

Predictability of multispecies competitive interactions in three populations of Atlantic salmon *Salmo salar*

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Juvenile Atlantic salmon *Salmo salar* from three allopatric populations (LaHave, Sebago and Saint-Jean) were placed into artificial streams with combinations of four non-native salmonids: brown trout *Salmo trutta*, rainbow trout *Oncorhynchus mykiss*, Chinook salmon *Oncorhynchus tshawytscha* and coho salmon *Oncorhynchus kisutch*. Non-additive effects, as evidenced by lower performance than predicted from weighted summed two-species competition trials, were detected for *S. salar* fork length (L_F) and mass, but not for survival, condition factor or riffle use. These data support emerging theory on niche overlap and species richness as factors that can lead to non-additive competition effects.

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Globally, species introductions, whether planned or unintentional, have become so common that native species are often in competition with more than one ecologically similar non-native species (Cox, 2004). The combined effects of competition with multiple non-native species are largely unknown, so a simple additive function of two-species competition effects is typically used to predict outcomes (Weigelt *et al.*, 2007). Some studies examining multispecies competition support the simple additive function of two-species competition effects as reported from studies in both plants (Weigelt *et al.*, 2007) and animals (Young *et al.*, 2009), yet other studies have found non-additive effects (plants: Dormann & Roxburgh, 2005; animals: Wootton, 1993). Indeed, the influence that non-additive effects of competition can have on the performance of focal native species appears to be highly variable, with native species' performance (*e.g.* population growth) increasing, decreasing, or remaining unchanged (Levine, 1976; Stone & Roberts, 1991).

Atlantic salmon *Salmo salar* L. 1758 in Lake Ontario, Canada is a prime example of a native extirpated species whose re-introduction may be impeded by the presence of multiple non-native competitors. Four non-native salmonid species have been introduced over the past century and are now found in the lake and its tributaries: brown trout

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Salmo trutta L. 1758, rainbow trout *Oncorhynchus mykiss* (Walbaum 1792), Chinook salmon *Oncorhynchus tshawytscha* (Walbaum 1792) and coho salmon *Oncorhynchus kisutch* (Walbaum 1792) (Jones & Stanfield, 1993; Crawford, 2001). Three candidate populations of *S. salar* are being considered for re-introduction comprising those of Lac Saint-Jean (Saint-Jean) from Quebec, Canada, Sebago Lake (Sebago) from Maine, U.S.A. and LaHave River (LaHave) from Nova Scotia, Canada. It has been recently shown that these populations have genetic differences in behaviours, including aggression (Van Zwol *et al.*, 2012), so it is conceivable that the populations may differ in their competitive abilities when exposed to multiple non-native salmonids. Such difference across populations could also add to the complexity of understanding species competitive interactions.

A series of artificial stream tanks were set-up (25 cm × 240 cm) at the Ontario Ministry of Natural Resources and Forestry (OMNRF) Codrington Research Facility, Codrington, Ontario, Canada, to examine non-additive effects of competition on *S. salar*. The tanks mimicked the natural stream environment by containing two types of microhabitats: a 160 cm riffle section (mean ± s.d.: high current 20 ± 6 cm s⁻¹, low depth 28 ± 3 cm) followed by a 80 cm pool section (low current 7 ± 3 cm s⁻¹, high depth 68 ± 3 cm). Juveniles of all salmonid species were provided by the OMNRF, with details on the broodstock and rearing described in the study of Houde *et al.* (2015). Saint-Jean juveniles were not available in the first year. Six treatments were used in each of the 2 years with each treatment containing 32 fish: *S. salar* alone (LaHave only, Sebago only, or Saint-Jean only); two species (16 *S. salar* with 16 of one non-native salmonid species); multispecies (16 *S. salar* with four of each non-native salmonid species). Each treatment was represented by two replicates. Initial body sizes and treatment means are presented in Tables SI and SII (Supporting Information). Juveniles were kept in the artificial stream tanks for 10 months (September to July) in each year. Examinations of the treatment effects for *S. salar* in the first year have been previously published by Houde *et al.* (2015). Here, the non-additive effects of multispecies competition are reported.

At 3 months (in December), all juveniles were removed from the artificial stream tanks, lightly anaesthetized with MS-222, measured for fork length (L_F) and mass (M) and then allowed to recover before being returned to the tank. Condition factor (K) was calculated as $K = 100 M L_F^{-3}$. The next day, for riffle use, a trained observer took counts of each salmonid species within the riffle section at 1200 hours. At 10 months (in July the following year), all juveniles were removed from the artificial stream tanks and counted to examine survival. Body size measurements were not examined at this time because differential mortality across treatments affected densities in the tanks, which confounded such analyses.

Observed and predicted multispecies competition effects were compared for the *S. salar* traits using the method described by Weigelt *et al.* (2007). First, observed effect estimates (E_O) for each *S. salar* replicate were extracted using linear models that contained a fixed effect for artificial stream tank identity and no intercept. Next, predicted effect estimates of multispecies competition (E_P) on *S. salar* were calculated based on a simple additive function of the observed estimates for two-species treatment replicates, weighted by the number of artificial stream tanks ($n = 8$):

$$E_P = n^{-1} \sum_{i=1}^n E_{O_i}, \quad (1)$$

where i denotes a replicate of a given two-species treatment. The deviations between predicted and observed multispecies effects for each trait were then tested for a significant difference from zero across all populations and years combined using one-sample t -tests. A non-significant difference would indicate that the multispecies competition effects on a particular trait was additive. Next, to examine the deviations within populations and years, 95% C.L. were generated for each deviation using a re-sampling routine as described in Supporting Information. A re-sampling routine was used in these latter analyses because it provides more robust estimates of the C.L. than parametric approaches due to the low number of replicates that were available at the individual population and year level. Also, to compare across traits and populations, Hedge's g effect sizes and 95% C.L. were calculated (Hedges & Olkin, 1985) for each trait and each population relative to global deviation using all of the observed deviations.

Across all populations, significant deviations between observed and predicted multispecies effects were detected for *S. salar* L_F and M , but not for survival, K or riffle use (Table I). The global deviation using all of the observed data was -0.181 (95% C.L.: -0.247 , -0.115). The deviations of L_F and M were significantly more negative than expected and had negative Hedge's g effect sizes, indicating that the *S. salar* juveniles had worse performance (*i.e.* lower L_F and M) than predicted by the additive model. Examining individual populations and years, most traits did not differ in the magnitude of the deviation with the exception of riffle use in year 2 (Table I). Specifically, Sebago juveniles had the largest deviations followed by Saint-Jean juveniles and LaHave juveniles. Sebago juveniles also had larger deviations for survival than both LaHave and Saint-Jean juveniles in year 2, but the opposite occurred in year 1 with Sebago juveniles having the smallest deviations (Table I). Comparing the three populations using all of the observed deviations, Sebago had a negative effect size of -0.254 (95% C.L.: -0.285 , -0.223), whereas LaHave and Saint-Jean had positive effect sizes of 0.265 (0.234 , 0.286) and 0.074 (4.00×10^{-5} , 0.148), respectively.

The analysis suggests that native species may have lower performance in sympatry with multiple, non-native species than predicted by two-species competition models. Across three populations of *S. salar*, negative deviations for L_F and M were found, indicating reduced performance for these two traits in the multispecies treatment than was predicted based on an additive model of two-species treatment effects. Other studies have similarly found non-additive effects of multispecies competition with native species underperforming in fitness-related traits (Wootton, 1993). Interestingly, there were few differences in these deviations across the three *S. salar* populations within traits. The result was unexpected as the populations differ in behavioural aspects, such as aggression, that could influence competitiveness (Van Zwol *et al.*, 2012). Nevertheless, the data suggest that re-introduction efforts of *S. salar* in Lake Ontario, regardless of the source population, should avoid streams containing large numbers of non-native salmonids.

Non-additive effects of competition may result from varying degrees of niche overlap among species (Stone & Roberts, 1991; Huisman & Weissing, 1999, 2001, 2002). It is well known that *S. salar* have high niche overlap with *S. trutta* and *O. mykiss* for riffle microhabitat (*i.e.* shallow, fast-moving water with a gravel substratum; Hearn & Kynard, 1986; Vehanen, 2006). Conversely, *S. salar* typically has little stream niche overlap with *O. tshawytscha* and *O. kisutch*, which instead prefer pool microhabitat (Heland & Beall, 1997; Holecek *et al.*, 2009). Given that *S. trutta* and *O. mykiss* are typically more aggressive than *S. salar* (Hearn & Kynard, 1986; Vehanen, 2006), these

TABLE I. Summary of the deviations between predicted and observed multispecies effects for three populations of *Salmo salar*. Streams 1 and 2 are the artificial stream tank identities representing replicates for the multispecies treatment. Significance using all the deviations for a trait was determined by a one-tailed *t*-test of the deviations. Confidence limits (95% C.L.) for the populations were created using re-sampling procedures. Hedge's *g* effect sizes (and 95% C.L.) for the traits were calculated relative to the global deviation using all of the observed deviations

Trait	Stream 1	Stream 2	95% C.L.	Pair-wise <i>P</i> -value
Survival				
Year 1				
LaHave	0.086	-0.226	-0.453, 0.469	LA-SE <0.001
Sebago	-0.570	-0.218	-0.742, -0.430	
Year 2				
LaHave	0.031	-0.156	-0.359, 0.188	LA-SE <0.001
Sebago	0.172	0.172	0.219, 0.328	LA-SJ >0.05
Saint-Jean	-0.273	0.039	-0.469, 0.164	SE-SJ <0.001
<i>t</i> -test <i>P</i> -value		>0.05		
Hedge's <i>g</i>	0.156	(0.082, 0.230)		
L_F (cm)				
Year 1				
LaHave	-0.221	-0.157	-0.566, 0.180	LA-SE >0.05
Sebago	-0.218	-0.474	-0.797, 0.093	
Year 2				
LaHave	-0.252	-0.271	-0.793, 0.300	LA-SE >0.05
Sebago	-0.300	-0.277	-0.765, 0.191	LA-SJ >0.05
Saint-Jean	-0.317	-0.148	-0.889, 0.330	SE-SJ >0.05
<i>t</i> -test <i>P</i> -value		<0.001		
Hedge's <i>g</i>	-0.376	(-0.450, -0.301)		
M (g)				
Year 1				
LaHave	0.001	-0.003	-0.043, 0.041	LA-SE >0.05
Sebago	-0.037	-0.045	-0.078, -0.003	
Year 2				
LaHave	-0.324	-0.365	-1.394, 0.870	LA-SE >0.05
Sebago	-0.717	-0.697	-1.776, 0.471	LA-SJ >0.05
Saint-Jean	-0.482	-0.480	-1.772, 1.003	SE-SJ >0.05
<i>t</i> -test <i>P</i> -value		<0.001		
Hedge's <i>g</i>	-1.230	(-1.312, -1.148)		
K ($100 \times \text{g cm}^{-1}$)				
Year 1				
LaHave	-0.285	-0.223	-0.809, 0.295	LA-SE >0.05
Sebago	-0.354	-0.691	-1.117, 0.131	
Year 2				
LaHave	-0.008	0.027	-0.038, 0.062	LA-SE >0.05
Sebago	0.003	0.009	-0.028, 0.048	LA-SJ >0.05
Saint-Jean	-0.012	-0.011	-0.043, 0.020	SE-SJ >0.05
<i>t</i> -test <i>P</i> -value		>0.05		
Hedge's <i>g</i>	0.800	(0.723, 0.878)		

TABLE I. Continued

Trait	Stream 1	Stream 2	95% C.L.	Pair-wise <i>P</i> -value
Riffle use				
Year 1				
LaHave	-0.078	-0.078	-0.109, -0.031	LA-SE >0.05
Sebago	0.008	-0.055	-0.094, 0.133	
Year 2				
LaHave	0.070	-0.055	-0.023, 0.250	LA-SE <0.001
Sebago	-0.047	-0.109	-0.125, -0.039	LA-SJ <0.05
Saint-Jean	-0.039	0.086	-0.063, -0.008	SE-SJ <0.05
<i>t</i> -test <i>P</i> -value		>0.05		
Hedge's <i>g</i>	0.694	(0.617, 0.770)		

L_F , fork length; M , mass; K , condition factor; LA, LaHave; SE, Sebago; SJ, Saint-Jean (pair-wise population comparisons).

species may displace *S. salar* from riffle to pool microhabitat (Hearn & Kynard, 1986). In the multispecies treatment, those displaced *S. salar* would encounter competition with *O. tshawytscha* and *O. kisutch*, which might contribute to the non-additive effects that were observed. Indeed, theoretical models suggest that species with niche overlap can co-exist until the number of species matches the number of limiting resources (Huisman & Weissing, 1999, 2001). This threshold tends to be lower in lower diversity habitats because of a reduced capacity for niche separation (Young, 2001). The riffle and pool microhabitats commonly occupied by juvenile salmonids, and simulated in this study, are a relatively simple habitat and might limit the potential for niche separation and thereby contribute to the observed non-additive effects.

In conclusion, non-additive competitive interactions were detected in multispecies assemblages of salmonids, which reduced the performance of *S. salar* juveniles from three source populations. These non-additive effects may be caused by high niche overlap with *S. trutta* and *O. mykiss*, as well as by an increase in the number of potentially competing species in relatively simple stream habitats.

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Supporting Information

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

Table SI. Summary of the initial body sizes of fry (age 0+ parr) for three populations of *Salmo salar* and four non-native salmonid species (*Salmo trutta*, *Oncorhynchus mykiss*, *Oncorhynchus tshawytscha* and *Oncorhynchus kisutch*).

Table SII. Summary of survival and fitness-related traits for three populations of *Salmo salar* and four non-native salmonid species (*Salmo trutta*, *Oncorhynchus mykiss*, *Oncorhynchus tshawytscha* and *Oncorhynchus kisutch*).

Appendix SI. Method for producing 95% C.I. for the deviations and comparing *Salmo salar* populations.

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