Performance of four salmonids species in competition with Atlantic salmon

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ABSTRACT

Economically and culturally important salmonid species often compete with Atlantic salmon (*Salmo salar*) released from stocking programs or that escaped during aquaculture production. Such competitive interactions may lower the individual fitness of these species by reducing survival and body growth. Here, we exposed juvenile brown trout (*S. trutta*), rainbow trout (*Oncorhynchus mykiss*), Chinook salmon (*O. tshawytscha*), and coho salmon (*O. kisutch*) to juvenile Atlantic salmon in artificial streams for 10 months. Survival and fitness-related traits of the four species were not negatively impacted by the presence of Atlantic salmon. The results suggest that brown trout and rainbow trout have better competitive abilities than Atlantic salmon, and that Chinook salmon and coho salmon have limited competitive interactions with Atlantic salmon. Although we discuss certain environmental conditions that can favor Atlantic salmon as a competitor at the juvenile life stage, Atlantic salmon may have little impact on the productivity of these four species.

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Introduction

Salmonids, such as Pacific salmon (*Oncorhynchus* sp.), Atlantic salmon (*Salmo salar*), rainbow trout (*O. mykiss*), and brown trout (*S. trutta*), have been intentionally introduced globally to provide fisheries, contributing millions of dollars to local economies (Crawford and Muir, 2008; Gozlan et al., 2010). Salmonid aquaculture has also been expanding globally and may be a source of unintentional introductions of salmonids into foreign locations (Naylor et al., 2000; Bostock et al., 2010). The intentional and unintentional introductions of salmonids have inadvertently created the potential for interspecific competition with native salmonids (Crawford, 2001). On one hand, this interspecific competition may limit the production of these intentionally introduced salmonids (Gozlan et al., 2010). On the other hand, interspecific competition may negatively impact the production of culturally or economically important native salmonid populations (Hearn, 1987; Fausch, 1988). A better understanding of interspecific competition among salmonids is therefore relevant for both supporting local economies and conserving native biodiversity (Simberloff and Stiling, 1996; Gozlan et al., 2010).

Interspecific competition is typically greater between species with higher ecological niche overlap than those with lower overlap (Hutchinson, 1957; Maskell et al., 2006). Salmonids are territorial at juvenile life stages and tend to compete for similar resources in nursery streams (Kalleberg, 1958; Gibson, 1981; Scott et al., 2005b), but there are differences in the degree of niche overlap between species (e.g.

Gibson, 1981; Heland and Beall, 1997). Competing individuals may reduce niche overlap by utilizing sub-optimal habitats (MacArthur and Levins, 1967; Berg et al., 2014; Houde et al., 2016), which may reduce survival and growth (Hearn and Kynard, 1986). Species that are more aggressive may be more likely to secure optimal resources than those that are less aggressive (Holway and Suarez, 1999). Overall, the extent of interspecific competition between salmonid species pairs should covary with both the degree of niche overlap and interspecific differences in aggressive behaviour.

Concerns have been expressed that Atlantic salmon may negatively impact the production of culturally important native salmonids on the West Coast of North American where escapes from aquaculture net pens sometimes occur (Naylor et al., 2000; Bostock et al., 2010). Wild reproduction and population establishment from aquaculture escapes have been identified as a potential threat to native populations of Pacific salmon such as Chinook salmon (*O. tshawytscha*), coho salmon (*O. kisutch*), and rainbow trout, among others (Volpe et al., 2001; Piccolo and Orlikowska, 2012; Fisher et al., 2014). As these species support significant fisheries and are the focus of conservation efforts on the West Coast (Willson and Halpuka, 1995), potential ecological effects from aquaculture escapes and establishment of Atlantic salmon are a significant concern (Piccolo and Orlikowska, 2012; Fisher et al., 2014). Each of these species as well as brown trout were historically introduced into the Laurentian Great Lakes and became naturalized (Crawford, 2001; Stanfield et al., 2006). Ironically, rehabilitative stocking of Atlantic salmon in Lake Ontario, where it was historically native (Crawford, 2001), has been identified as a potential concern for affecting the production of these naturalized introduced salmonids that support economically important fisheries (Dietrich et al., 2008), which has been

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an issue for resistance to the restoration of Atlantic salmon (e.g. Johnson and Chalupnicki, 2014). Although native species are highly valued from a management context, naturalized populations of introduced salmonids are also valued components of fisheries management objectives (OMNRF, 2015). With management agencies employing risk-based frameworks for fisheries management, identifying potential challenges for sustainability is essential for proactive policy decisions (OMNRF, 2015).

Atlantic salmon has been shown to have high niche overlap with brown trout and rainbow trout in nursery streams, where each species tend to utilize riffle microhabitats (e.g. Hearn and Kynard, 1986; Armstrong et al., 2003, but see Johnson and McKenna, 2015). However, brown trout and rainbow trout tend to be more aggressive than Atlantic salmon (e.g. Gibson, 1981; Vehanen, 2006; Van Zwol et al., 2012a), suggesting that both species may be better competitors than Atlantic salmon under equal habitat conditions. In contrast, Atlantic salmon tend to have low niche overlap with Chinook salmon and coho salmon in nursery streams, as these latter species generally prefer pool microhabitats (e.g. Heland and Beall, 1997; Holecek et al., 2009), although Johnson and Chalupnicki (2014) showed that juvenile Atlantic salmon and Chinook salmon used similar habitat in two Lake Ontario tributaries. All three species also tend to be equally aggressive (e.g. Gibson, 1981; Scott et al., 2005b). Further studies are warranted to test these expectations of the outcome of interspecific competition between Atlantic salmon and these four other species.

Here, we focus on the performance of four salmonid species, brown trout, rainbow trout, Chinook salmon, and coho salmon, exposed to interspecific competition with Atlantic salmon. The present study is different from our previous studies using the same artificial streams, which instead focused on the performance of Atlantic salmon in the context of restoration (Van Zwol et al., 2012b,c; Houde et al., 2015a,b,c). Additionally, whereas another study by Van Zwol et al. (2012a) focused on interspecific competitive effects of Atlantic salmon on brown trout and rainbow trout during 7 day trials, the present study examines for the first time the performance of all four naturalized salmonid species in the Great Lakes, and over a considerably longer time frame of 10 months.

Methods

Study species and populations

Fry (age 0 + parr) of the four species were provided by Ontario Ministry of Natural Resources and Forestry (OMNRF) fish culture stations and were transported to the OMNRF Codrington Research Facility, Codrington, Ontario in spring 2011. Brown trout and rainbow trout were produced using hatchery parents with ancestry to the Ganaraska River, ON. Coho salmon and Chinook salmon were produced using naturalized parents from the Credit River, ON. Fry from the LaHave and Sebago Atlantic salmon populations were derived from offspring produced in fall 2010 that were reared at Codrington. The LaHave population has been bred in captivity in Ontario since wild egg collections from the LaHave River, Nova Scotia, Canada ended in 1995. The Sebago population was imported into Ontario as wild egg collections from Panther River, Maine (a supplemented tributary of Sebago Lake) in 2006. Fry ($n = 125$) were held in species-specific tanks (18 L) and fed to satiation daily until transferred to the artificial streams.

Experimental set-up

Artificial stream tanks (width = 25 cm, length = 240 cm) were arranged in six rows each containing six tanks at Codrington. The substrate was composed of two parts gravel (2–64 mm) and one part cobble (65–256 mm) and the tanks contained two types of microhabitat: a 160 cm riffle section (mean ± 1SD and range, velocity = 20 ± 6 and 3–59 cm/s, depth = 28 ± 3 and 23–33 cm) followed by an 80 cm

pool section (velocity = 7 ± 3 and 3–15 cm/s, depth = 68 ± 3 and 63–73 cm). There was no additional structure within the tanks. The substrate composition, water depth, and water velocity parameters are within the natural ranges preferred by all five salmonid species (Johnson and Kucera, 1985; Morantz et al., 1987; Bisson et al., 1988; Armstrong et al., 2003; Holecek et al., 2009). Fish were exposed to ambient water from Marsh Creek (temperature = 8.5 ± 2.5 and 1.9–15.4 °C) that was partially recirculated throughout the tanks rows with refreshing rate of 0.7 L/s.

Totals of 32 fish were placed into each artificial stream tank using a substitutive design (Fausch, 1998). The three treatments were each species alone (e.g. 32 brown trout), species with LaHave Atlantic salmon in equal numbers (e.g. 16 brown trout and 16 LaHave Atlantic salmon), and species with Sebago Atlantic salmon (Electronnic Supplementay Material (ESM) Table S1). Tanks were randomly assigned a treatment and there were two replicates per treatment. The species differed in body size (see Table 1), but these differences are similar to those encountered in the nursery streams where the stocked fish experience interspecific competition.

Fish remained in the tanks for 10 months (September to July). During this period, the fish were given a competition-inducing 3% body mass ration per day (e.g. Garner et al., 2008) September to December and May to July, and a 1% body mass ration per day January to April, coinciding with colder water temperatures. Rations were delivered at the upstream end of the streams once a day or twice a day with the ration divided in half. Greater details on the study species and experimental set-up are described in Houde et al. (2015a).

Survival, body size, and riffle use

The four species were measured for survival and three fitness-related traits (body length, mass, and condition; Fausch, 1984, 1998). Riffle use was also examined, as it is a utilized microhabitat of juvenile brown trout and rainbow trout, as well as Atlantic salmon (Hearn and Kynard, 1986; Armstrong et al., 2003). Measurements were collected on October 28, November 29, and July 24. On these dates, all juveniles were removed from the artificial stream tanks, lightly anaesthetized with MS-222, measured for length (nearest 0.1 cm) and mass (nearest 0.01 g), and then allowed to recover before being returned to their tank. Condition was calculated as $100 \times mass / length^3$ (Fulton, 1904). To quantify riffle use, a trained observer took counts of the individuals of each salmonid species within the riffle section at mid-day the day after body size measurements. Riffle use was also examined by taking photographs the day before collecting body size measurements, but the data were not collected for all measurement dates. The analysis was therefore limited to the observer data, although the photographic data showed similar riffle use results patterns (data not shown).

Statistical analysis of traits

Survival, body length, mass, condition, and riffle use of the four salmonids were analyzed using R 3.2.1 (available at http://www.r-project.org/). Statistical significance was set at $\alpha = 0.05$. Individual values were used for body size measurements and tank values were used for survival (proportion relative to initial count) and riffle use (proportion in the riffle section). Binomial models (or quasi-binomial models if there is dispersion) were used for survival and riffle use. Linear mixed-effects models using the R *lmerTest* package were used to examine effects for body length, mass, and condition. All models contained fixed effects for *species*, *treatment*, and *species × treatment* and the mixed-effects models contained a random effect for *artificial stream tank* identity. The traits were examined at the 3 month mark (November 29) and at the 10 month mark (July 24) because over winter mortality caused differences in juvenile densities that may influence these traits (ESM Tables S1 and S2). Data from the remaining sample times are available from the authors.

Table 1

Summary of the initial body sizes of fry (age 0 + parr) for the four focal species (brown trout *Salmo trutta*, rainbow trout *Oncorhynchus mykiss*, Chinook salmon *O. tshawytscha*, and coho salmon *O. kisutch*) and two populations of Atlantic salmon *S. salar*.

Presented are means ± 1SD. Different uppercase letters indicate significant differences assessed using Tukey's post-hoc multiple comparisons within species and populations for each row ($p < 0.05$). Sample sizes were: $n = 128$ for each of the four focal species; and $n = 224$ for each Atlantic salmon population.

Traits	Salmonid species				Atlantic salmon populations	
	Brown trout	Rainbow trout	Chinook salmon	Coho salmon	LaHave	Sebago
Length (cm)	6.0 ± 0.7[A]	6.0 ± 0.6[A]	8.2 ± 0.6[B]	8.5 ± 1.0[C]	5.8 ± 0.4[D]	5.6 ± 0.5[E]
Mass (g)	2.44 ± 0.92[A]	2.20 ± 0.70[AD]	5.92 ± 1.68[B]	6.67 ± 2.29[C]	2.17 ± 0.49[D]	2.01 ± 0.52[D]
Condition ($100 \times$ g/cm³)	1.05 ± 0.06[A]	0.99 ± 0.06[B]	1.05 ± 0.10[A]	1.05 ± 0.06[A]	1.09 ± 0.06[C]	1.14 ± 0.06[D]

Results

Within the four species, there were few significant differences in the responses to the two Atlantic salmon population treatments, i.e. species together with LaHave or Sebago Atlantic salmon (ESM Table S3; Fig. S1). We therefore pooled these two population treatments together as a general 'species with Atlantic salmon' treatment for the analysis. Additionally, in a separate experiment using the same artificial streams one year later which included another Atlantic salmon population treatment (Lac Saint-Jean from Quebec) but no species alone treatment, we also found that within the four species there were few significant differences in the response to the three Atlantic salmon population treatments (ESM Table S3; Fig. S2).

There were no significant treatment effects for survival and riffle use at either 3 or 10 months (Table 2; Fig. 1). However, there were significant treatments by species effects for body length and mass at 10 months but not at 3 months. Brown trout and rainbow trout were longer and heavier when held with Atlantic salmon than when reared alone. In contrast, Chinook salmon and coho salmon body length and mass were similar when reared alone or with Atlantic salmon at either time. For all four species, there were no significant effects of the presence or absence of Atlantic salmon on body condition (Table 2; Fig. 1).

Table 2

Summary of model results for traits of the four focal species (brown trout- *Salmo trutta*, rainbow trout- *Oncorhynchus mykiss*, Chinook salmon- *O. tshawytscha*, and coho salmon- *O. kisutch*). Displayed are quasi-binomial model results for survival and riffle use and linear mixed-effects results for body length, mass, and condition. Species and treatment were coded as fixed effects in all models and mixed-effects models contained a random effect for artificial stream tank identity. The two treatments were each of the four species alone and species with Atlantic salmon (LaHave and Sebago Atlantic salmon population treatments were pooled).

Trait	3 months			10 months		
	df	F-statistic	p-Value	df	F-statistic	p-Value
Survival						
Species	3, 16	2.31	0.115	3, 16	4.51	0.018
Treatment	1, 16	0.06	0.805	1, 16	0.07	0.791
Species × treatment	3, 16	0.88	0.471	3, 16	0.36	0.779
Length						
Species	3, 487	170.42	<0.001	3, 9.8	11.42	0.002
Treatment	1, 487	0.94	0.334	1, 9.8	15.86	0.003
Species × treatment	3, 487	1.64	0.180	3, 9.8	8.07	0.005
Mass						
Species	3, 487	147.32	<0.001	3, 467	7.85	<0.001
Treatment	1, 487	2.49	0.116	1, 467	15.87	<0.001
Species × treatment	3, 487	0.95	0.513	3, 467	7.30	<0.001
Condition						
Species	3, 17.8	18.60	<0.001	3, 13.4	12.43	<0.001
Treatment	1, 17.8	0.04	0.846	1, 13.4	0.63	0.441
Species × treatment	3, 17.8	1.10	0.374	3, 13.4	0.99	0.428
Riffle use						
Species	3, 16	6.54	0.004	3, 16	10.07	<0.001
Treatment	1, 16	0.04	0.847	1, 16	0.28	0.602
Species × treatment	3, 16	1.63	0.222	3, 16	0.56	0.647

Discussion

We found that there was little negative impact of Atlantic salmon on the survival and fitness-related traits of the four other salmonid species. Atlantic salmon tend to be less aggressive than brown trout and rainbow trout (e.g. Gibson, 1981; Vehanen, 2006), but just as aggressive as Chinook salmon and coho salmon (e.g. Gibson, 1981; Scott et al., 2005b). Consistent with these other studies, brown trout and rainbow trout had smaller body sizes when reared alone than when with Atlantic salmon; that is, intraspecific competition for both species was greater than interspecific competition with Atlantic salmon (Fausch, 1998). Furthermore, supporting evidence that Chinook salmon and coho salmon have similar competitive abilities as Atlantic salmon, Chinook salmon and coho salmon had similar body sizes whether alone or with the Atlantic salmon. Other studies have also observed no negative impacts of Atlantic salmon on the performance of brown trout (e.g. Vehanen, 2006; Van Zwol et al., 2012a), rainbow trout (e.g. Coghlan et al., 2007; Van Zwol et al., 2012a), Chinook salmon (e.g. Scott et al., 2005b), and coho salmon (e.g. Heland and Beall, 1997). Collectively these studies indicate that these species are unlikely to be negatively impacted by competition with other species of lower or similar competitive ability.

Beyond the degree of spatial niche overlap and differences in competitive abilities between species, another important consideration for evaluating the extent of interspecific competition is the degree of temporal overlap. Juvenile Atlantic salmon typically reside in streams for 2 years in North America before outmigrating as smolts (Klemetsen et al., 2003). Similarly, juvenile brown trout and rainbow trout typically reside in streams for 2 years (range 1–3 years) with some individuals that remain residents (Fausch and White, 1986; Klemetsen et al., 2003). In contrast, juvenile Chinook salmon and coho salmon have shorter residence times of 2 to 3 months and 1 year, respectively (Fausch and White, 1986). Spatially and temporally brown trout and rainbow trout may be exposed to higher interspecific competition with Atlantic salmon relative to Chinook salmon and coho salmon. Although we used age 0 + fish, which covered the residency period of Chinook salmon and coho salmon, similar results to the present study were observed for age 1 + brown trout and rainbow trout using the same artificial streams (Van Zwol et al., 2012a). Collectively these data suggest that Atlantic salmon have little negative impact on the survival and growth of all four other species.

Comparisons of the results using artificial streams to natural systems may have limitations. The use of artificial streams has the advantages of controlling environmental variables, such as water velocity and depth, and increasing replication which otherwise can be more difficult to achieve using natural streams (Fausch, 1988, 1998). On the other hand, a meta-analysis suggests that artificial streams can overestimate the magnitude (but not direction) of competitive effects as compared to natural streams (Korsu et al., 2010). In particular, laboratory studies may produce stronger responses to interspecific competition because of a generally smaller spatial scale relative to natural systems. Although the fish density in the artificial streams was likely higher than that experienced in natural streams, suggesting the potential for scale effects (e.g. Riley et al., 2005), a previous study found similarities in both the direction and magnitude of Atlantic salmon responses to competition with
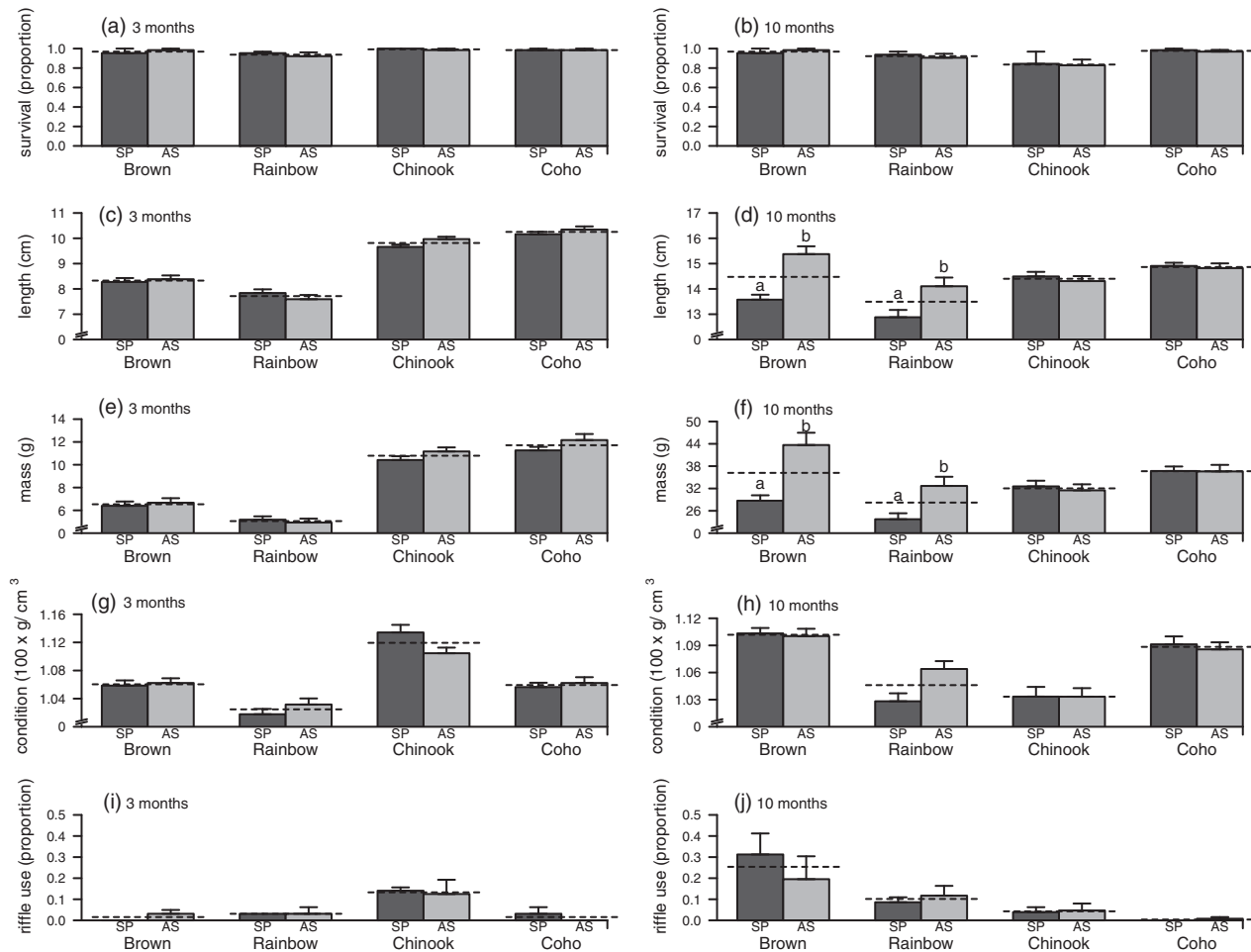
Fig. 1. Traits for the four focal species (brown trout- *Salmo trutta*, rainbow trout- *Oncorhynchus mykiss*, Chinook salmon- *O. tshawytscha*, and coho salmon- *O. kisutch*) in artificial stream tanks at 3 and 10 months. Treatment symbols are SP = species alone, AS = species with Atlantic salmon (LaHave and Sebago Atlantic salmon population treatments were pooled). Displayed are means and 1SE for treatments. Dashed lines are the means for the species across treatments. Different lowercase letters indicate significant differences assessed using Tukey's post-hoc multiple comparisons within species ($p < 0.05$).

rainbow trout between the same artificial streams and natural streams sites (Houde et al., 2016). Regardless, certain conditions within natural systems may influence the outcome of interspecific competition (Finstad et al., 2011). For example, the growth of juvenile rainbow trout may be lower if Atlantic salmon are given prior residency (i.e. 3 days, Volpe et al., 2001) or if Atlantic salmon are stocked at a high density into a natural stream (Dietrich et al., 2008). Stream gradients and temperature will also likely influence competitive outcomes and microhabitat use between brown trout, rainbow trout, and Atlantic salmon (Armstrong et al., 2003; Coghlan et al., 2007; Dietrich et al., 2008; Johnson, 2016); and as adults, spawning Atlantic salmon may also interact with spawning individuals of the four species (Scott et al., 2003, 2005a). It would also be useful to compare multispecies performance in natural as well as experimental systems (Fausch, 1998), so future studies should examine competitive interactions of these species in natural streams and over their life cycles.

Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.jglr.2016.10.017.

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