

# The effect of competition among three salmonids on dominance and growth during the juvenile life stage

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**Abstract** – Although non-native species can sometimes threaten the value of ecosystem services, their presence can contribute to the benefits derived from the environment. In the Great Lakes, non-native brown trout (*Salmo trutta*) and rainbow trout (*Oncorhynchus mykiss*) support substantial recreational fisheries. With current efforts underway to restore once-native Atlantic salmon (*Salmo salar*) to Lake Ontario, there is some concern that Atlantic salmon will impede non-native contributions to the recreational fishery because Atlantic salmon exhibit niche overlap with brown trout and rainbow trout, particularly during the juvenile life stage. We therefore examined competition and growth of juvenile Atlantic salmon, brown trout and rainbow trout in semi-natural streams. We found that brown trout were the most dominant and had the greatest growth rate regardless of what other species were present. Rainbow trout were more dominant than Atlantic salmon and consumed the most food of the three species. However, in the presence of brown trout, rainbow trout fed less frequently and exhibited negative growth as compared to when the rainbow trout were present with only Atlantic salmon. These data suggest that, outside of density-dependent effects, Atlantic salmon will not impact stream production of brown trout and rainbow trout.

**Key words:** competition; behaviour; Atlantic salmon; non-native; trout

## Introduction

Invasive species, more generally the presence of non-native species, can threaten ecosystem processes and the associated services. For instance, the introduction of non-native species can adversely affect native species through competition, predation or displacement at the individual level (Race 1982; Hamilton et al. 1999; Morita et al. 2004; Blanchet et al. 2007). Non-native species that exhibit niche overlap with ecologically similar native species can drive competition for food and shelter (Hearn & Kynard 1986), and unless the species diverge in resource use, the native species may become extirpated (Morita et al. 2004). Indeed, controlling invasive species in the Great Lakes are estimated to cost Canada and the United States over \$1 billion a year (reviewed by Lovell et al. 2006). Sustainably managing natural resources and their ser-

vices thus often requires limiting competitive interactions of native and non-native species.

On the other hand, non-native species can contribute to ecosystem processes and services and can sometimes even facilitate the restoration of native species (Ewel & Putz 2004). For example, while the introduction of zebra mussels (*Dreissena polymorpha*) in inland waters of North America has typically been associated with a number of negative biotic and abiotic changes, the species enhances both water clarity and quality, increasing light transmittance and enabling greater growth of benthic plants and filtering of a wide range of particles from the water column (reviewed by MacIsaac 1996). The increased water clarity and quality has enhanced the growth of native wild celery (*Vallisneria americana*) and water star-grass (*Zosterella dubia*, Zhu et al. 2006) and has also enhanced services through water activities including

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recreational diving (Jones et al. 2006). Introduced non-native salmonids in the Great Lakes provide another example, as these species have strengthened local economies through the recreational fisheries (Toth & Brown 1997; Brown & Connelly 2009).

In Lake Ontario, non-native salmonid species routinely stocked include brown trout (*Salmo trutta*), rainbow trout (*Oncorhynchus mykiss*), chinook salmon (*O. tshawytscha*) and coho salmon (*O. kisutch*) (Crawford 2001; Mills et al. 2003). Current efforts are now underway to restore a once-native top predator of the lake, the Atlantic salmon (*Salmo salar*). Atlantic salmon were extirpated at the end of the 20th century (MacCrimmon 1977). Atlantic salmon and naturalised brown trout and rainbow trout, however, share similar habitat (Hearn & Kynard 1986; Harwood et al. 2002; Heggenes et al. 2002), and evidence suggests that intense competition for resources could occur among these species (Volpe et al. 2001; Scott et al. 2005; Stradmeyer et al. 2008). For example, brown trout may restrict habitat use of the lesser-aggressive Atlantic salmon (Heggenes et al. 1999). Indeed, there is concern that competition between Atlantic salmon, brown trout and rainbow trout will hinder both the restoration effort and the current ecological services provided by the non-native species (e.g., Dietrich et al. 2008). Thus, it is essential to examine the potential impact of stocking Atlantic salmon in streams with juvenile brown trout and rainbow trout.

Using semi-natural stream environments, we examined dominance, feeding behaviours and growth rates of juvenile Atlantic salmon, brown trout and rainbow trout. Behavioural interactions of these three salmonid species largely occur in streams during the juvenile life stage, and this life stage is critical for recruitment and population viability (see Elliott 1990; Good et al. 2001). We predicted that, if brown trout and rainbow trout were more dominant competitors than Atlantic salmon, as past research suggests (Harwood et al. 2001; Volpe et al. 2001; Armstrong et al. 2003), performance of the trout species would not be affected by the presence of Atlantic salmon.

## Methods

### Study species

The experiment evaluated 1.5-year-old Atlantic salmon (*S. salar*), brown trout (*S. trutta*) and rainbow trout (*O. mykiss*) reared from brood stocks created by Ontario Ministry of Natural Resources (OMNR) in support of the effort to restore Atlantic salmon in Lake Ontario (L. Grieg, B. Ritchie, L. Carl & C. A. Lewis, unpublished data). Juvenile mortality among salmonids is high (Elliott 1990; Good et al. 2001), so

restoration efforts in Lake Ontario stock various age groups of Atlantic salmon including 1.5-year-old individuals. Fish were obtained from OMNR Harwood Fish Culture Station (Harwood, Ontario, Canada) and OMNR Normandale Fish Culture Station (Normandale, Ontario, Canada) and were of the same age and culture history as those stocked in Lake Ontario streams. Similar to local stocking conditions, the yearlings of these species differed in size. Prior to the start of the experiment, fish were held for 1 month at the OMNR Codrington Fisheries Research Facility (Codrington, Ontario, Canada) in flow-through tanks with an average density of 0.6 fish·l<sup>-1</sup> (in large groups, >250 fish per tank) and were exposed to a natural light cycle and fed trout chow (Corey Aquafeeds, New Brunswick, Canada).

### Experimental set-up

Semi-natural stream channels were constructed to perform six trial blocks examining behaviour and growth between May and July 2009 at the Codrington hatchery. The channels were designed to provide substrate and flow conditions similar to those used by trout and Atlantic salmon found in southern Ontario streams (Gibson 1973; Hearn & Kynard 1986). The stream channels were 2.4 m in length and 0.5 m in width and divided into a riffle (0.2 m deep by 1.6 m long) and pool (0.6 m deep by 0.8 m long). Ambient flow in the riffle was 0.18 ± 0.05 m·s<sup>-1</sup> (±SD) and 0.027 ± 0.025 m·s<sup>-1</sup> in the pool. Water from the hatchery's surface-water head pond (gravity-fed system) was piped to each of the stream channels through a headbox inside the hatchery, ensuring equal flow to all stream channels. Water temperature in the stream channels over the trials was 9.8 ± 1.4 °C (±SD). For greater detail of the design of the stream channels, the reader is referred to the study of Van Zwol et al. (2012a).

A trial block used nine stream channels and consisted of three replicates of three treatments with 12 individuals in each replicate: Atlantic salmon with brown trout (six salmon, six trout), Atlantic salmon with rainbow trout (six salmon, six trout) and Atlantic salmon with both trout species (four salmon, four of each trout species). Six trial blocks were performed using a total of 288 Atlantic salmon (=6 blocks × 3 replicates × [6 + 6 + 4 fish across the three treatments containing Atlantic salmon]), 180 brown trout and 180 rainbow trout (=6 blocks × 3 replicates × [6 + 4 fish across the two treatments containing a given trout species]). Fish density in the stream channels was held constant at 10 fish·m<sup>-2</sup>, which is at the high end of those found in streams in Ontario, yet this set-up allowed us to effectively determine the relative strengths of intraspecific and

interspecific competition between the species (see Fausch 1998). There were seven trial start dates as logistical constraints at the onset of the experiment resulted in one trial block having a pair of dates, with the commencement of three treatments followed by six treatments.

At the beginning of each trial block, fish were haphazardly selected using similar catch effort and sedated with MS-222. Initial mass and total length were measured, and fish were individually tagged below the dorsal fin with a coloured 2-cm vinyl anchor tag (Floy Tag & Mfg. Inc., Seattle, Washington, DC, USA) for later recognition in video analysis. Tags were applied to either the left or right of the dorsal fin to ensure all fish within each tank could be uniquely identified. Fish recuperated in a flow-through holding tank prior to being placed in the appropriate stream channel. The placement of each treatment in the nine stream channels was determined by a random number generator.

### Behavioural analysis

Behavioural observations of the fish began the day after tagging (day 1) and continued for 7 days, in the morning (0800–1230 h) and afternoon (1400–1830 h). Three high-definition camcorders (Sony HDR-XR200V, Toronto, ON, Canada) were used to record a stream channel with one camera above the pool and two equally spaced above the riffle. The fields of view from the three cameras covered the entire stream channel to ensure that all behaviours could be observed. Camcorders were attached to a portable rig situated approximately 1 m above the water; the rig allowed the cameras to be easily moved among the nine channels. Two rigs were constructed (six cameras in total), enabling two stream channels to be recorded simultaneously before moving the rigs to the next pair of stream channels. The rigs were left in place for 15 min prior to recording to allow the fish time to acclimate to the presence of the camcorders. The fish were then recorded for 30 min.

Trout chow (Corey Aquafeeds; Fredericton, New Brunswick, Canada) and frozen bloodworms (Chironomidae; Hikari<sup>®</sup>, Kyorin Co., Ltd, Himeji, Hyogo, Japan) were alternately provided each minute (~1 g trout chow or 50–100 bloodworms each minute) for the first 10 min of the morning recording session (~2% of biomass in each stream channel). Food items were released at the top and middle of a stream channel, with the current carrying food items through the stream channel to simulate natural invertebrate drift. The order in which stream channels were recorded was determined each day using a random number generator.

Behavioural data from 4 days of each trial were analysed, comprising days 1, 3, 5 and 7. Each time

an action occurred, the recording was paused with actor, act and recipient recorded. Aggressive behaviours comprised chasing, charging and nipping, which were summed for each individual and divided by the number of hours of video observed for the tank (see Keenleyside & Yamamoto (1962) for definitions of behaviours). These data were used to calculate a dominance score for each fish using David's score, which uses both an individual's initiated and received aggression while accounting for repeated interactions between group members (see David 1988; Gammell et al. 2003 for details of the calculation). The higher the David's score achieved, the higher the dominance status of the fish.

Feeding acts were recorded for each fish and defined as snapping or biting movements that were not directed towards other fish in the stream channel, in addition to bites directed at the substrate of the channel for food items that had settled out of the water column (see Brown & Brown 1996). The number of feeding acts was used to calculate food consumption rate by dividing the number of distinct acts by the number of hours of video observed for the tank. No differentiation was made between consumption of blood worms versus trout chow in the calculation.

On the final day of each trial block (day 8), fish were collected from the stream channels for final mass and length measurements. Netting of fish started at the channels farthest from the headbox. Using initial and final mass measurements, standard growth rate (SGR) was calculated as follows:  $SGR = 100 \times [\ln(\text{final mass}) - \ln(\text{initial mass})] / \text{days fed}$  (e.g., Bernier et al. 2004).

### Statistical analysis

Behavioural data for Atlantic salmon have been discussed in detail elsewhere (Van Zwol et al. 2012a,b); thus, analyses in the current manuscript focus on brown trout and rainbow trout. The Atlantic salmon data presented here represent a subset of those presented in the study of Van Zwol et al. 2012a,b and are used as a comparison to values from the two trout species.

Differences in initial mass and total length of the species were analysed using one-way analysis of variance (ANOVA). We then used linear mixed models to examine the effects of species and treatment on food consumption rate, standard growth rate and David's score. Treatment was nested within species, initial mass was treated as a covariate, and channel number and trial block were entered as nominal, random factors. If a random factor was nonsignificant ( $P > 0.05$ ), the factor was removed from the final model using a backwards stepwise analysis. When

the treatment effect was statistically significant, individual ANOVAS were run for each species with treatment as the main effect. Initial mass was also included in these ANOVAS as were any significant random factors identified in the original analysis.

Linear mixed models were also used to examine the relationship between David's score and food consumption rate or standard growth rate. Treatment was included as a main effect, David's score was entered as a covariate, and the interaction between treatment and David's score was also included. Channel number and trial block were again included in the initial models as nominal, random factors. These latter mixed models were run separately for data from brown trout and rainbow trout.

Food consumption rate data were normalised using a logarithmic ( $x + 1$ ) transformation prior to statistical analyses. *Post hoc* tests of pairwise comparisons used Tukey's HSD. All statistics were performed using JMP 4 (version 4.0.2; SAS Institute Inc., 2000, Cary, NC, USA), and *P*-values presented are two-tailed probabilities ( $\alpha \leq 0.05$ ).

### Results

Mass varied among species ( $F_{2,645} = 137.1$ ,  $P < 0.001$ ) as both Atlantic salmon ( $40.3 \pm 15.0$  g, mean  $\pm$  SD) and brown trout ( $39.4 \pm 13.6$  g) were significantly heavier than rainbow trout ( $20.6 \pm 9.6$  g) (Tukey's HSD,  $P < 0.05$ ); there was no difference in mass between Atlantic salmon and brown trout (Tukey's HSD,  $P > 0.05$ ). Total length varied among all three species ( $F_{2,645} = 198.0$ ,  $P < 0.001$ ); Atlantic salmon ( $165 \pm 22$  mm) were the longest, followed by brown trout ( $151 \pm 18$  mm) and finally rainbow trout ( $125 \pm 18$  mm; Tukey's HSD,  $P < 0.05$ ). Treatment means of each variable for each species are presented in the Appendix S1.

We recorded 19,985 feeding behaviours and 15,881 aggressive behaviours from 648 h of video recording. The linear mixed models revealed that the species significantly varied in food consumption rate, standard growth rate and David's score (Table 1, Appendix S1). Brown trout had the highest overall David's score and standard growth rate, but lowest food consumption rate; rainbow trout consumed more food and achieved higher David's scores than Atlantic salmon, but the two species had similar growth rates (Fig. 1).

Within rainbow trout, food consumption rate, standard growth rate and David's score were significantly higher in the treatment with just Atlantic salmon than when both brown trout and Atlantic salmon were present (Table 1, Fig. 1). For brown trout, there was no difference in these three variables across the two treatments (Fig. 1). In contrast, for Atlantic salmon,

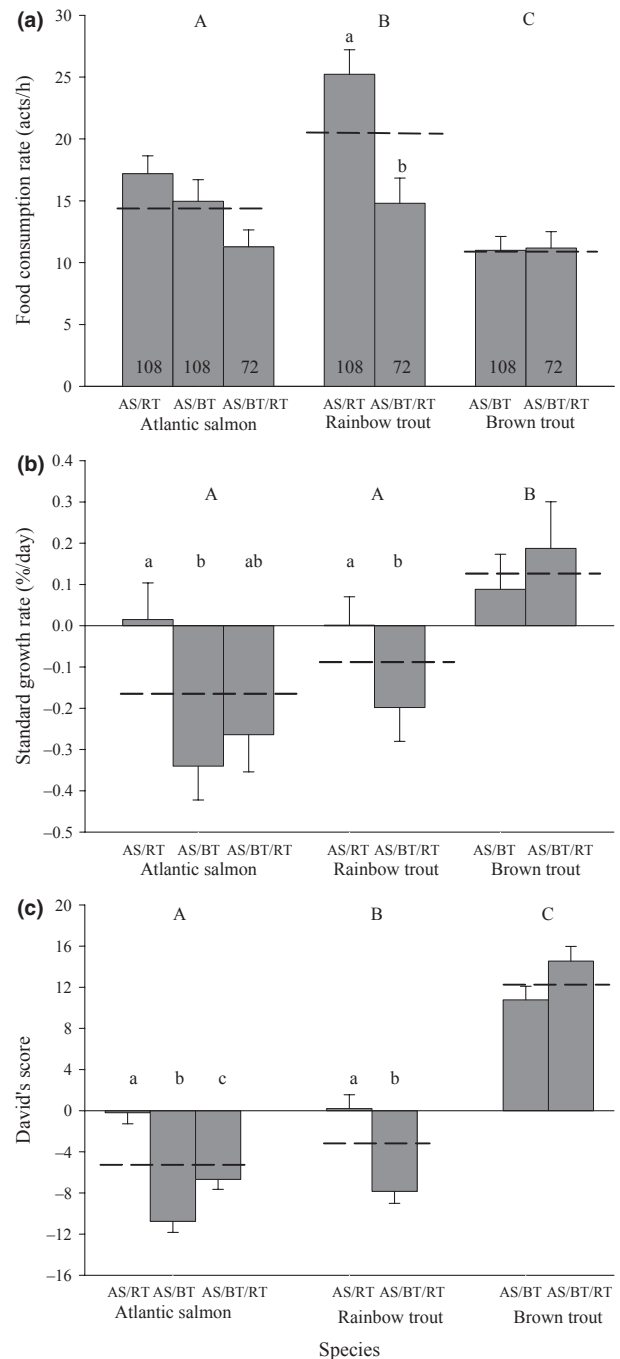


Fig. 1. The influence of mixed-species competition on behaviour and growth in juveniles of three salmonids. Data presented are means and standard errors for (a) food consumption rate, (b) standard growth rate, and (c) David's score, an index of dominance. Mixed-species treatments were conducted in semi-natural stream channels and comprised Atlantic salmon (*Salmo salar*) with rainbow trout (*Oncorhynchus mykiss*) (AS/RT), Atlantic salmon with brown trout (*Salmo trutta*) (AS/BT), and Atlantic salmon with both brown trout and rainbow trout (AS/BT/RT). Dashed lines denote means of each species across treatments, with uppercase letters corresponding to homogeneous subsets ( $P < 0.05$ ). Lowercase letters denote homogeneous subsets across treatments within species. Food consumption rate data were  $\log_{10}(x+1)$  transformed prior to statistical analyses but are displayed untransformed. Numbers of fish in each treatment for each species are indicated at the base of the bar plots in panel (a).

Table 1. Summary of linear mixed model results of behaviour and growth in three juvenile salmonids. Analyses examined food consumption rate (acts per h), standard growth rate (%/day) and David's score (an index of dominance) across three treatments that involved competition between Atlantic salmon (*Salmo salar*), brown trout (*Salmo trutta*) and rainbow trout (*Oncorhynchus mykiss*).

Variable	Effect	F	d.f.	P
Food consumption rate	Model ( $R^2 = 0.15$ )	8.41	13, 634	<0.001
	Species	12.5	2, 634	<0.001
	Treatment [species]	6.70	4, 634	<0.001
	Initial mass	7.05	1, 634	0.010
	Trial (random)	8.31	6, 634	<0.001
Standard growth rate	Model ( $R^2 = 0.14$ )	8.00	13, 634	<0.001
	Species	10.3	2, 634	0.006
	Treatment [species]	3.66	4, 634	<0.001
	Initial mass	4.23	1, 634	0.040
	Trial (random)	11.7	6, 634	<0.001
David's score	Model ( $R^2 = 0.42$ )	67.0	7, 640	<0.001
	Species	153	2, 640	<0.001
	Treatment [species]	19.8	4, 640	<0.001
	Initial mass	82.7	1, 640	<0.001

Species and treatment nested within species were coded as main effects, initial mass was entered as a covariate, and trial start date and tank number were entered as random factors. Nonsignificant random factors were removed from the final model.

all three variables were highest when Atlantic salmon were alone with rainbow trout. David's score and standard growth rate were both lowest when Atlantic salmon were with only brown trout, while food consumption rate was lowest when Atlantic salmon were in the treatment with both brown trout and rainbow trout, albeit this last effect was marginally nonsignificant ( $P = 0.075$ ; Fig. 1). Across all species, initial mass was positively related to David's score and food consumption rate, but negatively related to standard growth rate (data not shown, but see Table 1 for significance values).

In rainbow trout, David's score was not correlated with either food consumption rate ( $F_{1,170} = 2.85$ ,  $P = 0.093$ ) or standard growth rate ( $F_{1,170} = 0.933$ ,  $P = 0.34$ ; Fig. 2). For brown trout, there was a positive relationship between David's score and food consumption rate ( $F_{1,170} = 25.2$ ,  $P < 0.001$ ; Fig. 2). This relationship did not differ significantly between the two treatments (interaction between David's score and treatment:  $F_{1,170} = 3.43$ ,  $P = 0.066$ ). There was no relationship, on the other hand, between David's score and standard growth rate in brown trout ( $F_{1,170} = 4.67$ ,  $P = 0.32$ ; Fig. 2).

### Discussion

With programmes in place to restore once-native Atlantic salmon to Lake Ontario, there is concern that these fish will negatively affect naturalised non-native salmonids that contribute to local recreational fisheries. Here, we studied agonistic interactions and

growth of juvenile Atlantic salmon, brown trout and rainbow trout in semi-natural stream channels. We found that brown trout were the most dominant and had the highest growth rate, that rainbow trout were intermediate and that Atlantic salmon were least dominant and had the lowest growth rate. Given that dominant fish typically are able to monopolise higher-quality feeding areas (e.g., Gibson 1973; Höjesjö et al. 2005), our data suggest that brown trout and rainbow trout will not be negatively affected by the presence of Atlantic salmon. Indeed, we found that rainbow trout and Atlantic salmon were most impacted by the presence of brown trout.

Dominant individuals typically have preferential access to food and resources and consequently have better growth (Nakano 1995; Ryer & Olla 1996; Martin & Moore 2008). Höjesjö et al. (2005) found that less-competitive Atlantic salmon consumed fewer food items as they were excluded from foraging areas by more-aggressive brown trout, a pattern that has been similarly observed in other taxa (Yamagishi et al. 1974; Monaghan & Metcalfe 1985; Gatz et al. 1987). Our results further these findings as we found a significant, positive relationship between dominance and food consumption for brown trout and a marginally nonsignificant relationship for rainbow trout. While the dominant individuals likely did not consume every food item, anecdotally we noted that those individuals were efficient in preventing subordinates from eating by chasing or biting them during feeding. Interestingly, when all three species were present, brown trout, which were typically more dominant than either Atlantic salmon or rainbow trout, consumed about the same amount of food as Atlantic salmon, but less than rainbow trout. It may be that brown trout spent more time in agonistic interactions and less time capturing food (see Cutts et al. 2002). Regardless, brown trout still had the highest growth rates of the three species, implicating better food conversion efficiency for the brown trout (e.g., Abbott & Dill 1989). Nevertheless, increased food consumption and growth rate appear to be advantages associated with high social status in salmonids.

Many studies have examined pairwise competition between species, yet in the wild organisms rarely encounter only single-competitor environments. Furthermore, it has been shown that competition for food and shelter is most intense in environments with three or more ecologically similar species (Inouye et al. 1980; Mittelbach 1988; Bengtsson 1993). Here, we examined the heterospecific interactions of three ecologically similar salmonids and found that the trispecies treatment influenced each species differently. The presence of all three species sharply lowered food consumption, growth and dominance of rainbow

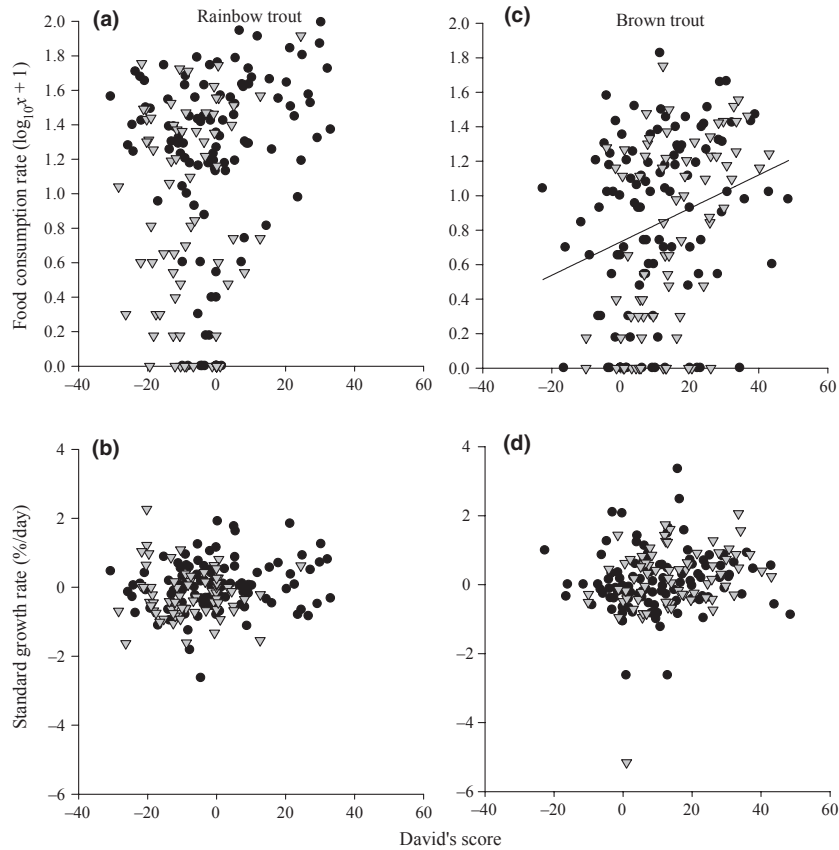


Fig. 2. The relationship between dominance and growth during mixed-species competition in juveniles of three salmonids. Scatterplots denote the relationship between David's score (an index of dominance) and either food consumption rate or standard growth rate for rainbow trout (*Oncorhynchus mykiss*) (a and b) or brown trout (*Salmo trutta*) (c and d). Mixed-species treatments were conducted in semi-natural stream channels and comprised Atlantic salmon (*Salmo salar*) with either rainbow trout or brown trout (circles), or Atlantic salmon with both brown trout and rainbow trout (triangles). Food consumption rate data were  $\log_{10}(x + 1)$  transformed. The solid line denotes the only significant linear relationship based on a linear mixed model (see text for details).

trout compared to conspecifics that were just with Atlantic salmon. Atlantic salmon performed poorly in both the pairwise competition treatment with brown trout and the trispecies treatment but had higher growth when only with rainbow trout. For brown trout, the trispecies treatment did not influence the species' food consumption, growth or dominance compared with the pairwise treatment. These patterns suggest that brown trout are a better competitor than the other two species and are affected mostly by competition with conspecifics, whereas Atlantic salmon and rainbow trout are negatively affected by the presence of brown trout.

Community ecologists have long understood that competition between ecologically similar species can result in spatial separation or shifts in resource use if the species continue to live in sympatry (e.g., Werner & Hall 1977; Langeland et al. 1991). Although brown trout and Atlantic salmon have historically coexisted in rivers in Europe (Höjesjö et al. 2005), they tend to occupy different reaches of the stream, largely driven by the aggressive behaviour of brown trout (Arm-

strong et al. 2003; also see Stradmeyer et al. 2008). Our study confirmed the dominance of brown trout over Atlantic salmon and clearly showed that brown trout are also dominant over rainbow trout. Historically, rainbow trout and Atlantic salmon have not coexisted, yet studies indicate considerable niche overlap (e.g., Hearn & Kynard 1986). In our study, rainbow trout performed better when alone with Atlantic salmon, obtaining similar dominance scores to the salmon and displaying the highest level of growth, than when with Atlantic salmon and brown trout. Similar results were reported by Blanchet et al. (2008), suggesting that, despite apparent niche overlap, Atlantic salmon are not a major impediment to rainbow trout. We predict, however, that these two species will show spatial segregation from the considerably more dominant brown trout in stream tributaries of Lake Ontario.

In conclusion, although more studies are needed, particularly over the entire stream residency period and during other life stages, our data suggest that the addition of Atlantic salmon to Lake Ontario will not

negatively impact brown trout or rainbow trout and the ecological services these fishes provide. Rather, our data suggest that, if spatial segregation in streams is not possible, brown trout may need to be managed to increase the performance and production of rainbow trout and Atlantic salmon.

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### Supporting Information

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

**Appendix S1.** Summary of body size, behaviour, and growth of three juvenile salmonids.

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