Letter

Effects of exotic salmonids on juvenile Atlantic salmon behaviour


Abstract – We examined the effects of two salmonid species, chinook salmon (Oncorhynchus tschawytscha) and brown trout (Salmo trutta), both exotic species to Lake Ontario, on behaviour and foraging success of juvenile Atlantic salmon (S. salar), a native species to Lake Ontario, in an artificial stream. We found that both exotic species have effects on Atlantic salmon behaviour, but that neither had an effect on foraging success. These results may explain why the Atlantic salmon re-introduction programme in Lake Ontario has had little success, as more than 3 million exotic salmonids are released in Lake Ontario streams annually.

Introduction

Atlantic salmon (Salmo salar) was an abundant native species in Lake Ontario, but was extirpated by 1896 likely by a combination of overfishing, habitat destruction and erection of barriers to spawning migration (Netboy 1968; MacCrimmon 1977; Dunfield 1985; Parrish et al. 1998). Sporadic attempts between the 1880s and 1980s to re-introduce the species did not produce a self-sustaining population. Successful re-introduction of a species to parts of its former range is dependent upon a variety of factors, such as the number and frequency of releases, removal of the causes of species loss and presence of ecologically similar exotic species (Griffith et al. 1989; Kleiman 1989; Fischer & Lindenmayer 2000). Previous efforts to re-establish Atlantic salmon in Lake Ontario were unsuccessful likely because the riverine habitat had not been restored (introduced populations failed to reproduce successfully; Emery 1985).

Management agencies in Canada and USA have been stocking non-native salmonids in Lake Ontario annually since the 1960s, to enhance recreational angling (Crawford 2001). Several of the exotics, including rainbow trout (Oncorhynchus mykiss), chinook salmon (O. tshawytscha), coho salmon (O. kisutch) & brown trout (S. trutta), have established spawning populations in Lake Ontario tributaries (Stewart et al. 1999; Hickey 2002; Stewart & Shaner 2002). Establishment of spawning populations of these exotics suggests that habitat in Lake Ontario and its tributaries is again appropriate for Atlantic salmon because of their similar habitat requirements (Glova & Field-Dodgson 1995; Fausch 1998; Harwood et al. 2002; Armstrong et al. 2003). Nonetheless, recent efforts to re-introduce Atlantic salmon to Lake Ontario have yet to produce a self-sustaining population (Stewart & Shaner 2002).

Establishment of the exotic salmonids, while suggestive of suitable habitat, may pose an ecological barrier to the re-introduction of Atlantic salmon because there is substantial overlap in resource use among species (Glova & Field-Dodgson 1995; Fausch 1998; Harwood et al. 2002; Armstrong et al. 2003).
Exotic salmonids have been shown to limit the success of native salmonid recovery programmes elsewhere. For example, Harig et al. (2000) found that re-introduction of cutthroat trout (O. clarkii) to streams in eastern Colorado, USA, was most successful when exotic salmonids (rainbow trout and brook charr, Salvelinus fontinalis) were prevented access to the stream. In the Salmon River basin (Idaho, USA) brook charr (an exotic) appear to cause a reduction in the survival rate of native chinook salmon (Levin et al. 2002).

We examined the hypothesis that the ecologically similar exotic salmonids contribute to the lack of success in re-introducing Atlantic salmon to Lake Ontario. Previously, Scott et al. (2003) demonstrated that adult chinook salmon (O. tshawytscha) have negative effects on adult Atlantic salmon during spawning, causing increased levels of agonistic behaviour, delayed spawning and reduced postspawning survival. However, mathematical modelling suggests that this influence by itself is not likely to inhibit establishment of a self-sustaining population (Wilson 2003; R.J. Scott, unpublished data). Both models suggest that the most sensitive period of Atlantic salmon life-cycle to mortality is the early life stages, including the period of juvenile in-stream foraging. Jones & Stanfield (1993) found that removal of all exotic salmonids from several experimental enclosures resulted in increased juvenile Atlantic salmon growth and survival. Whereas the mechanism of this effect is reasonably well known for rainbow trout (competition for foraging sites; Volpe et al. 2001) it is unknown for the other exotic salmonids present in Lake Ontario tributaries.

We examined the mechanisms of effect between juvenile Atlantic salmon and other salmonids. Specifically, we predicted that the exotic salmonids would have negative effects on social interactions and foraging success by juvenile Atlantic salmon. We tested these predictions in competition trials involving Atlantic salmon, chinook salmon and brown trout in an artificial stream.

**Methods**

**Species**

We examined the effects of chinook salmon and brown trout on Atlantic salmon. We chose these particular species for several reasons. First, chinook salmon is the most abundantly stocked exotic salmonid in Lake Ontario (Crawford 2001). Although juveniles of this species migrate from riverine to lacustrine habitat earlier than those of other exotic salmonids (some of which do not migrate at all), there is ample temporal and spatial overlap during which they may interact with juvenile Atlantic salmon. Additionally, we could find no published research on interactions between Atlantic and chinook salmon juveniles. Secondly, brown trout and Atlantic salmon have a long history of sympatry in Europe and there is a substantial body of published research examining interactions between them there (e.g., Harwood et al. 2001, 2002; Armstrong et al. 2003). However, brown trout and Atlantic salmon did not overlap historically in North America. Consequently, Atlantic salmon niche breadth may be broader in North America than in Europe (because of competitive release) and therefore the potential for interaction with brown trout may be greater. We did not include coho salmon in our study because coho salmon stocking in Lake Ontario has declined substantially during the past decade (Crawford 2001). We did not include rainbow trout because there are numerous studies of Atlantic salmon–rainbow trout interactions (e.g., Hearn & Kynard 1986; Jones & Stanfield 1993; Volpe et al. 2001).

All fish used in this study were raised in Ontario Ministry of Natural Resources Fish Culture Stations for their salmonid stocking programmes. The fish that we observed were representative (e.g., culture history, age, size) of those stocked in the streams during the spring and summer in Ontario, Canada (see Table 1). Competitive outcome in salmonids is often size dependent and most studies attempt to control for this effect by using similar-sized fish. However, Atlantic salmon juveniles released into Lake Ontario tributaries are smaller than the chinook salmon and brown trout juveniles released into the same tributaries. We felt that we could better represent the present situation by using juveniles that were representative of those released in the stocking programme.

**Experimental procedure**

We obtained all fish in the early spring and held in 800 l flow-through tanks at 11 °C and 12:12 h light:dark cycle and fed them *ad lib* (Transition Diet; Martin Mills Inc., Elmira, ON, Canada). We set aside a random set of fish each day and deprived them of food for 24 h to ensure feeding motivation (Cutts et al. 2002). These fish were transferred to an artificial stream. In the Salmon River basin (Idaho, USA) brook charr (an exotic) appear to cause a reduction in the survival rate of native chinook salmon (Levin et al. 2002).

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<table>
<thead>
<tr>
<th>Treatment</th>
<th>Atlantic salmon</th>
<th>Chinook salmon</th>
<th>Brown trout</th>
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<tbody>
<tr>
<td>4 ATS</td>
<td>44.46 ± 7.17</td>
<td></td>
<td></td>
</tr>
<tr>
<td>8 ATS</td>
<td>46.07 ± 8.03</td>
<td></td>
<td></td>
</tr>
<tr>
<td>4 ATS + 4 CHI</td>
<td>46.40 ± 6.74</td>
<td>54.14 ± 9.03</td>
<td></td>
</tr>
<tr>
<td>4 ATS + 4 BRT</td>
<td>44.04 ± 6.26</td>
<td></td>
<td>63.49 ± 5.81</td>
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</tbody>
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Table 1. Size of fish (fork length, mm) used in each of the experimental treatments. Values are mean ± standard deviation. Sample size for each was 40 except in the eight Atlantic salmon (ATS) treatment, which had a sample size of 80.

...
**O. tschawytscha** and *S. trutta*, on juvenile Atlantic salmon behaviour

![Fig. 1. Overhead view of the artificial stream used in the competition experiment (modified from Grand 1997). The stream measured 0.5 m wide × 1.9 m long by 0.5 m high and was constructed of clear glass to allow behavioural observations. The bottom of the stream was covered with natural stream substrate (gravel and cobble). The stream was filled with freshwater (11 °C) to depth of 30 cm and a centrifugal pump created a current of 20 cm s⁻¹ (average current of juvenile Atlantics salmon territories in a wild population; Keeley & Grant 1995). Arrows indicate the direction of water flow and dashed lines the location of 4-mm mesh barriers. The outside walls of the artificial stream were transparent whereas the central divider was opaque. The solid black lines show the location of the centrifugal pump and water outflow and the black dots at the upstream end of each section indicate the location of the feeding tubes.](image)

stream (Fig. 1) 30 min prior to each trial. We placed 50 natural food items (larval Trichoptera and Ephemeroptera collected from a local river) in a 4 l container filled with freshwater. The container was elevated 30 cm above the water surface and a siphon (Tygon tubing) drained all the water from the pail to the stream over 20 min. A stir-plate kept the food items suspended so that individual food items were introduced into the stream through the siphon in a random manner.

We made continuous recordings of conspecific and heterospecific agonistic interactions (charge, chase, bite, frontal display and lateral display). At the end of each trial, we removed all fish from the artificial stream, killed them with an over-dose of anaesthetic (40–60 ppm clove oil) and preserved them in 10% formalin. Later, we measured each fish (fork length), removed its gut contents and dried them to a constant mass at 55 °C.

**Experimental design**

The total bottom area of our stream tank available for use by the fish was 0.95 m² so there was enough room for three to four feeding territories (Keeley & Grant 1995) for 45.4 mm fork length Atlantic salmon. Therefore, we used four Atlantic salmon in our baseline treatment. In each additional treatment we added four more Atlantic salmon (density control), chinook salmon or brown trout for a total of four treatments, (i) four Atlantic salmon, (ii) eight Atlantic salmon, (iii) four Atlantic salmon plus four chinook salmon and (iv) four Atlantic salmon plus four brown trout. We replicated each of the four treatments 10 times.

**Data analysis**

We used one-way ANOVA (Sokal & Rohlf 1995) to test for effects of our treatments on total rate (number per 20 min) of interactions involving Atlantic salmon (i.e., interactions involving two Atlantic salmon plus those involving one Atlantic salmon and one member of the other species present). One-way ANOVA was also used to test for effects of our treatments on interactions (number per 20 min) involving pairs of Atlantic salmon. We used MANOVA followed by univariate analyses to test for effects of other species present on different aspects of Atlantic salmon interactions (Quinn & Keough 2002). Specifically, we tested whether the overall effect on Atlantic salmon interaction rate was the result of increased interactions among Atlantic salmon or if it was a result of interactions with the heterospecific individuals and finally, whether it was a result of Atlantic salmon initiated or other species initiated interactions. Probability of type I error was adjusted to account for multiple tests (Quinn & Keough 2002).

We randomly selected Atlantic salmon for our trials and in doing so we introduced size variation that could influence foraging success. For example, larger juvenile salmonids are typically better at monopolizing resources (such as food and space) than smaller individuals (O’Conner et al. 2000). We used ANCOVA to examine the effects of treatment and Atlantic salmon size (fork length; covariate) on dry gut content mass (Rawlings 1988) simultaneously. Fork length and dry gut mass were both log-transformed to linearize the relationship between the variables prior to analysis.

**Results**

**Behaviour**

There was a significant effect of the treatments on the total rate of agonistic interaction involving Atlantic salmon (Fig. 2, top panel; \(F_{3,36} = 13.72, \ P = 0.001\)) and this appears to be the effect of interactions with the other species present as there was no effect of the treatments on interaction rate between Atlantic salmon (Fig. 2, bottom panel; \(F_{3,36} = 0.565, \ P = 0.642\).

MANOVA suggests that the group centroids are different among the treatments (Fig. 2, bottom panel; Wilk’s \(\lambda_{3,16} = 0.495; \ P = 0.009\)) and subsequent univariate tests of differences among treatments in the direction of interaction suggests that Atlantic salmon directed equal amounts of agonistic behaviour toward chinook and brown trout (\(F_{1,18} = 0.679; \ P_{\text{adjusted}} = 0.841\),...
but receive far more agonistic interactions from chinook salmon than from brown trout ($F_{1,18} = 16.007; P_{\text{adjusted}} = 0.0016$).

Foraging success
Mass of dried gut contents increased with Atlantic salmon fork length in the same way among the four treatments (Fig. 3; $F_{3,158} = 0.205, P = 0.893$). However, although there was an effect of fish size on gut contents (Fig. 3; $F_{1,161} = 5.179, P = 0.024$), there was no effect of the treatments (Fig. 3; $F_{3,161} = 1.223, P = 0.303$).

Discussion
The results of our study clearly demonstrate that both brown trout and chinook salmon have an effect on the behaviour of Atlantic salmon in an artificial stream. More importantly, this study demonstrates the mechanisms of those effects; brown trout and chinook salmon influence juvenile Atlantic salmon agonistic behaviour but neither appears to have an effect on foraging success under laboratory stream conditions. Atlantic salmon agonistic behaviour and foraging success typically reflect an optimal trade-off between the site-specific costs and benefits of holding a feeding territory such that net energy gain is maximized (Keeley & Grant 1995, 1997). Therefore, changes in agonistic behaviour without a subsequent change in foraging success could reduce an individual’s net energy gain and long-term growth if those effects occur frequently and persistently in nature. For example, both species in our study caused a dramatic increase in agonistic behaviour (and thus elevated activity) by juvenile Atlantic salmon but had no effect on their foraging success. Therefore, both exotic species could cause increase in energy expenditure in the wild and subsequently reduce early growth in juvenile Atlantic salmon. Early growth is critical to survival and reproduction for salmon (Metcalfe & Monaghan 2001). Smaller juvenile Atlantic salmon have lower overwinter survival than larger ones (Jensen & Johnsen 1984) and they tend to grow more slowly (Huntingford & de Leaniz 1997; Cutts et al. 1998; O’Connor et al. 2000). As chinook salmon emigrate from riverine habitat during their first summer, there is an opportunity for Atlantic salmon to recover growth after the chinook salmon leave but prior to their first winter. For example, Morgan & Metcalfe (2001) showed that although fish deprived of food early grew slower than fed fish, they did catch up
in size once they were allowed to feed again. Despite this, the nonfed fish were still smaller than their fed counterparts following the winter. So, the effect of slow growth early is likely to persist beyond the initial year (Metcalfe & Monaghan 2001). Additionally, slow growing juveniles smolt at a smaller size and mature older at a larger size than fast growing juveniles (Hutchings & Jones 1998; Jonsson et al. 2001). Although maturing at a large size may seem to be beneficial as larger fish tend to produce more and larger gametes, in the case of Atlantic salmon in Lake Ontario it may be a detriment because larger Atlantic salmon spawn earliest in a spawning season. Spawning earlier would increase the temporal overlap of spawning Atlantic salmon with spawning chinook salmon (see Scott et al. 2003) and thus increase the period of net energy loss for Atlantic salmon.

Exotic species have affected re-introduction of a number of species across a broad range of taxa, including many salmonid populations (e.g., Harig et al. 2000; Levin et al. 2002). Understanding the mechanisms that are responsible for the effect of exotics on native species is critical to making decisions regarding re-introduction efforts (Caughley & Gunn 1996). Our results clearly show that the effects of interspecific interactions in these juvenile salmonids can be significant. Our results suggest that attempts to re-introduce Atlantic salmon to Lake Ontario streams may be difficult if brown trout or chinook salmon are present in those streams.

Furthermore, our results emphasize the potential devastating effect that exotic Pacific salmonids may have on declining and imperiled native populations of Atlantic salmon on the Atlantic coast of North America. There exists no physical barrier to range expansion by these exotics from the Great Lakes to the Atlantic coastal region (Hickey 2002). On the contrary, the design of our experiment does not allow inferences regarding the effect of Atlantic salmon on the exotics that we studied. Therefore, using our results to predict the effect or success of Atlantic salmon that are invading the west coast of North America would not be prudent. Finally, we have shown clear effects of two exotic species in Lake Ontario on Atlantic salmon in an artificial stream and discussed their relevance to natural streams. However, it is clear that our conclusions must be validated in a natural setting.

**Resumen**

1. Examinamos el impacto de dos salmónidos exóticos, *Onchorhyncus tshawytscha* y *Salmo trutta* introducidos en el Lago Ontario, sobre la comportamiento y éxito alimenticio de individuos juveniles del salmón del Atlántico (*Salmo salar*), especie autóctona del lago Ontario, en un río artificial.

2. Encontramos que ambas especies introducidas producen impactos sobre *S. salar*, sin embargo los mecanismos son diferentes. La ocurrencia de *O. tshawytscha* causó un aumento dramático en el comportamiento agonístico, mientras que *S. trutta* ocasionó una disminución marcada en el éxito alimenticio del salmón del Atlántico.

3. Estos resultados pueden explicar por qué el programa de reintroducción del salmón del Atlántico en el lago Ontario ha tenido poco éxito con más de tres millones de salmones exóticos que son liberados, anualmente, en los ríos del Lago Ontario.

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**References**


