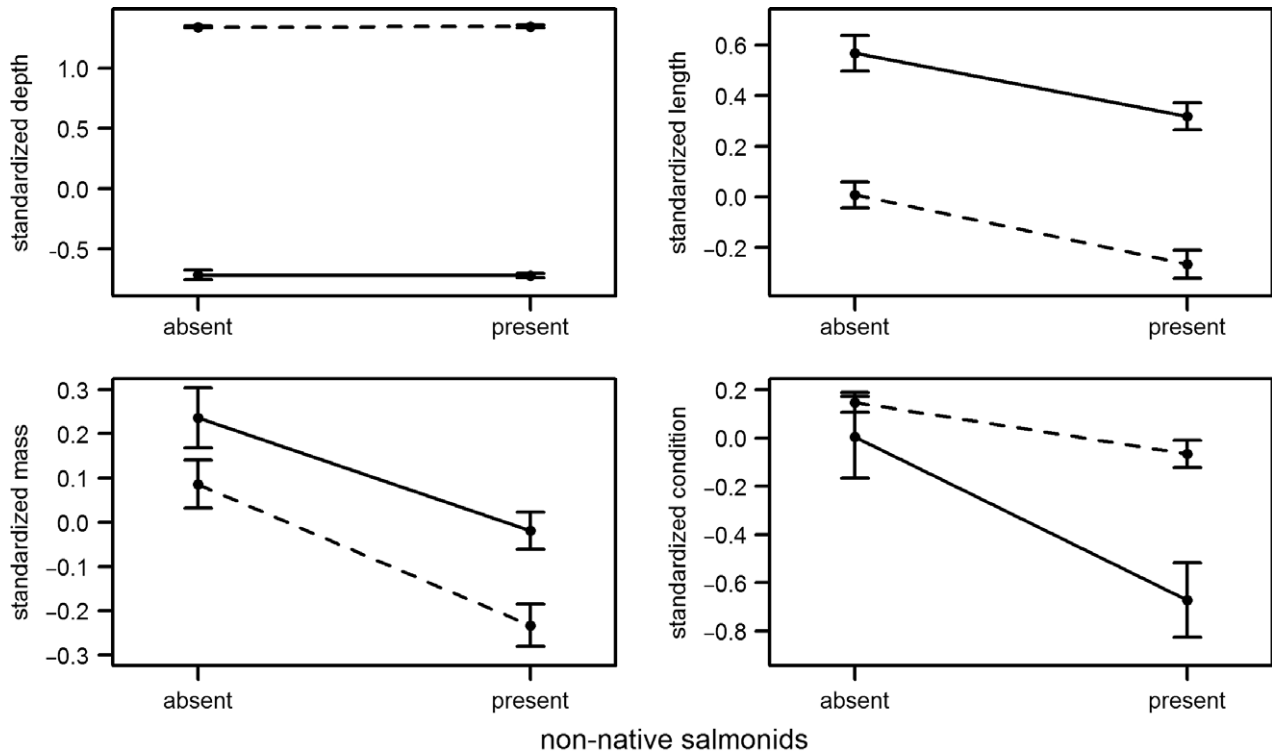
Fig. 3. Standardised water depth, body length, mass, and condition for of Atlantic salmon (*Salmo salar*) in natural and artificial streams. Displayed are means ± SE in the presence or absence of rainbow trout. Solid lines represent natural stream data; dashed lines represent the artificial stream data.

observed that Sebago salmon avoided agonistic interactions with rainbow trout relative to LaHave salmon. This difference in behavioural tactics may underlie the difference we detected in performance when in competition with a non-native species.

Effects of interspecific competition may be similar in natural and artificial environments. We examined the effects of competition with rainbow trout on the traits of Atlantic salmon in both natural and artificial streams (Houde et al. 2014). We found that Atlantic salmon responses to competition were similar in both environments. A meta-analysis by Korsu et al. (2010) found that effects of competition were similar in direction, but differed in magnitude between environments. The direction and magnitude may have been more similar in our study (for three of the four traits we examined) because we used a paired-family design, that is a subset of eight families per population in the artificial streams from those families that were released in the natural streams. Our data suggest that there is merit in performing controlled experiments first in artificial environments as a primary test for performance and fitness reductions due to interspecific competition (also see Fausch 1998). Artificial environments may also provide insight into target variables, such as the importance for controlling for physical habitat, before taking the research into the more complex natural environment.

Our results have implications for the restoration of native species populations. The presence of non-native salmonids has been identified as an important feature of the environment that may be an impediment to the restoration of Lake Ontario Atlantic salmon (Jones & Stanfield 1993; Crawford 2001 COSEWIC 2006, 2010). We found that the Sebago population had better performance (i.e. larger body size and better condition) with rainbow trout in a natural stream than the LaHave population. Stocked Sebago-origin salmon also appear to co-exist with naturalised and stocked rainbow trout and brown trout in Lake Champlain (Marsden et al. 2010), whereas the LaHave population has not previously been examined in wild sympatry with rainbow trout (Dimond & Smitka 2005). More broadly, our results suggest using candidate populations that are from environments that are similar to the reintroduction environment ('ecological analogues'). Ecologically suited candidate populations may possess genetic adaptations important to their establishment and fitness in the reintroduction environment (Meffe 1995; Moritz 1999; Jones 2003, 2013). More broadly, identifying ideal candidate populations may also require an examination of the performance of several populations in response to important features of the reintroduction environment (Meffe 1995). Finally, we found that the presence of ecologically similar non-native species reduced fit-

ness-related traits of a native species in both natural and artificial environments. We suggest that native species reintroductions that minimise ecological niche overlap with non-native species in an attempt to maximise the success of the reintroduction.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Two natural stream sites within Duffins Creek for examining the effects of interspecific competition with rainbow trout on Atlantic salmon (*Salmo salar*).

Appendix S2. Details of the fry size and handling for natural stream release of LaHave and Sebago Atlantic salmon (*Salmo salar*).

Appendix S3. Details of the genetic assignments for LaHave and Sebago of Atlantic salmon (*Salmo salar*).