Competition among juvenile Atlantic salmon (*Salmo salar*) and steelhead (*Oncorhynchus mykiss*): relevance to invasion potential in British Columbia

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Abstract: Atlantic salmon (*Salmo salar*) are routinely captured in both freshwater and marine environments of coastal British Columbia (Canada). Recent evidence suggests that this species is now naturally reproducing in Vancouver Island rivers. Our objective was to quantify the performance of each species in intra- and inter-specific competition by assessing the competitive ability of Atlantic salmon sympatric with native niche equivalent steelhead – rainbow trout (*Oncorhynchus mykiss*). Significant behavioural differences, particularly with respect to agonism, were observed between species; however, the status of an individual as resident or challenger was the best predictor of performance. Resident fish always outperformed challengers, regardless of species. Thus, we suggest that Atlantic salmon may be capable of colonizing and persisting in coastal British Columbia river systems that are underutilized by native species, such as the steelhead.

Résumé : On capture couramment des saumons atlantiques (*Salmo salar*) dans des milieux marins ou dulcicoles du littoral de la Colombie-Britannique (Canada). Des données récentes permettent de penser que cette espèce se reproduit maintenant de façon naturelle dans les cours d'eau de l'île de Vancouver. Notre objectif était de quantifier la performance de chaque espèce dans la concurrence intra- et interspécifique en évaluant l'aptitude concurrentielle des saumons atlantiques sympatriques du saumon arc-en-ciel (*Oncorhynchus mykiss*) indigène, dont la niche est équivalente. Des différences de comportement significatives ont été notées, particulièrement sur le plan de l'agonisme, mais c'est le statut d'un individude résident ou de challengeur qui constituait le meilleur prédicteur de la performance. Les poisson résidents dépassaient toujours les challengeurs, quelle que soit l'espèce. Nous jugeons donc que le saumon atlantique est en mesure de coloniser et d'occuper de façon permanente les systèmes côtiers de Colombie-Britannique sous-utilisés par les espèces indigènes comme le saumon arc-en-ciel.

[Traduit par la Rédaction]

Introduction

Aquaculture produces the most valuable export crop in British Columbia, namely, farmed salmon, and approximately 80% of production is Atlantic salmon (*Salmo salar*). Pacific coast aquaculturalists prefer Atlantic salmon, owing to a consistently better market price and its superior performance under culture compared with native species (Keller and Leslie 1996). The balance of production is made up of chinook (*Oncorhynchus tshawytscha*) and coho (*Oncorhynchus kisutch*) salmon. Atlantic salmon are raised in freshwater hatcheries to smolts and then transferred to marine net pens, where they remain and grow to market size. The majority of marine net pen facilities in British Columbia are located off the northeast and west coasts of Vancouver Island. The first capture of a free-ranging Atlantic salmon in British Columbian waters occurred in 1987, and adults are now routinely encountered during the marine commercial salmon season and are also seen in many Vancouver Island rivers from summer through winter each year (McKinnell et al. 1997; Thomson and Candy 1998). In August 1998, the first naturally reproduced Atlantic salmon were captured in the Tsitika River on the northeast coast of Vancouver Island (Volpe et al. 2000). The 12 fish sampled represent the first documented evidence of successful feral spawnings (2 year-classes captured) of aquaculture-escaped Atlantic salmon in British Columbia.

As reports of free-ranging Atlantic salmon become commonplace, and particularly since the discovery of the Tsitika River juveniles, the potential for naturalization of Atlantic salmon in British Columbia has become a contentious issue. Previous failed introductions in British Columbia and elsewhere have been cited as evidence that current aquaculture escapees pose little ecological threat (Needham 1995). Atlantic salmon were introduced to British Columbia early last century but, despite considerable effort, all attempts failed to establish a self-sustaining population (Carl and Guiguet 1958).

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Table 1. Starting densities, weights, and lengths of fish in the three replicate experiments are listed, with the time frame and temperature profile for each replicate.

	Experimental block		
	1	2	3
No. of fish in low-density channels	4	4	2
No. of fish in mixed and high-density channels	8	8	4
No. of fish of each species in mixed channels	4	4	2
Mean start weight of steelhead (g)	0.55	1.09	1.14
Mean start weight of Atlantic salmon (g)	0.55	1.05	1.63
Mean start length of steelhead (mm)	38.7	49.3	47.1
Mean start length of Atlantic salmon (mm)	37.1	48.7	54.3
Residents introduced to channel	22 June	15 June	31 July
Challengers introduced to channel	25 June	18 July	3 August
Experiment ends	6 July	29 July	14 August
Temperature (°C)			
Mean	17.0	18.2	18.5
Range	15.1–17.9	15.0–19.1	16.3–19.1

The cause(s) of these failed introductions remains unknown. Regardless, aquaculture-escapee salmon encounter different biological and physical parameters today than those released earlier this century. As such, it is important to determine colonization potential and future downstream effects of contemporary escapes in a scientific manner.

Juvenile steelhead – rainbow trout (*Oncorhynchus mykiss*) display significant niche overlap with Atlantic salmon and, under limiting circumstances, are likely to come into vigorous competition for resources (Gibson 1981; Hearn and Kynard 1986). We assumed that, if the presence of Atlantic salmon was to affect native populations, the effect would be first and perhaps most vigorously manifested in, although not necessarily restricted to, sympatric steelhead. Our objective was to quantify the performance of each species in intra- and inter-specific competition by assessing the competitive ability of Atlantic salmon sympatric with native niche equivalent steelhead.

Methods

Fish

All experiments were conducted using a single cohort of young-of-the-year fish of each species. We collected progeny of Vancouver Island aquaculture broodstock (McConnel strain) Atlantic salmon from a local commercial aquaculture facility. Fish were reared to emergence and, at 119 days post-hatch (2 June 1998), were haphazardly sampled from pooled spawnings (three females, six males) and moved to the University of Victoria's Aquatic Facility (UVicAF), where they were held under aquaculture-like conditions until required. Steelhead were F_1 progeny of wild adults (three females, six males) taken from the Salmon River, Vancouver Island. Fish were maintained at the Vancouver Island Trout Hatchery (Duncan, B.C.) until transported to UVicAF at 38 days post hatch (also 2 June 1998). Animals were chosen haphazardly from rearing tanks containing mixed pools of progeny.

Fish were held in standard 410-L circular rearing tanks for 20 days prior to the start of the first experiment. The steelhead holding tank was augmented with structural diversity, including cobble substrate and artificial structure, to simulate a more natural environment. While in the holding tanks, steelhead were fed a "high forage rate" (see below) mixture of chironomid larvae and *Daphnia*, the same forage they would encounter in the experimental channels. Atlantic salmon were maintained in an aquaculture-like environment (bare tank) and fed commercial pellet food to satiation. The outdoor holding tanks were equipped with opaque lids, so fish were exposed to natural photoperiod. Temperature in the tanks varied between 15 and 19°C over the course of the experiments, which ran from 22 June to 14 August 1998 (Table 1).

Experimental procedure

A primary objective was to quantify the strength of intraspecific and interspecific competition of sympatric juvenile Atlantic salmon and steelhead. The per capita effect of steelhead on themselves (intraspecific competition or a_{ss}) was measured as the reduction in performance (weight loss) between steelhead at high density and steelhead at low density. The effect of Atlantic salmon on steelhead (interspecific competition or a_{as}) was defined as the change in performance between steelhead sympatric with Atlantic salmon at high density and steelhead alone at low density. Per capita coefficients of intra- and inter-specific competition for Atlantic salmon (a_{aa} and a_{sa}, respectively) were calculated in a similar fashion. Analyses of intra- and inter-specific competition often yield confounded data (Underwood 1986 and references therein; Fausch 1997) as a result of not adequately separating intraspecific from interspecific effects. Because the low-density, high-density, and mixed channels had n, $2n$, and n of steelhead and (or) Atlantic salmon, we could unambiguously separate intraspecific from interspecific effects. Thus, six combinations of fish were used: conspecific Atlantic salmon at low and high density; steelhead at low and high density; and two mixed-species channels, both at high density. These six combinations were each replicated at high and low forage levels, bringing the total number of channels to 12 for the full design. The design was replicated three times as time blocks (see Table 1). Steelhead and Atlantic salmon began the first two replicates at a similar mean size; however, by experiment (time replicate) 3, Atlantic salmon were much heavier than steelhead (Table 1). This was due to the more rapid relative growth of Atlantic salmon in the holding tanks. Both species grew over the course of the experiments and, to compensate, densities had to be halved during replication three (Table 1).

In each of the 12 experimental channels, fish were subjected to a combination of four treatments: (1) species composition (intra- or inter-specific), (2) order of introduction (resident or challenger), (3) fish density (high or low), and (4) forage abundance (high or low) (Fig. 1). For the high-density and mixed channels, four resident fish were acclimatized to the channels for 3 days prior to the introduction of four challenger fish. For the low-density channels, four fish were added at once. Observations began immediately after the introduction of the challengers and continued for 10 days.

Fig. 1. Schematic representation of the experimental design for one full experiment. Two replicates of six channels were used in each of three experiments: one replicate provided with a high forage level and the other with a low forage level. By comparing results from appropriate channels, intraspecific (a_{ss}, a_{aa}) and interspecific (a_{sa}, a_{as}) competition can be evaluated, as well as the role of residency (assembly). The relevant comparisons are illustrated by brackets between the experimental populations being compared. Within each channel, the number and species of fish (AS, Atlantic salmon; ST, steelhead) are given. The top set indicates the initial fish introduced into the channels, i.e., the *residents*. After a 72-h acclimatization, the fish indicated by the bottom set were introduced, i.e., the *challengers*. Note that both the high-density single- and mixed-species channels had residents and challengers, while low-density single-species channels had only residents.
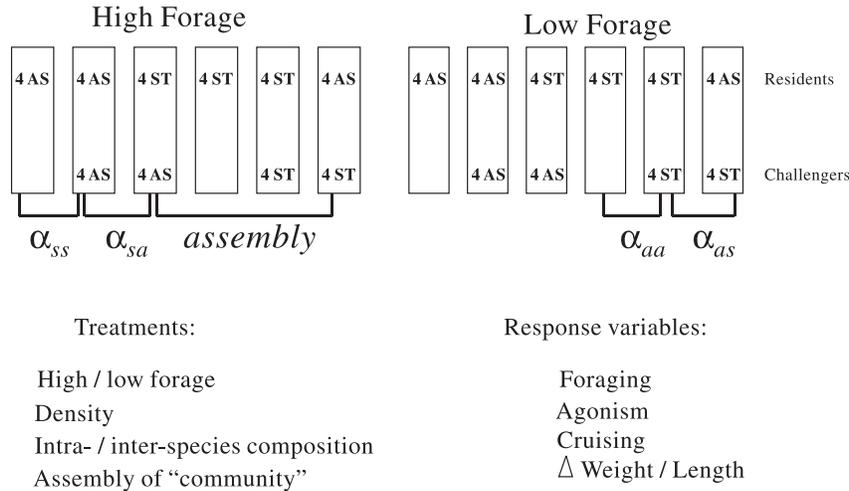

Fig. 2. Schematic representation of a single experimental channel viewed from above. Water entered from a single inlet behind a mesh partition that fish could not pass but which allowed free passage of forage items. Six identical half-bricks provided the only structure in the channel (all channels had the same number of bricks, regardless of composition or density). Water was removed via dual gravity-driven outlets. Ball valves on both the inlet and outlet allowed precise control of flow rates.
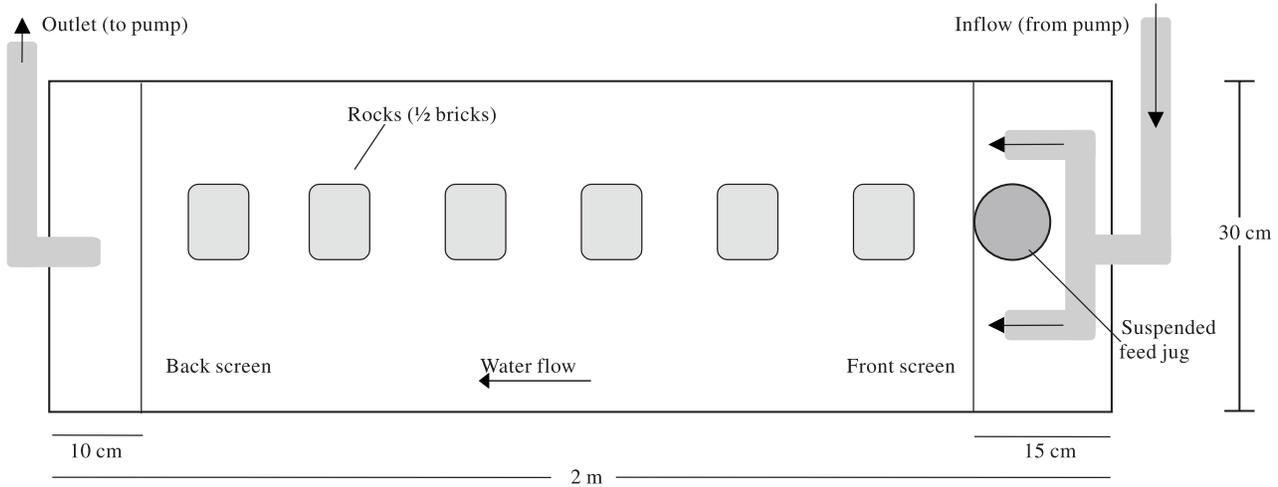
Prior to each experiment, fish haphazardly selected from the holding tanks were starved for 12 h to clear the gut, anesthetized with clove oil (Keene et al. 1998), measured (fork length), weighed, and randomly assigned an identifying fin clip. After being measured and weighed, fish were graded, to minimize size differences, and added to randomly chosen channels as residents. By the third replicate, the size difference between species was too great to effectively control for size (Table 1). After a 72-h acclimatization period, during which the resident fish were provided with half the experimental forage level, similarly treated challengers were added to the channels and the forage levels increased to full ration. We used fin notches ("V"-shaped clips) to identify individuals at the beginning and end of each experiment (notches could not be distinguished by observers when fish were in the channels). Some individuals had no notches, while others had notches on one or two of

the following fins: adipose, right or left ventral, upper or lower tips of the caudal. Because the duration of each experiment was only 13 days, the regeneration of the clips was not an issue, allowing us to remove only a very small portion of tissue while maintaining individual discrimination.

Food consisted of equal parts frozen adult *Daphnia s*pp. and chironomid larvae. Daily rations provided the caloric equivalent of a commercially prepared diet at high and low forage levels (based on standard feeding protocols prepared by EWOS Inc.). Food was dispensed via an inverted 4-L plastic jug suspended above each channel upstream of the top fence (Fig. 2). The jugs were partially filled with shaved ice and the appropriate ration for 1 day, shaken to distribute the forage items, and then filled with dechlorinated filtered water and frozen solid overnight. When frozen, the forage items were randomly distributed throughout the jug, which re-

Table 2. Main response variables per 5-min observation, together with total sampling effort.

| | Experimental block | | | |
	1	2	3	Mean
Δweight (g)				
Steelhead	0.00	–1.03	0.00	–0.34
Atlantic salmon	–0.04	–0.14	–0.08	–0.09
Δlength (mm)				
Steelhead	0.90	0.00	1.43	0.78
Atlantic salmon	1.30	0.61	1.12	1.01
Counts/5 min				
Intraspecific agonism				
Steelhead	1.40	2.15	0.72	1.42
Atlantic salmon	0.22	0.19	0.20	0.20
Interspecific agonism				
Steelhead	0.51	0.56	0.34	0.47
Atlantic salmon	0.11	0.15	0.27	0.18
Forage				
Steelhead	5.92	2.23	1.61	3.25
Atlantic salmon	4.91	2.51	1.35	2.92
Cruise				
Steelhead	5.60	7.82	8.03	7.15
Atlantic salmon	1.43	1.28	2.04	1.58
Total no. of 5-min observations				
Steelhead	127	128	104	na
Atlantic salmon	82	130	110	na

Note: Values for each variable are adjusted for sampling effort and represent the total number of observations across all treatments. Agonism values are means across all treatments. Interspecific-agonism values are adjusted to account for the different number of conspecific and interspecific individuals available for interaction relative to the focal individual.

quired approximately 24–26 h to thaw completely. A hole punched in the lid of each jug allowed the thawing water and forage to drip into the channel. Forage entered the channel unpredictably over the thawing period. Freshly prepared jugs were provided when the previous day's jug was completely empty.

Both species showed normal feeding behaviour upon entering the channels. Even though Atlantic salmon had not encountered natural drifting forage before entering the channels, we did not note any delay in acceptance of drift forage. Both species fed exclusively on moving drift, ignoring any forage item that came to rest on the substrate or on the front and rear fences.

Experimental channels were 2.0 m long, 0.3 m wide, and 8 cm deep. Natural light and photoperiod were provided by overhead skylight windows. All channels were surrounded by opaque black fabric, to minimize disturbance. Six cement bricks ($6 \times 6 \times 3.5$ cm) treated with a biologically inert sealer (Thompson's Water Seal®) were placed in each channel, to serve as current refuges, and were the only structures in the channels (Fig. 2). All bricks were identical, to ensure that any observed territoriality was a function of the brick position in the channel and not of the brick itself. A single layer of river cobble (2–3 cm in diameter) covered the remainder of the bottom of each arena. Victoria municipal water that had been dechlorinated with thiosulphate was provided in a partial-recirculation system (15% replacement per cycle), at a rate of 40 L·min^{-1}, providing a maximum surface velocity of 0.25 m·s^{-1}. Water temperature varied from 15 to 19°C over the course of the experiment. Water chemistry was maintained by passing water through a series of sand filters, charcoal beds, a biofilter, and an aeration tower every cycle.

Experimental stocking density was determined in a pilot experiment using steelhead. Two raceways were stocked to what was considered excess (15 steelhead). Each channel allowed emigration

through a one-way trap to a refuge, an adjacent suboptimal channel with minimal flow and no food. Fish in the primary channel experienced natural photoperiod and a high-ration diet. After 48 h, relative positions and densities of fish were assessed for 15 min every 3 h (Hearn and Kynard 1986). All territories were considered stable if positions were held static for three consecutive observation periods. We replicated this with a new group of fish five times. Final densities ranged from 6 to 10. The modal density of eight fish per channel was chosen as the high density. We halved this to four individuals in the low-density channels.

Observation protocol

Fish in all 12 channels were observed daily, with observation periods covering 24 h. Channels and focal fish were chosen at random. Visual night observations were conducted under deep-red illumination (wavelengths greater than 640 nm). Three Sylvania S14 lamps (11 W, 130 V, deep red; Albright Lighting Ltd., Victoria, B.C.) illuminated each channel from a height of 1 m. The spectral output of the lamp was chosen to minimize the stimulation of the red-sensitive cone photoreceptors found in salmonids, thus mimicking night conditions (peak absorbance 576 nm; Hawryshyn and Harosi 1994). Because the spectrum of these lights capitalized on the absorbance differences between salmonid and human eyes, we were able to visually observe fish in what they perceived as relative darkness.

Over each 10-day experimental period, observation sessions of focal fish lasted 5 min (total times given in Table 2). During this period, all activities undertaken by the focal fish were recorded in one of three categories: forage, agonism, and cruise. These were defined, respectively, as the number of prey consumed; counts of attacks, charges, or chases performed or received by focal fish; and counts of nondirectional movement of focal fish. All interspecific-agonism values were corrected, to account for species asymmetry in mixed channels. A focal fish had three potential intraspecific and four interspecific targets.

Data analysis

All fish were weighed and measured at the end of each experiment, to calculate the competition coefficients. Our behavioural data are non-independent (only one behaviour could be executed at a time to the exclusion of all others), so we used principal-component analysis (PCA) on the correlation matrix, to reduce the number of variables (McPeek 1990). The principal component (PC) scores were used as dependent variables in a stepwise generalized linear model (GLM). The stepwise GLM adds and subtracts main and interaction effects (experiment, density, forage level, species), to determine which subset of variables combine to give the simplest adequate model of the PC based on Akaike's (1974) information-criterion value. The best-fit models were further simplified by eliminating any terms with a Mallow's (1973) C_p value of less than one. The terms of each GLM were then subjected to a fixed-effect analysis of variance (ANOVA) and tested for significance. A multivariate analysis of variance (MANOVA) was not necessary, as the PCs are, by definition, uncorrelated. All analyses were performed in S-PLUS version 4.5 (Mathsoft International, Inc., Seattle, Wash.).

Results

Overall we found that steelhead cruised 4.5 times more than Atlantic salmon and committed five acts of agonism for each similar act executed by Atlantic salmon (Table 2). Over the course of each of the three experiments, both species lost weight and grew only modestly in length (Table 2).

Steelhead were 2.1 times more likely to be agonistic towards a conspecific than towards an Atlantic salmon. Atlantic salmon were 2.2 times more likely to attack a steelhead

Table 3. Per capita weight change of Atlantic salmon and steelhead at low- and high-ration levels and different densities, and mean agonism, forage, and cruise counts per 5-min observation period at different densities.

	Steelhead			Atlantic salmon			
	Low density	High density	Mixed	Low density	High density	Mixed	p
Δweight (g)							
Low ration	–0.093	–0.064	–0.026	–0.052	–0.075	–0.062	—
High ration	–0.047	–0.057	–0.004	0.003	–0.097	–0.069	—
Agonism							
Intraspecific	1.230	2.430	1.003	0.250	0.310	0.082	<0.001*
Interspecific	—	—	0.470	—	—	0.180	0.18
Forage	3.34	3.26	3.21	2.63	3.57	2.75	0.67
Cruise	8.40	6.54	7.50	2.51	1.68	1.01	<0.001*

     * p value significant at <0.05.

than a conspecific ("mixed" columns, Table 3). Interspecific agonism in Atlantic salmon increased markedly with age, while in steelhead, it peaked during experiment 2 and declined sharply in experiment 3, when Atlantic salmon were larger than steelhead (Table 1). Number and types of clips used for individual identification were evenly distributed among species and treatments. No relationship between clips and performance (weight change) was observed in a multiple regression analysis ($p > 0.08$).

Nine fish (3.8%) were lost owing to mortality (four Atlantic salmon and five steelhead). All but one individual of each species were accounted for—they had jumped out of the channel over or through a retaining screen. Calculations were adjusted to account for asymmetric densities due to mortality.

Behaviour at different densities

High-density treatments increased the level of agonism in steelhead ($p < 0.001$) (Table 3) but made little difference to foraging and cruising rates (Table 3). A similar but less pronounced pattern was seen with Atlantic salmon: agonism increased at high density ($p = 0.033$) (Table 3), foraging showed only moderate change, and cruising dropped markedly (Table 3).

In mixed channels, steelhead targeted conspecifics more than twice as often as Atlantic salmon, while showing little change in other behaviours (Table 3). Atlantic salmon sympatric with steelhead showed a 67% reduction in intraspecific agonism (Atlantic salmon in low-density channels vs. Atlantic salmon in mixed channels; Table 3) and a 2.2:1 bias towards interspecific agonism. Little change was noted in Atlantic salmon foraging rate and, as in the intraspecific high density treatment, cruise rate dropped markedly.

Principal-component analyses

Intraspecific and interspecific channels were examined separately, owing to the differences in competitive relationships in each.

Intraspecific

The first three PCs accounted for 80% of the total variation (Table 4). The first PC (PC1) is related to agonism. Fish in channels with a high frequency of agonism were likely to display low growth and reduced foraging rates. The second PC (PC2) is correlated with activity levels. More sedentary

fish were less agonistic and more likely to show reduced growth. The third PCS (PC3) shows a residual positive correlation between foraging and agonism.

Interspecific

The first three PCs accounted for 91% of the total variation (Table 4). PC1 is activity with a positive correlation among intra- and inter-specific agonism and cruising. PC2 reveals a negative relationship among growth and cruising—fish with reduced growth rates are more sedentary. PC3, as with the intraspecific PC scores, shows a residual positive relationship between foraging and intraspecific agonism. Increased foraging comes at a cost of increased intraspecific agonism, regardless of whether the individual is in a single-species or mixed channel.

Treatment effects on behaviour

Intraspecific

Agonism (PC1) increased later in the season as the fish grew. Steelhead were more aggressive than Atlantic salmon (Table 5), but the difference decreased with time (block). Steelhead were more active than Atlantic salmon (PC2) under all conditions.

Interspecific

In sympatry as in allopatry, steelhead were more active and aggressive than Atlantic salmon (Table 6) under all conditions.

Diurnal versus nocturnal activity

At night, steelhead increased their rates of both intra- and inter-specific agonism and markedly reduced their foraging and, to a lesser extent, cruising (Table 7). Atlantic salmon increased intraspecific agonism at night by 122% and interspecific agonism by 32%. Foraging also increased slightly, but cruising activity dropped dramatically (Table 7).

Resident versus challenger effects

Resident–challenger status had a pre-eminent effect on predicting performance. Resident fish outperformed challengers in all instances, regardless of other treatment effects (Table 8). In the simplest terms, on average across all fish, residents gained weight and challengers lost weight (Fig. 3).

Table 4. Loadings for intra- and inter-specific principal-component analysis.

	Principal component					
	1	2	3	4	5	6
Intraspecific loadings						
Cruise	0.191	−0.838	−0.046	0.411	0.304	
Forage	−0.450	0.046	0.835	0.269	0.147	
Δlength	−0.498	−0.313	−0.136	−0.700	0.396	
Δweight	−0.532	−0.333	−0.163	0.122	−0.751	
Intraspecific agonism	0.479	−0.289	0.519	−0.503	−0.405	
% cumulative variation	37.6	62.7	80.0	92.0	100.0	
Interspecific loadings						
Cruise	0.477	−0.437	−0.137	−0.280	−0.001	0.696
Forage	−0.116	−0.144	0.932	−0.100	−0.264	0.130
Δlength	−0.394	−0.471	−0.121	0.725	−0.154	0.241
Δweight	−0.026	−0.707	−0.117	−0.336	−0.175	−0.585
Intraspecific agonism	0.530	−0.199	0.285	0.420	0.596	−0.259
Interspecific agonism	0.567	0.164	−0.051	0.311	−0.722	−0.176
% cumulative variation	42.8	73.9	91.2	96.6	99.5	100

Note: The percent cumulative variation accounted for by the addition of each principle component is given below each set of loading values.

Table 5. ANOVA of terms associated with the minimum adequate model of intraspecific principal component (PC) scores.

	df	SS	F	p
Agonism (PC1)				
Block	2	27.18	14.34	0.000
Density	2	1.29	0.68	0.510
Species	1	10.82	11.43	0.002
Block:density	4	1.00	1.05	0.310
Residuals	26	27.46		
Activity (PC2)				
Species	1	26.51	48.35	0.000
Residuals	34	18.64		
Foraging and agonism (PC3)				
Block	2	21.80	46.52	0.000
Density	2	1.19	2.54	0.096
Species	1	1.15	4.89	0.035
Residuals	30	7.03		

Table 6. ANOVA of terms associated with the minimum adequate model of interspecific principle component (PC) scores.

	df	SS	F	p
Agonism (PC1)				
Species	1	13.72	8.01	0.018
Residuals	10	17.13		
Growth (PC2)				
Species	1	11.22	10.06	0.001
Residuals	10	11.15		
Foraging and agonism (PC3)				
Block	2	10.33	17.49	0.002
Species	1	0.17	0.59	0.468
Food level	1	0.01	0.02	0.886
Residuals	7	1.44		

high-density channels had a greater number of foraging opportunities and, on average, gained more or lost less weight than their low-density counterparts.

The pattern of resident fish out-competing challengers was most obvious among those individuals that showed the greatest weight change—either positive or negative. The 20 fish (10% of the study population) that recorded the greatest gain or loss of weight were examined for a pattern that might predict the observed dramatic change in weight. Of the five potential predictive factors, resident–challenger status was highly significant ($F_{[1,14]} = 9.8$, $p = 0.011$), whereas all other factors shared no predictive power (all $F < 1.0$).

Coefficients of competition

Steelhead showed better per capita mass change at low forage, whereas Atlantic salmon performed better in high-forage situations (Table 9). The high degree of steelhead intraspecific agonism is reflected in the competition coefficients. At the low forage rate, the per capita effect of steelhead on steelhead (a_{ss}) is roughly double that exerted by Atlantic salmon on steelhead (a_{as}) and increases to four times at high forage levels. The effect of Atlantic salmon on

This pattern was equally prominent in conspecific channels and mixed channels. Even when both residents and challengers lost weight, challengers lost at least twice as much weight as residents (Table 8). Forage level did not have a consistent effect, as low-ration fish did not always lose more weight than their high-ration counterparts (Table 8).

Resident steelhead showed better overall performance at high density, which was opposite to our a priori prediction (Table 8). Steelhead at high density lost only 0.007 and 0.004 g per capita in high- and low-forage channels, respectively, compared with 0.093 and 0.047 g per capita in high- and low-forage channels, respectively, at low density. We suspect that dominant individuals can be more effective at restricting access to profitable feeding areas when at low-density than when at high density. At high density, a dominant individual must defend a profitable position against seven other fish, while a dominant individual at low density has only three other fish to exclude. Therefore, owing to the diluted attention of the dominant fish, subordinates in the

Table 7. Behaviour counts observed during day (06:30–19:59) and night (20:00–06:29) and percent change in activities from day to night.

	Steelhead			Atlantic salmon		
	Day	Night	% change	Day	Night	% change
Intraspecific agonism	1.02	1.49	+46	0.09	0.20	+122
Interspecific agonism	0.60	0.74	+23	0.23	0.14	+39
Forage	4.53	1.91	–58	1.91	2.46	+29
Cruise	6.53	5.41	–17	2.92	1.14	–61
No. of observation sessions	243	116	—	211	111	—

Note: Data are from all three experiments and counts are standardized per 5-min observation session.

Table 8. Per capita change in mass (g) of resident versus challenger fish; data are arranged to contrast the effects of density and ration.

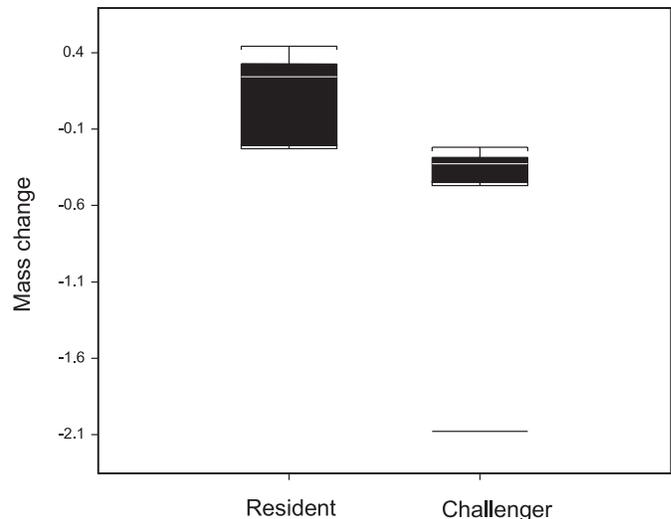|	Steelhead			Atlantic salmon		
	Resident	Challenger	% change	Resident	Challenger	% change
Low ration						
Intraspecific low density	–0.093	—	—	–0.052	—	—
Intraspecific high density	–0.007	–0.122	–1643	–0.061	–0.090	–48
Interspecific (high) density	–0.016	–0.036	–125	0.110	–0.235	–314
High ration						
Intraspecific low density	–0.047	—	—	0.003	—	—
Intraspecific high density	–0.004	–0.110	–2650	–0.058	–0.137	–136
Interspecific (high) density	0.029	–0.021	–172	0.071	–0.209	–394

itself is double that of steelhead on Atlantic salmon at the low forage level, but this difference diminishes at the high forage rate.

The coefficients of competition are more informative when analyzed separately for resident and challenger effects (Table 10). For steelhead, the direction of effect between resident and challenger fish is greatest in intraspecific channels, reflecting the dominant role of intraspecific agonism in steelhead performance. For Atlantic salmon, the distinction is not nearly so great. However, in mixed channels, Atlantic salmon do well as residents when challenged by steelhead, but relatively poorly as challengers (Table 10).

Discussion

Atlantic salmon and steelhead have only rarely come into contact in the wild and so there are few studies contrasting their competitive ability in sympatry. The few studies that have explicitly addressed this issue concluded that steelhead and Atlantic salmon are likely to compete for resources with relative success that is likely to vary with environmental parameters (Gibson 1981; Hearn and Kynard 1986; Jones and Stanfield 1993). Here, steelhead performance was superior relative to Atlantic salmon, but intraspecific (a_{ss}), not interspecific (a_{as}) agonism is the greater influence on performance. The average per capita competitive influence from an Atlantic salmon across all treatments is less than half that from another steelhead. However, the resident–challenger status of the individual greatly affects this generalization.

Greater aggression does not automatically translate to superior competitive ability. Interspecific competition can only be evaluated relative to intraspecific competition (Underwood 1986; Fausch 1997). Steelhead were greater than five times more aggressive than Atlantic salmon, but targeted other

Fig. 3. Box plot of relative weight change of resident and challenger fish (both species combined).

steelhead 2.1:1 over Atlantic salmon in mixed channels. In the same channels, Atlantic salmon showed an agonistic bias of 2.2:1 towards steelhead. As a result, replacement of steelhead with Atlantic salmon had little net effect on the number of agonistic interactions in which an individual steelhead was likely to be involved. Overall, Atlantic salmon did not perform as well as steelhead, but did show superior performance as residents.

Many fish lost mass over the course of the experiments. The sparse experimental environment, minimal depth, and limiting forage supply are likely the causes of this observation. A similar study of brown trout (*Salmo trutta*) found

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Table 9. Coefficients of competition (a) of steelhead and Atlantic salmon at high and low forage levels.

	a_{ss}	a_{as}	a_{aa}	a_{sa}
Low ration	+0.029	+0.067	–0.023	–0.010
High ration	–0.010	+0.043	–0.100	–0.072

Note: a_{ss}, steelhead intraspecific; a_{as}, Atlantic salmon – steelhead interspecific; a_{aa}, Atlantic salmon intraspecific; a_{sa}, steelhead – Atlantic salmon interspecific.

that only fish in channels augmented with woody debris with high forage rates gained mass. Those in control channels (not augmented, high and low forage) and in augmented channels at low forage rates all lost mass (Sundbaum and Näslund 1998). The lack of sufficient structure to provide visual isolation resulted in increased activity levels and corresponding energy expenditure. Greater augmentation of our channels may have served to reduce overall energy expenditure. Also, our channels were shallow (8 cm) and may have artificially amplified interspecific agonism by not allowing effective partitioning of the water column. Atlantic salmon were usually found in contact with the substrate, while steelhead remained in the water column. If the channels were deeper, it is possible that microhabitat partitioning might reduce interactions and result in lower energy expenditure. Finally, we observed that fish of both species did not pursue forage after it was in contact with the substrate. Since forage items were slightly negatively buoyant, they did occasionally drop from the column before being consumed, resulting in a net shortfall of forage (food was allotted to channels based on the assumption of a near 100% foraging efficiency and on energy budgets of relatively inactive aquaculture fish). Also, unlike the situation in the wild, the option of emigrating from vigorously contested areas was not an option here. These factors do detract from the "naturalness" of our simulations, but modifications to ameliorate them would reduce interspecific interactions and thus biotic resistance to Atlantic salmon. Our experimental conditions are likely harsher, in terms of intra- and inter-specific competition, than may be expected in the wild and, therefore, estimates of Atlantic salmon performance are, if anything, conservative.

Atlantic salmon showed a marked increase in aggression and foraging at night. Wild Atlantic salmon have demonstrated increased nocturnal activity (Gries et al. 1997). Our experimental design did not allow us to partition Atlantic salmon nocturnal performance by residents and challengers but it is possible that overall poor diurnal performance could be ameliorated by a combination of increased nocturnal Atlantic salmon agonism and foraging activity and reduced nocturnal foraging and cruising by steelhead.

Competitive exclusion has been suggested as a potential factor affecting some Atlantic salmon augmentation–re-establishment programs (Kennedy and Strange 1986). In British Columbia, adult Atlantic salmon are, at times, numerous in many coastal rivers, particularly in northern Vancouver Island (Thomson and Candy 1998). Competitive exclusion by natives during the juvenile stage and a suggested but unidentified deficiency in Atlantic salmon colonization ability have been argued as reasons escapees are not likely to colonize (Needham 1995). In our experiments, Atlantic salmon did not perform well when "released" (i.e.,

Table 10. Coefficients of competition (a) of resident versus challenger steelhead and Atlantic salmon at high and low forage levels.

	Steelhead		Atlantic salmon	
	Resident	Challenger	Resident	Challenger
Low ration				
a_{ss}	+0.086	–0.029	—	—
a_{as}	+0.077	+0.057	—	—
a_{aa}	—	—	–0.009	–0.038
a_{sa}	—	—	+0.162	–0.183
High ration				
a_{ss}	+0.043	–0.063	—	—
a_{as}	+0.076	+0.026	—	—
a_{aa}	—	—	–0.061	–0.140
a_{sa}	—	—	+0.068	–0.212

Note: a_{ss}, steelhead intraspecific; a_{as}, Atlantic salmon – steelhead interspecific; a_{aa}, Atlantic salmon intraspecific; a_{sa}, steelhead – Atlantic salmon interspecific.

challengers) into habitat already occupied by steelhead. However, when juvenile Atlantic salmon are allowed a residency period of 3 days, the ability to resist competitive intrusion of both steelhead and other Atlantic salmon competitors increases. This phenomenon was not limited to Atlantic salmon; resident steelhead likewise outperformed both intra- and inter-specific challengers. In some cases, the difference in performance was dramatic—up to 2650% improvement was observed between resident and challenger steelhead at high ration. In all cases, the differences were so large that prior residency became the only meaningful predictor of performance. Re-analysis of the data taking this into consideration shows that the top-performing group overall are resident Atlantic salmon in mixed channels at low food ration. If Atlantic salmon are resistant to interspecific competition after a short settlement period in isolation, habitats in the wild underutilized by niche equivalent competitors are more likely to be colonized.

The asymmetry of performance observed between residents and challengers is intriguing but the phenomenon is not new. Braddock (1949) described the "prior residence" effect in work with the platyfish (*Platypoecilus maculatus*). Significant prior residency advantage has been documented in juvenile Atlantic salmon with a separation of as little as 1 day between the introduction of challengers to conspecific residents (Huntingford and Garcia de Leaniz 1997), significantly less separation time than the 3 days used here. Prior residency has also been found to be a significant predictor of success for juvenile Atlantic salmon (Cutts et al. 1999*a*, 1999*b*; O'Connor et al. 2000). The prior residency effect may be widespread in salmonids, as both underyearling brown trout (*S. trutta*) and chinook salmon (*O. tshawytscha*) also show a significant prior residency advantage in interspecific competition (Glova and Field-Dodgson 1995).

In addition to other teleosts (Rauch 1996; Itzkowitz et al. 1998), prior-residency effects have been described in a wide array of taxa (Sandell and Smith 1991; Baugh and Forester 1994; Figler et al. 1999). The phenomenon is hypothesized to be the result of a resident's knowledge of the territory and, thus, its potential value. Armed with this information, a

resident's defence of the territory is likely to be more vigorous than a naive challenger's attempts to usurp it (Krebs 1982). Further, residents may be habituated to the test environment, while challengers may be more fearful and therefore less likely to engage in aggressive acts (Figler and Einhorn 1983). By augmenting the physical environment in the steelhead holding tank, we tried to minimize the physical differences between it and the experimental channels. Atlantic salmon did not receive such treatment (the holding tank was intentionally left bare, to simulate culture conditions); therefore, if there were negative effects in transferring fish between holding and experimental environments, we expect it affected Atlantic salmon to a greater degree than steelhead.

Residence effects are usually detected when competitors are of similar size. Therefore, residence effects may be more prominent in intraspecific competitions, as contestants are more likely to be similarly sized. Interspecific life-history differences are more likely to result in one species dominating, owing to a size advantage that may or may not be temporally stable. For instance Glova and Field-Dodgson (1995) observed that species dominance changed with time as the size advantage of earlier-emerging chinook dissipated. The threshold intraspecific size difference at which prior-residence advantage can be overcome is variable and has been estimated to be 10% total length for blennies (*Parablennius marmoreus*; Rauch 1996) and 6% for coho salmon (*O. kisutch*; Rhodes and Quinn 1998). Although the fish used in the majority of our experiments were standardized for size, Atlantic salmon were, on average, larger than steelhead; however, because each was maintained on different forage, direct comparisons are not possible. Field observations suggest that Atlantic salmon may have a size-at-age advantage over steelhead. A comparison of wild-reared Atlantic salmon and steelhead of similar ages from the Tsitika River, British Columbia, showed that Atlantic salmon were more than 50 and 100% larger than steelhead at 0+ and 1+ stages, respectively (Volpe et al. 2000). Atlantic salmon eggs require longer incubation than steelhead eggs—500 and 375 degree-days, respectively (Jobling 1995)—which translates into an approximately 25 day shorter incubation for steelhead eggs at 5°C. However, Atlantic salmon generally spawn in the fall or early winter (Scott and Scott 1988), whereas steelhead generally spawn in the spring (Scott and Crossman 1973). There is a high probability that, by spawning months ahead of steelhead, juvenile Atlantic salmon could exhibit a size–development advantage sufficient to overcome any advantage to steelhead through faster embryonic development. To date, only a single feral population has been studied, but the significantly larger size-at-age of the juvenile Atlantic salmon relative to sympatric steelhead (Volpe et al. 2000) supports this prediction.

Attempts to introduce Atlantic salmon to southern British Columbian rivers in the early half of this century failed. During this period (1905–1933; Carl and Guiguet 1958), coastal river systems would have been at or near saturation and vacant niche space would have been sparse, with suitable habitat saturated with native residents. We have demonstrated that Atlantic salmon do not perform well when introduced under such conditions. However, these conditions no longer exist. Steelhead populations in 12 of the 19 major river sys-

tems on Vancouver Island's east coast have been classified as "high risk"—population estimates over the past decade have been less than 20% of their long-term means (Bruce Ward, B.C. Ministry of Fisheries, University of British Columbia, 2204 Main Mall, Vancouver, BC V6T 1Z4, Canada, personal communication). The situation is much the same across the entire coast of British Columbia, as niches broaden in response to severely depressed and, in some cases, locally extirpated native populations (Slaney et al. 1996). Unlike the situation earlier this century, suitable rearing habitat is no longer likely to be limiting, and the potential for successful Atlantic salmon colonization has increased as a result. Juvenile Atlantic salmon may come to occupy such habitat directly, via escape from stream-side hatcheries or lake rearing pens (McKinnell et al. 1997), or through natural reproduction of free-ranging adults (Volpe et al. 2000).

Temporal segregation benefiting Atlantic salmon may result from life-history differences between Atlantic salmon and native salmonids in British Columbia. Atlantic salmon show considerable life-history variability across the native range. Spawning time usually ranges from September to December (Scott and Scott 1988) but may extend into March (Garcia de Leániz et al.1987). Free-ranging Atlantic salmon observed in British Columbian rivers do not begin to show spawning colouration until late fall, suggesting a spawning time near the end of this distribution (Volpe 1998, 1999, 2000). In a pilot experiment to assess the spawning capability of aquaculture-production fish, none of the 50 Atlantic salmon used displayed spawning characters (physical or behavioural) until mid-January (Volpe et al. 2001). Based on these data, we suggest that much of Atlantic salmon spawning activity may occur after most of the spawning activity of the five fall-spawning native *Oncorhynchus* species but before that of spring-spawning steelhead. If so, native adult spawner densities would be low at this time, resulting in minimal competition for redd sites. Atlantic salmon may superimpose their redds on those of earlier-spawning Pacific salmon or have theirs superimposed by those of spring-spawning steelhead. Superimposition has been demonstrated to be a significant factor in determining spawning success in space-limited systems (Hayes 1987). Currently in coastal British Columbia, low numbers of both Atlantic salmon and steelhead suggest superimposition is not, for the time being, likely to be a significant issue.

Early deposition of eggs from a successful Atlantic salmon mating would see progeny emerging from the redd in advance of steelhead. The Atlantic salmon used in this study hatched more than 2 months before the steelhead. If successful establishment of Atlantic salmon depends, in part, on settlement in isolation, a 2-month head start on the competition would prove to be a significant factor.

These data also have implications for enhancement and other management initiatives using stocked fish. Hatchery-reared fish introduced as part of wild stock augmentation programs have been shown to be deficient in numerous characters important for survival and fitness (Olla et al. 1998; Utter 1998). However, we are not aware of any such studies that have explicitly tested the role of residency in calibrating the performance of wild and introduced cultured stocks. The observed reduction in performance of hatchery-reared fish may be partly explained by their simply being challengers. In our

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simple test environment, an acclimatization period of only 3 days was necessary to produce significant performance differences in both species during intra- as well as inter-specific trials. Hatchery-reared fish released during augmentation programs may face similar challenges in the wild.

Our data demonstrate that Atlantic salmon are capable of colonizing vacant or underutilized habitat and of successfully defending that habitat against subsequent challenges from steelhead. These data also suggest that predicting the fate of feral Atlantic salmon in coastal British Columbia can be accomplished only by considering the native salmonid demographics and physical parameters of each contaminated system.

Acknowledgements

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