Differences in antipredator behaviour between wild and hatchery-reared juvenile Atlantic

salmon

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Abstract

Differences in antipredator behaviour between wild and hatchery-reared juvenile Atlantic salmon

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Captive rearing may elicit environmental or genetically-based changes to salmonid antipredator behaviour, which may reduce its survival when released into the wild. While this subject has received considerable attention, there has been little research using fish reared for a short period of time (2 generations or less of captive breeding). In addition, few studies have tested wild-caught and hatchery-reared fish originating from the same population and none have done so under natural conditions. Hence, I conducted a semi-natural field study comparing the antipredator behaviour of wild-caught, F1 (offspring of wild-caught adults) with that of F2 (second generation) hatchery-reared juvenile Atlantic salmon (from the same source population) to standardized predation cues. Wild-caught salmon exhibited strong antipredator responses to the predation threat, while F1 and F2 salmon showed weaker responses. Interestingly, F1 salmon showed stronger responses than F2 salmon. The observation that wild-caught and F2 salmon were consistently different supports the hypothesis that even one full generation of hatchery rearing may be sufficient to select for maladaptive responses to predators under natural conditions. The observation that F1 salmon were intermediate to wild-caught and F2 salmon suggests that individual experience may also play a significant role on the

observed reduced antipredator response. Given the current decline of many salmonid populations across North America and the controversy regarding the effectiveness of hatchery programs for conservation use, the results of this study suggest that minimizing hatchery time may reduce the behavioural differences between wild and hatchery-reared fishes.

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General Introduction

Predation is a major evolutionary selection pressure, shaping the use of habitat, foraging habitats, territorial defence and reproduction strategies of potential prey individuals (Lima & Dill 1990). Predation can also have a profound affect on a prey individual's morphology and life history strategy (Lima & Dill 1990; Chivers et al. 2001a). In response to predation, prey individuals have evolved a large number of morphological and physiological antipredator adaptations, such as, cryptic and aposematic colouration (Blest 1957; Edmunds 1974; Jarvi et al. 1981), chemical defences (Kubanek et al. 2002) and chemical alarm signals (Pfeiffer 1974; Blum 1985; Smith 1992; Hardie et al. 1999). Prey can reduce the chance of being preyed upon by trying to avoid being detected by predators through predator avoidance strategies (via shifts in habitat use, activity time, or reduced movement), or by trying to escape a predator during an encounter (Sih 1985). Individuals that are unable to respond to a predation threat will become a meal for a predator, resulting in a total loss of fitness.

Avoiding predators, however, comes at a cost. Often prey individuals are forced to trade-off time and energy available for foraging, reproduction and territorial defence with predator avoidance behaviour (Sih 1980; Lima et al. 1985; Gilliam & Fraser 1987). In almost all cases, local predation risk is temporally and spatially variable and the prey, therefore, may adjust the form and intensity of their antipredator behaviour in order to increase their overall fitness (Lima & Dill 1990). For example, predation risk may change at night compared to during the day or may fluctuate depending on the location (Dorner et al. 1999). Prey individuals are able to display a threat-sensitive antipredator response, in which prey individuals balance predator avoidance with other activities by adjusting

the magnitude of their antipredator response to reflect the magnitude of the perceived predation threat (Helfman 1989). In other words, individuals can modify the intensity of their antipredator behaviour in response to varying degrees of predation risk. By showing a threat-sensitive antipredator response, prey may be able to optimize the trade-off between antipredator response and other activities (Helfman 1989; Helfman & Winkleman 1997). Numerous studies have supported the threat-sensitive hypothesis over a wide variety of taxa, including terrestrial invertebrates (Persons & Rypstra 2001), aquatic invertebrates (Rochette et al. 1997), amphibians (Rohr & Madison 2001), reptiles (Amo et al. 2004), birds (Lima 1992a, 1992b), mammals (Swaisgood et al. 1999; Wirsing et al. 2007) and fishes (Winkelman 1996; Chivers et al. 2001b; Brown et al. 2006a). There are, however, conditions in which individuals shift this threat-sensitive antipredator response towards a more hazard-prone or hazard-averse behaviour. Hazard-prone individuals display reduced antipredator responses when exposed to predation risk compared to hazard-averse individuals, who show an increased antipredator response (Lemke and Ryer 2006). For example, increased hunger level has been shown to shift behavioural tactics towards a more hazard-prone response under increased predation threat (Aubret et al. 2007).

In order for prey individuals to display threat-sensitive predator avoidance behaviour, prey must first be able to accurately access local predation risk (Brown et al. 2006b). To detect the threat of predation, prey individuals may use numerous sensory modalities, including visual, olfactory, auditory, tactical and electrical (Smith 1992). An alarm signal (chemical, visual or auditory) may be emitted by an individual as a response to detecting danger, allowing nearby individuals to become aware of the danger present,

independent of any benefits to the sender (Smith 1992). Numerous studies have

demonstrated that individuals release an alarm signal when faced with a predator (see

Brown et al. 1999; Fichtel et al. 2005; Magrath et al. 2007; Bura et al. 2009; reviewed in

Hollen and Radford 2009). For example, the Richardson's ground squirrel

(*Spermophilus richardsonii*) produce both audible and ultrasonic alarm calls that warn

conspecifics of danger and as a result, nearby individuals respond with increased

vigilance (Wilson and Hare 2006).

Within aquatic environments, prey individuals rely heavily on the use of chemical

alarm cues to assess local predation risk (Chivers and Smith 1998), due to the way in

which the cues are dispersed and transmitted in the water column (reviewed in Wisenden

2000). These chemical alarm cues have been extensively studied in multiple taxa,

including platyhelminthes (Wisenden and Millard 2001), arthropods (Wisenden et al.

2001; Laforsch et al. 2006), amphibians (Marvin and Hutchison 1995; Gonzalo et al.

2010) and fishes (Brown and Godin 1997; Larson and McCormick 2005). For instance,

when exposed to conspecific chemical alarm cue, aquatic larval caddisfly

(*Hesperophylax occidentalis*) displays an antipredator response by significantly reducing

movement (Gall and Brodie 2009).

Given the importance of antipredator behaviour, it is of concern that many

captive-bred animals either show a reduced antipredator response or no response at all

when exposed to a predator (Sutherland 1998; Caro 1999). This is partly because of

domestication, which may produce hazard-prone individuals due to intentional selection

for fast growth and, in turn, increased aggressiveness (Einum and Fleming 1997; Ferno

and Jarvi 1998). It may also be because captive-bred individuals lack predator

experience and therefore, do not respond to predation risk (Olla et al. 1998). Multiple

studies have demonstrated that captive-bred individuals have low survival rates when

released into the wild (reviewed in Fischer and Lindenmayer 2000), partly due to the fact

that they have never been previously exposed to a predator (Synder et al. 1996). Captive-

reared fishes (Berejikian 1995), amphibians (Kraaijeveld-Smit et al. 2006), birds

(Hakansson and Jensen 2008) and mammals (Zidon et al. 2009) have all been shown to

exhibit an antipredator response deficiency. For example, when captive-bred field mice

*Peromyscus polionotus subgriseu*s were exposed to a simulated model predator, they

were less likely to seek refuge than their wild counterparts (McPhee 2003). This reduced

antipredator response may result from the inadvertent selection of traits that are

unfavourable in the wild but beneficial in captivity and/or that captivity does not allow

individuals to acquire essential learned behaviours (experience), such as predator

recognition and avoidance (Seddon et al. 2007). Furthermore, recent studies have shown

that captive-bred individuals may be taught to avoid predators before being released into

the wild with mixed success (reviewed in Brown and Laland 2001).

The goal of this thesis is to compare the antipredator behaviour to chemical alarm

cues in wild-caught, first and second generation hatchery-reared juvenile Atlantic salmon

(*Salmo salar)* under semi-natural conditions. While many studies have looked at the

differences in antipredator response between hatchery-reared and wild fishes, only three

laboratory studies, one looking at behavioural responses (Alvarez and Nicieza 2003), one

looking at physiological responses (Hawkins et al. 2004) and the other testing survival

directly (Fritts et al. 2007) compared the antipredator response between first and/or

second generation hatchery-reared and wild fry. Only two (Hawkins et al. 2004 and

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Fritts et al. 2007) used fish from the same donor stock thereby eliminating the effect of population differences. In the first study, Alvarez and Niceiza (2003) found that F2 hatchery-reared juvenile Brown trout spent less time in refuges when exposed to predation risk compared to their wild counterparts. In the second study, Hawkins et al. (2004) found that there was a significant delay in the time between peak ventilatory response and onset in the decline phase in first generation hatchery-reared Atlantic salmon fry compared to wild fry, suggesting that the hatchery fry were slower to react to the potential predator. In the third study, Fritts et al. (2007) found that second generation hatchery-reared Chinook salmon fry had a 2.2% survival disadvantage compared to first generation fry during live predator encounters, which would likely, however, have little impact on population stability. Nonetheless, no studies have recorded detailed behavioural responses to predation risk using chemical alarm cues to examine the antipredator response between wild, first and second generation hatchery-reared Atlantic salmon fry. This study is unique in that by using wild, first and second generation hatchery-reared fry from the same donor population, it will allow us to differentiate between the effects of hatchery selection and prior experience on the observed antipredator response.

Introduction

Many of the world's fish species are threatened due to over-exploitation and habitat degradation from human activities (Brown and Day 2002). Large predatory marine fishes seem to be the most severely affected, with some populations declining as much as 99.9% from their historical size (Myers and Worm 2003; Hutchings and Reynolds 2004). In addition, many populations of Atlantic salmon (*Salmo salar)* in North America and Europe have been on the steady decline since the late 1970's (ICES 1997; Parrish et al. 1998). In Canada, there are multiple extirpated and declining Atlantic salmon populations, including the extirpated Lake Ontario population and the endangered Inner Bay of Fundy population, where it has been estimated to have declined by more than 95% in the last 30 years (see Parrish et al. 1998 for population details; COSEWIC 2009).

To mitigate the decline of fish stocks, hatchery programs have been implemented to supplement the fish present in the wild (Kostow 2009). However, there has been much criticism on the effectiveness of hatchery programs in increasing wild population stocks and much research has been devoted to this issue (Waples 1999; Fraser 2008; McClure et al. 2008). Hatchery-reared fishes, ranging from fry to the adult life stage, have been shown to have a reduced foraging efficiency (Bachman 1984; Reiriz et al. 1998), reduced swimming performance (Duthie 1997), reduced reproductive success (Fleming and Gross 1993; Berejikian and Tezak 2001), increased aggression (Mesa 1991; Deverill et al. 1999) and a reduced antipredator response when compared to their wild counterpart (Johnsson 1993; Alvarez and Nicieza 2003). These behavioural differences are thought to reduce survival and overall fitness of hatchery-reared fishes when released into the

wild (Fraser 2008). The differences in behaviour between hatchery-reared and wild

fishes are primarily due to the environmental conditions in the hatchery (experience) and

genetic divergence (hatchery selection) (Olla et al. 1998).

Prior experience has a large role in how an individual fish feeds and reacts to

predators and because of extreme differences in environmental conditions between

artificial rearing in a hatchery and in a wild environment, the fishes may be behaviourally

ill-equipped to forage and respond to predators in the wild (Brown and Day 2002). For

example, when hatchery-reared juvenile pink salmon (*Oncorhynchus gorbuscha)* were

first exposed to live prey items they displayed maladaptive behaviours such as an

antipredator response or no response at all (Godin 1978). The ability of fishes to

recognize and avoid predators consists of innate and learned aspects shaped by the

environment (Kelley and Magurran 2003). Since there is an absence of predators in a

hatchery setting, fishes do not have the prior experience needed to fully develop their

antipredator response. For example, when juvenile steelhead trout (*Oncorhynchus*

mykiss) were exposed to a live predator, the hatchery-reared predator naïve fry were

preyed upon the most (Berejikian 1995).

In addition, there is evidence that captive rearing has resulted in a genetic

divergence, both phenotypically and behaviourally between the hatchery strain and the

wild strain (Petersson et al. 1996; Huntingford 2004). The reason for this genetic change

is that natural selection pressures are altered or relaxed during the process of captive

rearing (Brown and Laland 2001). Removing the predation selection pressure for many

generations is more likely to result in a large-scale loss of antipredator response

compared with removal during an individual's lifetime (Brown and Laland 2001).

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Studies on guppies have shown that genetic responses to selection pressure removal can occur over a few (1-2) generations (Endler 1995; Reznick et al. 1997)

The ability of hatchery-reared fishes to show a similar antipredator response as its wild counterpart is critical for its survival in the wild. Despite much research into the effects of the hatchery environment on salmonid antipredator behaviour, many studies have compared multigenerational (greater than 3 generations) hatchery-reared salmonids with their wild counterparts of differing donor stocks (however, see Hawkins et al. 2004; Fritts et al. 2007). It is of critical importance to compare the effects of hatchery rearing between local wild and local hatchery populations, in order to control for genetic differences that may exist between non-local populations (Fraser 2008).

Aquatic organisms including prey fishes rely heavily on chemical alarm cues to detect the presence of and escape attack from predators (Chivers & Smith 1998; Wisenden 2000). Chemical alarm cues are substances released into the water column by injured prey fishes following mechanical damage to the epidermis, as would occur during a predation event (Smith 1992; Chivers & Smith 1998.). Following the release of chemical alarm cues, nearby conspecifics and certain sympatric heterospecifics show a dramatic, short-term increase in species typical antipredator behaviour, including increased area avoidance and shelter use, freezing, decreased activity levels, reduced foraging and mating, which all significantly increase the chance of survival during a predator encounter (Chivers & Smith 1998; Mirza & Chivers 2001a; Brown 2003). Furthermore, potential secondary predators are attracted to the emitted alarm cue odour and may attempt to hijack the initial predation event allowing the prey an opportunity for escape (Wisenden 2000). Chemical alarm cues have been demonstrated in several

salmonid species, including rainbow trout (*Oncorhynchus mykiss*; Mirza and Chivers 2001), brown trout (*Salmo trutta;* Mirza and Chivers 2001b), brook charr (*Salvelinus fontinalis;* Mirza and Chivers 2001b), chinook salmon (*Oncorhynchus tshawytscha*; Berejikian et al. 1999), Coho salmon (*Oncorhynchus kisutch*; Tierney et al. 2006) and Atlantic salmon (*Salmo salar*; Leduc et al. 2006).

In this study, I determined if there was a difference in antipredator response between wild-caught and hatchery-reared juvenile (0+) Atlantic salmon under semi-natural conditions. I compared four behaviours associated with an antipredator response in two populations of wild-caught and hatchery-reared fry bred for up to two generations in a hatchery. Conspecific chemical alarm cues were used to elicit an antipredator response. If prior experience is the sole factor affecting antipredator behaviour, then I predict that first and second generation hatchery fish should show a similar reduced intensity antipredator response compared to the wild salmon. On the other hand, if hatchery selection is the only mechanism influencing antipredator behaviour, then I predict that wild-caught and first generation hatchery-reared fish should display a similar antipredator response, with the second generation hatchery fish showing a reduced response. This prediction is based on the reasoning that the different selection pressures in the wild and in the hatchery between wild-caught and first generation hatchery fish have only operated for a short period of time, whereas in second generation hatchery fish there is a greater opportunity for differential selection to occur (Alvarez and Nicieza 2003). However, if hatchery selection and prior experience both have an effect on antipredator behaviour, then I predict that fry reared in the hatchery over two generations should show the most reduced antipredator response, followed by first generation

hatchery fry, and then the wild individuals. Also, I would expect no difference in overall

antipredator response intensity between individuals of equivalent rearing in the two

different populations (e.g. Population A wild-caught = Population B wild-caught). This

is the first study comparing the antipredator response to chemical alarm cues between

wild, first generation and second generation hatchery-reared Atlantic salmon fry of the

same donor stock under semi-natural conditions.

Material and Methods

Test Site

This experiment was conducted in the Little Southwest Miramichi River located in Northumberland County, New Brunswick, Canada (Figure 1) over two consecutive years between July 6 – August 9, 2009 and July 4 – 23, 2010. Two test sites were chosen approximately 100 metres downstream from the mouth of Catamaran Brook. The two test sites, each containing one plastic testing bin, were 25 metres apart and were chosen due to their similar physical characteristics (Table 1). A suite of physical variables were recorded throughout the testing period since several physical variables have been shown to influence and affect the behaviour and habitat choice of salmonids (Heggenes et al. 1999; Hedger at al. 2005). Before the start of the first trial, the pH and water temperature were recorded (using a portable Accumet pH meter and Hanna Waterproof pH tester, in 2009 and 2010, respectively), as well as water velocity (half-way between the substrate and surface using a Flo-Mate velocity meter), depth (using a 1 m measuring pole included with the Flo-Mate meter), air temperature, cloud and canopy cover. The pH, water velocity and depth were measured once a day, whereas the air temperature, water temperature, cloud and canopy cover were measured every fourth trial. The water velocity at each test site was measured inside each enclosure. Cloud cover was measured by estimating the amount of cover directly over the test site using an eight square grid with zero being no cover and eight being full cloud cover, which was later converted into percent coverage. Canopy cover was measured by estimating the amount of trees and branches directly over the test site using the same method as previously described.

Test Fish

All hatchery reared juvenile (young-of-year) Atlantic salmon were obtained from the Miramichi Salmon Association (MSA) hatchery located in South Esk, New Brunswick, approximately 45 kilometres from the testing location. The fish were transported in 100 litre metal containers containing either brook or well water. Upon arrival at the experimental site, the fish were placed in transparent 99 litre plastic holding bins (0.8 m x 0.46 m x 0.34 m) in Little Southwest Miramichi River to allow them to acclimatize to the more natural stream conditions. All hatchery fish spent a minimum of 24 hours in the holding bins and up to a maximum of three days before testing. The front and back of the holding bins were cut out and replaced with 3.175 mm wire mesh in order to allow for more natural flow conditions. Substrate, consisting of small to medium sized rocks, was added to the bottom of the bins to mimic the actual stream bed. To eliminate the chance of escape and predation, the holding bins were secured with a lid. In addition, the holding bins were tethered to a tree using rope to reduce the risk of being displaced by the current.

Two hatchery strains; first and second generation hatchery-reared salmon, originating from two different source populations Rocky Brook (RB) and Little Southwest Miramichi River (LSW) were used. For the purposes of this experiment, first generation (F1) hatchery-reared salmon was defined as the offspring of wild-caught parents used as broodstock, while second generation (F2) salmon were the progeny of parents (F1) who have spent their entire lives in captivity. First and second generation hatchery-reared salmon from Rocky Brook were classified as RB F1 and RB F2, respectfully, whereas first generation hatchery-reared Little Southwest Miramichi salmon

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was classified as LSW F1. Each fall wild adults are captured entering their native

spawning stream and are used as broodstock by the MSA hatchery (M. Hambrook,

Miramichi Salmon Association, South Esk, New Brunswick, personal communication,

2010). The adult broodstock collection from Rocky Brook included 5 females and 5

males, while the collection from Little Southwest Miramichi included 15 females and 15

males.

All wild juvenile (young-of-year) Atlantic salmon were captured with dipnets via

snorkelling. Wild-caught salmon originating from two different populations were used in

this experiment. Wild-caught fish from Little Southwest Miramichi River and Rocky

Brook were classified as LSW wild and RB wild, respectively. Rocky Brook is a

tributary of the Main Southwest Miramichi River (Riddell and Leggett 1981) and is

located approximately 50 kilometres from the testing location (Figure 2). LSW wild fish

were placed directly in a holding bin when caught, while RB wild fish were transported

as described above. All wild-caught fish spent a minimum of 24 hours in the holding

bins and up to a maximum of three days before testing. All hatchery-reared and wild-

caught salmon from both populations significantly differed in size (one-way ANOVA;

$F_{(4,227)} = 14.604$; $p < 0.001$; Table 2). However, even though there was a statistical

significance in length between strains and populations, there may not be any biological

significance because any potential predator would most likely be able to prey on the

salmon in both the lower (37 mm) and upper (43 mm) mean size range. It may be,

therefore, unlikely that the 6 mm mean size difference would have the potential to affect

the way in which the salmon respond to the alarm cue.

Stimulus preparation

Skin from juvenile Atlantic salmon was collected as the alarm cue stimulus on July 7th, 2009 and July 6th, 2010. All skin donors used were first generation hatchery-reared LSW salmon obtained from the MSA hatchery. Previous work in the LSW watershed demonstrates that there is no evidence to suggest population specific responses in Atlantic salmon to chemical alarm cues (Leduc et al. 2006). In 2009, parr (1+) fish were used, while in 2010, I used fry (0+) fish due to the fact that the MSA hatchery did not have any LSW parr (1+) fish available for sacrifice that year. Previous work on Atlantic salmon alarm cue has demonstrated that there is no evidence of age specific (0+ versus 1+) responses to alarm cue (Kim et al. 2009). Testing, therefore, parr (1+) alarm cue on salmon fry (0+) did not pose a problem. Immediately following their removal from the hatchery tanks, the fish were killed humanely with a single blow to the head (in accordance with Concordia Animal Care Committee Protocol AC-2008-BROW). In 2009, skin fillets were removed from both sides of the fish and directly placed in an ice-chilled beaker filled with untreated neutral well water. In 2010, due to the small size of the donor fish, the entire body (skin and skeletal tissue) excluding the head, tail, and internal visceral organs was used as the source of alarm cue and placed in an ice-chilled breaker filled with untreated neutral well water. Previous studies have shown that whole body homogenates are a reliable indicator of predation risk, can elicit an antipredator response, and therefore function as an alarm cue (Brown and Smith 1997; Brown and Godin 1999; Brown et al. 2009, Brown et al 2010). The skin fillets and body were homogenized, filtered through polyester filter floss and diluted with untreated well water resulting in alarm cue solutions of 0.1038 cm² · mL^{-1} for each year (see Table 3 for

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additional details on alarm cue preparation). Alarm cue solutions of 0.06 cm² · mL⁻¹ and

above have been shown to elicit a predictable antipredator response in salmonids (Leduc

et al. 2006; Kim et al. 2009; Ferrari et al. 2010; Leduc et al. 2010a). The solution was

frozen in 60 mL aliquots at -20 °C until needed. For this study, 2 320 mL of alarm cue

(240.82 cm² of skin) was used, while the rest was used for other studies. The frozen

solutions were thawed 1 hour prior to use. This preparation procedure has been shown to

elicit an antipredator response in cichlids (Roh et al. 2004), percids (Harvey and Brown

2004), cyprinids (Ferrari et al. 2006), centrachids (Marcus and Brown 2003) and

salmonids (Brown and Smith 1998; Kim et al. 2009).

Experimental protocol

Field observations were conducted between July 22 – August 9, 2009 and July

12 – 22, 2010. All fish were allowed to acclimatize in the holding bins for a minimum of

24 hours before being placed in a testing bin. Fish spent an average of 1.87 days in the

holding bins and a maximum of three days before being tested. Two testing bins,

identical to the holding bins, were used for this experiment. Once placed in a testing bin,

the fish were allowed to acclimatize for approximately 25 minutes prior to testing. I used

a short testing bin acclimatization period for two reasons; the first being that the testing

bins were identical to and in close proximity to the holding bins, therefore minimizing

stress. The second reason was due to time constraints as each fish was being tested

individually, therefore it would have been infeasible to wait extended periods of time

between each trial. Trials were conducted by a single observer (Chris Jackson)

snorkelling adjacent to the testing bin. Due to low water levels in 2010, 6 trials had to be

conducted by out of water observation. In these cases, the observer stood at an angle

behind the testing bin to ensure that no overhead shadow was created. Testing consisted of 20 minute trials divided into a 10 minute pre-stimulus and a 10 minute post-stimulus observation periods. The behavioural measures were recorded every minute for the duration of the trial. After the pre-stimulus observation period, the observer injected 20 mL of the stimulus (either alarm cue or stream water for the experimental or control treatments, respectively) using a 60 mL syringe. The stimulus was injected at mid-water depth and approximately 10 cm upstream of the wire mesh front opening in order not disturb the test fish. To ensure that the stimulus passed through the enclosures in a similar way, all injections were made into the current, which flowed directly through the front opening. After each individual trial, standard length was recorded and the fish was released approximately 50 metres downstream from the test site furthest downstream. The testing bins were removed at the end of the day and placed on shore.

Behavioural measures

To accurately assess the intensity of an antipredator response from direct exposure to a stimulus, four behaviour measures were recorded during each trial. Time spent moving (in seconds), time spent on substrate (in seconds) and the number of foraging attempts were recorded following exposure to both stimuli (stream water and alarm cue). Latency to resume foraging (in seconds) was recorded following exposure to the alarm cue stimulus only. These behavioural measures were chosen because they allow us to quantify the intensity of an antipredator response in juvenile Atlantic salmon (Leduc et al. 2007, Leduc et al. 2008, Kim et al. 2009) and may confer increased survival benefits to individuals displaying these antipredator response behaviours during live

predator encounters (Mathis and Smith 1993; Mirza and Chivers 2001; Mirza and Chivers 2003).

Time spent moving was measured when an individual changed its location by at least half a body length. Time spent on substrate was measured when an individual was resting motionless on the substrate bottom. A foraging attempt was defined as the movement of at least half a body length with a biting attempt toward a food item in the water column or on the substrate floor. Latency to resume foraging was defined as the time elapsed before an individual captured its first food item following exposure to an alarm cue stimulus (Gotceitas and Godin 1993).

Statistical analysis

Initially, I conducted a multivariate analysis of variance (MANOVA) for each population (RB and LSW) to assess the overall effects of treatment (alarm cue vs. stream water) and strain (W, F1, F2) on their antipredator response. I included time spent moving, time spent on the substrate and number of foraging attempts as the three behavioural measures. I calculated the change in each behavioural measure by subtracting the post stimulus value – the pre stimulus value and using these difference scores as dependant variables in all subsequent analyses. Strain and treatment were classified as the independent variables. Since the measured behavioural variables are likely high correlated, MANOVA's were used for most analyses (Quinn & Keough 2002). All data satisfied the assumption of normality.

Two subsequent MANOVA's, including the resulting one-way ANOVA's for the alarm cue analysis only, were conducted for each population to determine if the Atlantic salmon strains differed in their antipredator response as a result of treatment (stream

water compared to alarm cue). Strain was the independent variable, while the three behavioural measures were the dependent variables. Simple contrast comparisons were conducted in the RB population analysis to determine where the significant differences occurred, if any.

For latency to resume foraging, only the values for the alarm cue treatment were recorded in the field due to the fact that I was interested in comparing their response to alarm cue and not stream water. Separate one-way ANOVA's were performed for each population (LSW and RB) with latency to resume foraging as the dependent variable and strain as the independent variable. The analysis was performed in two different ways: one with all the behavioural data included and the other where I excluded the data for a particular fish if that individual did not resume foraging within the 10 minute post-stimulus observation period. The data for the LSW population were non-normally distributed, therefore, the behavioural scores were ranked and tested using the Kruskall-Wallis test, which is a nonparametric analysis of variance (Quinn and Keough 2002).

I also performed a separate one-way ANOVA for each population to determine if pre-stimulus foraging rates were different between strains. Pre-stimulus foraging rate was the dependent variable, while strain (wild, F1, F2) was the independent variable.

To determine if population differences between similar strains (RB wild vs. LSW wild, and RB F1 vs. LSW F1) could account for differences observed in the behavioural measures, two additional MANOVAs were performed, one for each strain. Time spent moving, time spent on the substrate and the number of foraging attempts were the dependent variables, while population (RB vs. LSW) was the independent variable. The assumptions of all MANOVA's and ANOVA's were tested, keeping in mind that the F-

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test in quite robust against violations of normality and homogeneity, especially with

equal sample sizes (Quinn & Keough 2002). All statistical analysis was performed with

SPSS 17.0.

Results

Habitat variables

In 2009, canopy cover was the only physical variable that was significantly

different between test sites (one-way ANOVA, p < 0.05; Table 1), whereas in 2010, none

of physical variables were significantly different between test sites (one-way ANOVA,

all p > 0.05; Table 1). There was, however, no significant difference in the measured

behavioural variables (time spent moving, time spent on substrate, number of foraging

attempts) between test sites in 2009 (MANOVA; $F_{(3,156)} = 0.482$, p = 0.695). Due to a

change in weather conditions between summers 2009 and 2010, many of the physical

variables measured (water velocity, pH, canopy cover, air temperature and water

temperature) were significantly different between years (Table 4). Likewise, there was no

significant difference in the recorded behavioural variables between years (MANOVA;

$F_{(3,228)} = 2.349$, p = 0.073).

Behavioural variables

Rocky Brook population analysis

Overall, I found that salmon showed a significant difference in their antipredator

response when exposed to alarm cue versus stream water (MANOVA; treatment p <

0.001; Table 5). I also found an overall significant difference in the magnitude of their

antipredator response depending on their rearing history (MANOVA; strain p = 0.026;

Table 5). When treatment was further analysized, I found no significant difference in

salmon antipredator response between strains when subjected to the stream water

treatment only (MANOVA; strain: $F_{(3,52)} = 1.898$; p = 0.141). There was, however, a

significant difference in antipredator response between strain when exposed to the alarm

cue treatment only (MANOVA; strain; p = 0.003; Table 6). In addition, there was an overall significant difference in time spent moving and the number of foraging attempts as a result of their rearing history (p < 0.05; Table 6; Figures 3 and 5, respectively). This suggests that RB salmon have different behaviours as a result of their rearing history. To further investigate these differences in antipredator responses, simple contrast comparisons revealed that wild salmon significantly reduced their foraging attempts compared to F1 salmon (p = 0.033; Table 7) and significantly reduced their time spent moving and number of foraging attempts compared to F2 salmon (p < 0.05; Table 7) when exposed to alarm cue compared to stream water. F1 salmon significantly reduced their time spent moving compared to F2 salmon when exposed to chemical alarm cue (p = 0.04; Table 7).

Despite the premise of RB wild salmon having a greater latency to resume foraging compared to F1 and F2 strains, I found no significant overall difference in latency between wild, F1 and F2 salmon (one-way ANOVA; $F_{(2,50)}$ = 0.937; p = 0.399; non-foragers excluded; Figure 6).

Additionally, I found that the pre-stimulus foraging rates were significantly different between wild, F1 and F2 salmon (one-way ANOVA; $F_{(2,109)}$ = 21.910; p < 0.001). A simple contrast test revealed that wild salmon foraged significantly more than F1 and F2 (p < 0.001), whereas F1 salmon foraged significantly more than F2 salmon (p = 0.022).

Little Southwest Miramichi population analysis

I found that, overall, salmon displayed a significant difference in their antipredator response when exposed to alarm cue versus stream water (MANOVA; treatment $p < 0.001$; Table 8). There was no overall significant difference in antipredator response between wild and F1 salmon (MANOVA; strain $p = 0.627$; Table 8). When treatment was analysized further, I found no significant difference in antipredator response between wild and F1 salmon when exposed to the stream water (MANOVA; strain: $F_{(3,56)} = 0.451$; $p = 0.718$; Figures 3-5) or alarm cue (MANOVA; strain: $F_{(3,56)} = 0.303$; $p = 0.823$; Figures 3-5) treatments. However, wild salmon did take significantly longer to resume foraging after expose to alarm cue than F1 salmon (one-way ANOVA; $F_{(1,53)} = 15.532$; $p < 0.001$; non-foragers excluded; Figure 6).

Additionally, I found that the wild salmon pre-stimulus foraging rates were significantly higher than F1 salmon (one-way ANOVA; $F_{(1,118)} = 5.759$; $p < 0.018$). These results are similar to the RB pre-stimulus foraging rate and suggest that when hatchery-reared fish are released into the wild, they may not be able to forage at an optimal level.

Behavioural differences between populations

When comparing populations, I found no significant difference in latency to resume foraging between RB and LSW wild ($F_{(1,38)} = 0.185$; $p = 0.670$; non-foragers excluded; Figure 6) suggesting similar antipredator responses between the two different populations. Furthermore, there was no significant difference in overall antipredator response between RB and LSW wild salmon (MANOVA; $F_{(3,78)} = 0.952$; $p = 0.420$)

In addition, when comparing LSW and RB F1 hatchery-reared salmon, I found no significant difference in their antipredator response intensities (MANOVA; $F_{(3,86)} = 2.234$; $p = 0.090$). There was also no significant difference in latency to resume foraging between RB and LSW F1 salmon ($F_{(1,39)} = 0.349$; $p = 0.558$; non-foragers excluded; Figure 6).

Discussion

Overall, these results suggest that while all strains exhibited some response to conspecific alarm cues, there was a stronger response among wild-caught young-of-year (YOY) and a weaker response among hatchery-reared YOY. The present findings illustrate that wild and hatchery-reared (first and second generation) juvenile Atlantic salmon exhibit an antipredator response when exposed to predation risk. These results are consistent with previous studies which have shown that both, hatchery-reared and predator naive salmonids, display innate antipredator responses to predation risk (Brown and Smith 1998; Berejikian et al. 1999; Scheurer et al. 2007). Moreover, extensive research conducted by Leduc et al. (2006; 2007; 2009; 2010b) has demonstrated that wild juvenile Atlantic salmon display an antipredator response when exposed to conspecific alarm cues similar to the responses found here.

One intriguing finding was that wild salmon had the highest baseline foraging rates compared to F1 and F2 hatchery strains. Literature suggests that hatchery-reared fishes display more hazard-prone behaviour patterns, including a reduced antipredator response and increased foraging rates, due to unnatural hatchery conditions (Olla et al. 1998). Laboratory studies demonstrate that hatchery-reared juvenile salmonids show decreased predator avoidance response intensities and tend to forage at a higher rate under increased predation risk than their wild counterparts, leading to a more hazard-prone behaviour (Johnsson 1993; Sundstrom et al. 2004). However, these results suggest that under more natural conditions, hatchery-reared salmon forage less than wild salmon, therefore displaying a more hazard-averse behaviour. This may be because hatchery salmon have not been previously exposed to live prey items and lack the appropriate

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experience to select proper food items when subjected to natural conditions (Brown and Laland 2003). Hatchery salmon may be behaviourally ill-equipped to forage under more natural conditions, however, a more in-depth analysis looking at foraging rates between wild and hatchery salmon over an extended period of time in a stream would be needed to draw any definite conclusions.

More importantly, this study suggests that wild, first and second generation hatchery-reared salmon display antipredator responses of dissimilar intensities. LSW F1 salmon were quicker to resume foraging following predator exposure compared to LSW wild salmon. There was no difference between the two strains for time spent moving, time spent on the substrate and the number of foraging attempts. In addition, RB F1 salmon displayed less of a foraging reduction and started foraging sooner than their wild counterparts when exposed to alarm cue. There was no difference in time spent moving and time spent on the substrate between both RB wild and F1 strains.

Differences in antipredator response intensities were also observed between first and second generation hatchery-reared salmon. While RB F1 and F2 salmon displayed similar antipredator responses in terms of time spent on the substrate, the number of foraging attempts and latency to resume foraging, RB F1 salmon spent less time moving than F2 salmon following predator exposure. Overall, the response pattern of Rocky Brook F1 salmon was intermediate between that of the wild-caught and F2 Rocky Brook strains. RB F2 displayed less of a foraging reduction and spent more time in motion than their wild counterparts when being exposed to alarm cue. This suggests that there may be an additive effect of prior experience and hatchery selection on the antipredator behaviour of hatchery salmon. If these two mechanisms (experience and selection) are

functioning additively then we would expect to see the F2 hatchery strain display the lowest intensity antipredator response followed by F1, which was what we observed.

Environmental conditions between test sites and years were unlikely to have an influence on the antipredator response of salmon. Canopy cover was significantly different between test sites in 2009; however, it did not affect the behavioural responses of the salmon. Also, the physical conditions between years did not have an influence on the behaviour of salmon. Canopy cover was significantly different between years because the testing bins were placed further into the stream in 2010 due to low water levels and therefore, the canopy could not cover the test sites. In addition, it can be argued that even though many of the variables were statistically different from each other, these differences may be biologically irrelevant as many of the physical variables fall within the range commonly recorded in the Little Southwest Miramichi River basin (Cunjak et al. 1993; Breau et al. 2007). In addition, Atlantic salmon can tolerate relatively high water temperatures (27-28°C) for a salmonid species (Lund et al. 2003), and a recent study has shown that juvenile (0+) Atlantic salmon do not alter their behaviour in high temperature (>23°C) events (Breau et al. 2007).

It is clear from these results that there are definite antipredator behaviour differences between wild and F1 hatchery-reared salmon. A proposed mechanism widely citied in current literature to account for these behavioural differences is the role of previous predator experience in shaping antipredator responses to predation risk. A hatchery setting lacks many of the natural aspects of a wild environment, most importantly predators, and as a result hatchery-reared individuals cannot develop the acquired predator recognition and avoidance behaviours needed to survive in the wild

(Brown and Day 2002). Consequently, the survival rate of hatchery-reared fishes into adulthood is extremely poor and reduces the usefulness of hatchery programs (Brown and Laland 2001). Berejikian (1995) found that during live predator encounters, wild (experienced) steelhead trout fry survived significantly better than their hatchery-reared (predator naïve) counterparts. Similarly, hatchery-reared (predator experienced) juvenile coho salmon consistently survived in greater numbers and for longer periods of time when exposed to a live lingcod (*Ophiodon elongates*) than did hatchery-reared (predator naïve) juvenile coho salmon (Olla and Davis 1989). In addition, Alvarez and Nicieza (2003) found that wild and first generation hatchery-reared juvenile brown trout differ in their predator avoidance behaviour with the F1 individuals using refuging less than their wild counterparts, which they argued could be explained by previous experience with predators. However, two of these studies, Berejikian (1995) and Olla and Davis (1989) used multi-generational hatchery-reared individuals, while Alvarez and Nicieza (2003) used fish from different donor stocks. It is crucial to highlight the importance to use test fish from the same source population to eliminate population differences, and after limited hatchery exposure (one to two generations) because this strategy is commonly used to limit behavioural differences between the hatchery-reared and wild individuals (Fritts et al. 2007).

These results also may indicate antipredator response differences between the F1 and F2 hatchery-reared salmon. Much of the literature has suggested that increased artificial culture time (rearing over multiple generations) and selection for fast growth (domestication) in aquaculture operations has resulted in dramatic antipredator behaviour differences between artificially cultured and wild individuals (Huntingford 2004). Many

other studies looking into the effects of domestication on antipredator behaviour have focused either on multi-generational (> 3-4 generations) artificially cultured salmonids (Berejikian 1995; Johnsson et al. 1996; Petersson and Jarvi 2006; Houde et al. 2010) or situations where there was strong intentional directional selection for faster growing salmonids used in aquaculture (Johnsson and Abrahams 1991; Fleming and Einum 1997; Yamamoto and Reinhardt 2003). Only one previous laboratory study, testing survival directly (Fritts et al. 2007) was conducted between first and second generation hatchery-reared individuals, from the same donor stock thereby eliminating the effect of population differences. Fritts et al. (2007) found that F1 hatchery-reared juvenile Chinook salmon had a 2.2% survival advantage compared to the F2 generation when exposed to a live predator, indicating that domestication can affect the vulnerability to predator after only one generation of hatchery rearing, however the effect was small and may be biologically insignificant. This domestication, or hatchery selection, is most likely due to relaxed predation selection pressure found in the hatchery and not selection based on growth because the hatchery does not intentionally select for fast growing individuals (M. Hambrook, Miramichi Salmon Association, South Esk, New Brunswick, personal communication, 2010). There may, however, be unintentional selection occurring (e.g. growth) that may be unaccounted for.

This study has demonstrated a difference in the antipredator response between wild and first generation hatchery-reared juvenile salmon, indicating that prior predator experience may play a significant role in shaping antipredator behaviour and, ultimately, the survival of hatchery-reared salmonids. A difference in the antipredator behaviour between first and second generation hatchery-reared salmon was also observed, which

may provide additional evidence that hatchery selection may occur in one generation of hatchery rearing, however, the effect may be less pronounced than previously expected. The differences in antipredator behaviour between wild caught and hatchery fish is probably due to the additive effects of a lack of experience and hatchery selection, due to larger antipredator response differences found between wild and second generation hatchery salmon compared to smaller differences found between either wild and F1 or F1 and F2 alone. I observed antipredator response differences between wild caught and F1 fish suggesting that prior experience may play a role in shaping antipredator behaviour. The observed difference between F1 and F2 fish suggest, since both lack prior experience, that hatchery selection can occur after one generation in the hatchery. The difference in behaviour between wild caught and F2 hatchery fish may suggest an additive effect of prior experience and hatchery selection on their antipredator behaviour. It is also crucial to stress that both F1 and F2 hatchery-reared salmon showed reduced baseline foraging rates compared to wild salmon, indicating that under natural conditions, they may be behaviourally ill-equipped to forage. This may result in reduced growth rates and even death due to starvation and can have drastic consequences when stocking hatchery-reared salmon.

Conclusion

Due to differences between hatchery and natural environments, salmonids reared in hatcheries have reduced antipredator behaviour (Fritts et al. 2007), feeding ability (Sundstrom and Johnsson 2001) and breeding success (Fleming and Gross 1993), which may result in rapid fitness declines and lower survival rates when released into the wild compared to wild salmonids (Araki et al. 2008). It is important, however, to note that possible alternative mechanisms to domestication (hatchery) selection exist. Fitness declines of hatchery-reared fish may also be due to epigenetic changes, accumulation of deleterious mutations or maternal effects (reviewed in Fraser 2008).

Attempts have been made to implement more natural rearing conditions as a possible solution to the behavioural deficits of hatchery fish caused by the unnatural abiotic and biotic environment of a hatchery (Einum and Fleming 2001). Structures, such as rocks and branches, underwater feeders and the addition of live prey items, overhead cover and the use of alarm cues/predator odours can all be used to add complexity to a hatchery rearing environment. For example, increasing habitat complexity (in-water structures, underwater feeders and live prey) has been shown to modify the behaviour of hatchery-reared salmonids which may significantly improve their post-release survival rates (Berejikian et al. 2000; Brown et al. 2003). In addition, the use the conspecific chemical alarm cues and predator odour may be used to condition hatchery (predator-naïve) fish to show an appropriate antipredator response when exposed to predator odour, which may improve survival in the wild (Brown and Smith 1998; Berejikian et al. 1999).

The method in which hatcheries release their fish for stocking could have significant effects on the native fish populations. Keeping in mind that the goal of most

hatcheries is conservation related (increasing the viability of wild populations), it is important to implement release practices that aim to reduce and minimize the negative impacts of hatchery-reared fish on their wild counterparts. For example, using local strains for stocking may help eliminate any population effects between the hatchery-reared and wild individuals. Releasing first generation (offspring of wild caught parents) fish may help reduce the impact of inadvertent hatchery selection as there is less opportunity for selection to occur. Additionally, stocking fish as eggs or young-of-year can minimize the effects of the unnatural hatchery environment on their behaviour by limiting hatchery exposure to a minimum. As mentioned previously, adding complexity to the hatchery rearing environment may also be of help to reduce behavioural differences between wild and hatchery fish in order to increase post-release survival of the hatchery individuals.

We need a better understanding of how the hatchery environment and incorporated strategies affect the behaviour and post-release survival of hatchery fishes in order for hatcheries to increase in efficiency and fulfill their objective. More studies are needed, ideally under natural conditions, directly comparing wild, F1 and F2 generations from the same population to help disentangle the effects of experience and hatchery selection on behaviour and survival of hatchery-reared fishes.

Table 1.   Mean value (±SE) of the physical variables between both test sites in two consecutive field seasons. One-way ANOVAs were used to assess differences between test sites for measured variables.

Variable	site 1	site 2	F	d.f.	P
	mean (±SE)				
2009					
water velocity (cm/s)	23.5±1.24	22.4±1.58	0.277	1, 32	= 0.603
depth (cm)	19.5±0.72	18.4±0.68	1.136	1, 32	= 0.294
pH	7.16±0.04	7.16±0.04	0.000	1, 32	= 1.000
cloud cover (%)	50.8±6.63	51.5±6.88	0.006	1, 64	= 0.937
canopy cover (%)	33.75±2.50	17.75±1.75	26.304	1, 64	< 0.001
air temperature (°C)	20.6±0.04	20.7±0.04	0.003	1, 64	= 0.958
water temperature (°C)	16.4±0.18	16.4±0.18	0.003	1, 64	= 0.954
2010					
water velocity (cm/s)	17.0±2.65	17.2±3.01	0.002	1, 10	= 0.968
depth (cm)	20.0±0.72	18.4±1.00	1.628	1, 12	= 0.226
pH	7.80±0.01	7.80±0.01	0.000	1, 14	= 1.000
cloud cover (%)	48.38±8.50	48.38±8.50	0.000	1, 44	= 1.000
canopy cover (%)	0.00±0.00	0.00±0.00	N/A	1, 44	N/A
air temperature (°C)	23.04±0.58	23.04±0.58	0.000	1, 44	= 1.000
water temperature (°C)	21.47±0.51	21.47±0.51	0.000	1, 44	= 1.000

Note: α = 0.05

Table 2. Mean standard length (mm ± SD) of the test fish for 2009, 2010 and for both years combined. Sample sizes are included in brackets and indicate the total number of fish tested.

Strain	2009 Mean (±SD)	2010	2009 Range	2010	2009 & 2010 Mean (±SD)
LSW wild	40.2 ± 4.09 (n=50)	36.6 ± 2.72 (n=10)	28.0-48.0	30.0-40.0	39.6 ± 4.10 (n=60)
LSW F1	42.2 ± 4.89 (n=30)	40.6 ± 2.63 (n=30)	34.0-58.0	35.0-45.0	41.5 ± 3.99 (n=60)
RB wild	N/A	37.0 ± 2.93 (n=22)	N/A	32.0-44.0	37.0 ± 2.93 (n=22)
RB F1	40.8 ± 2.94 (n=30)	N/A	34.0-46.0	N/A	40.8 ± 2.94 (n=30)
RB F2	44.8 ± 4.11 (n=50)	38.3 ± 2.06 (n=10)	38.0-60.0	35.-42.0	43.7 ± 4.54 (n=60)

Table 3.   Number of fish, total area of skin, and the volume of water needed to produce the desired chemical alarm cue concentration.

	2009	2010
Age Class	parr(1+)	fry(0+)
Number of fish sacrificed	17	725
Standard length (mm ± SD)	104.59 ± 4.08	39.05 ± 3.36
Skin area (cm²)	499.88	2 299.48
Water volume (mL)	4815.8	22 152.99
Dilution (cm²/mL)	0.1038	0.1038

Table 4.   Mean value (±SE) of the physical variables in 2009 and 2010. For each year, both test sites were pooled together. One-way ANOVAs were used to assess differences in physical variables among years.

Variable	2009	2010	2009	2010	F	d.f.	P
	mean (±SE)		Range				
water velocity (cm/s)	22.9±1.00	17.1±1.91	11.0-33.0	7.0-27.0	8.408	1, 44	= 0.006
depth (cm)	18.9±0.50	19.2±0.63	14.0-25.0	15.0-24.0	0.097	1, 46	= 0.757
pH	7.15±0.03	7.80±0.01	6.59-7.37	7.76-7.88	208.90	1, 48	< 0.001
cloud cover (%)	51.13±4.75	48.38±6.00	0-100	0-100	0.136	1, 110	= 0.713
canopy cover (%)	25.75±1.88	0.00±0.00	0-62.5	0-0	137.98	1, 110	< 0.001
air temperature (°C)	20.7±0.28	23.0±0.40	16.0-26.0	17.0-28.0	24.696	1, 110	< 0.001
water temperature (°C)	16.4±0.13	21.5±0.36	15.0-19.0	18.0-26.5	226.99	1, 110	< 0.001

Note: α = 0.05

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Table 5.   Results of the overall MANOVA for the RB population. Strain (wild vs.
              F1 vs. F2) and treatment (alarm cue vs. stream water) were included as
              independent variables. Significant effects when $P < 0.05$.

Multivariate test	F	d.f.	P
Strain	3.199	3, 105	= 0.026
Treatment	11.832	3, 104	< 0.001
Strain x treatment	0.590	3, 105	= 0.623

Table 6.   Results of the RB population MANOVA for the alarm cue treatment only. Strain (wild vs. F1 vs. F2) was included as the independent variable. Significant effects when P < 0.05.

	Multivariate test	F	d.f.	P
	Strain	5.140	3, 52	= 0.003
Behavioural measure	**Between-subjects effects**			
Time spent moving	Strain	4.345	1, 53	= 0.018
Time spent on substrate	Strain	1.120	1, 53	= 0.334
Number of foraging attempts	Strain	4.266	1, 53	= 0.019

Table 7.   Results of the simple contrast comparisons for the RB population. Strain
(wild vs. F1 vs. F2) was the independent variable while time spent
moving, time spent on the substrate and the number of foraging attempts
were the dependent variables. Significant mean difference when P < 0.05.

		Time moving		Time on substrate		Foraging attempts	
Fish Strain		**Mean diff. (±95% CI)**	**Sig.**	**Mean diff. (±95% CI)**	**Sig.**	**Mean diff. (±95% CI)**	**Sig.**
Wild	F1	-11.60 (±37.2)	0.534	15.68 (±60.3)	0.604	-3.50 (±3.20)	0.033
	F2	-42.77 (±33.0)	0.012	37.52 (±53.5)	0.166	-4.10 (±2.84)	0.006
F1	F2	-31.17 (±29.6)	0.040	21.83 (±48.0)	0.366	-0.60 (±2.55)	0.639

Table 8.   Results of the overall MANOVA for the LSW population. Strain (wild vs. F1) and treatment (alarm cue vs. stream water) were included as independent variables. Significant effects when $P < 0.05$.

Multivariate test	F	d.f.	P
Strain	0.584	3, 114	= 0.627
Treatment	8.782	3, 114	< 0.001
Strain x treatment	0.117	3, 114	= 0.950

Figure 1.   Location of the study area, indicated by the arrow, on Little Southwest
             Miramichi River. (Modified from Leduc et al. 2006).
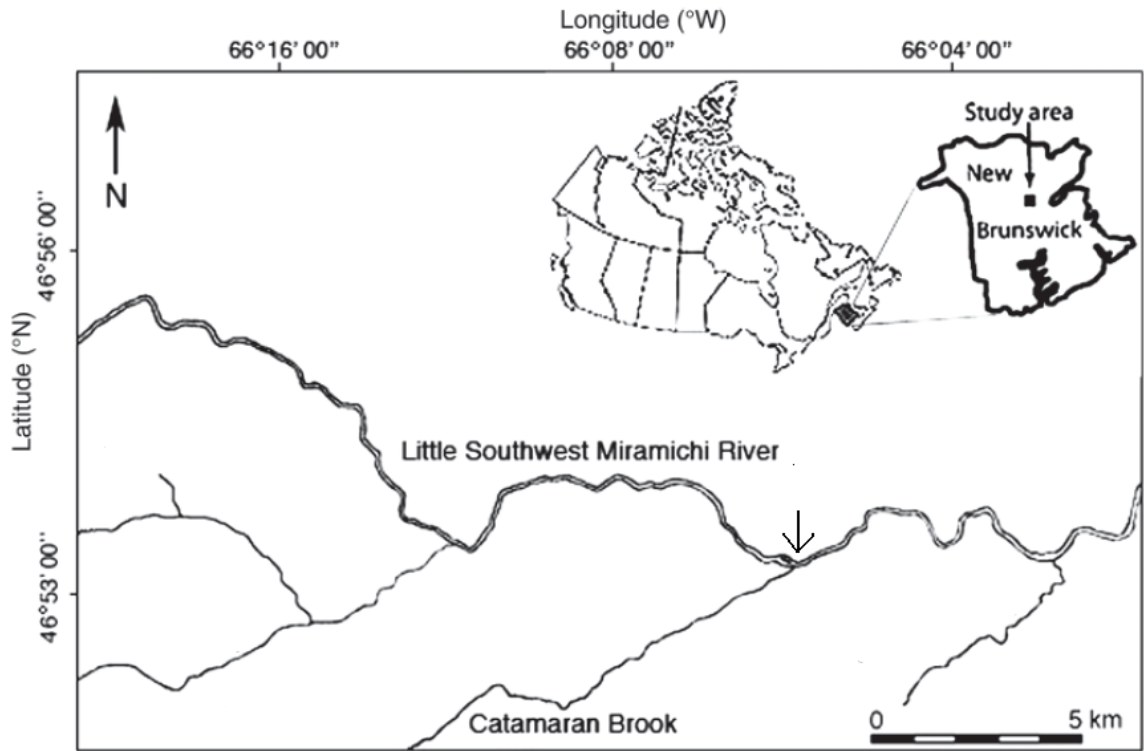
Figure 2.   Location of Rocky Brook in relation to Little Southwest Miramichi River.
             (Modified from Riddell and Leggett 1981).

Figure 3.   Boxplot displaying the median (± quartiles) change in time spent moving (in seconds) for wild (W), first (F1) and second (F2) generation hatchery-reared juvenile Atlantic salmon for both Rocky Brook (RB) and Little Southwest (LSW) populations exposed to either stream water (SW) or alarm cue (AC) treatment. Sample sizes: RB W = 22, RB F1 = 30, RB F2 = 60, LSW W = 60, LSW F1 = 60. Each strain received equal amounts of each treatment.
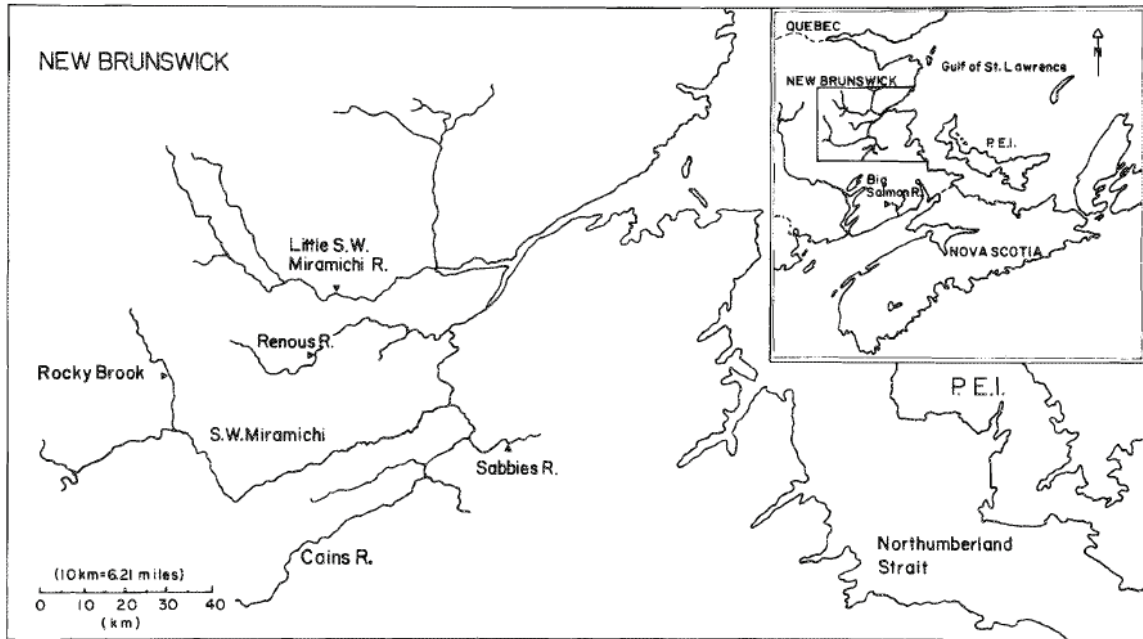

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Figure 4.   Boxplot displaying the median (± quartiles) change in time spent on the
                substrate (in seconds) for wild (W), first (F1) and second (F2) generation
                hatchery-reared juvenile Atlantic salmon for both Rocky Brook (RB) and
                Little Southwest (LSW) populations exposed to either stream water (SW)
                or alarm cue (AC) treatment. Sample sizes: RB W = 22, RB F1 = 30, RB
                F2 = 60, LSW W = 60, LSW F1 = 60. Each strain received equal amounts
                of each treatment.

Figure 5.   Boxplot displaying the median (± quartiles) change in the number of
foraging attempts for wild (W), first (F1) and second (F2) generation
hatchery-reared juvenile Atlantic salmon for both Rocky Brook (RB) and
Little Southwest (LSW) populations exposed to either stream water (SW)
or alarm cue (AC) treatment. Sample sizes: RB W = 22, RB F1 = 30, RB
F2 = 60, LSW W = 60, LSW F1 = 60. Each strain received equal amounts
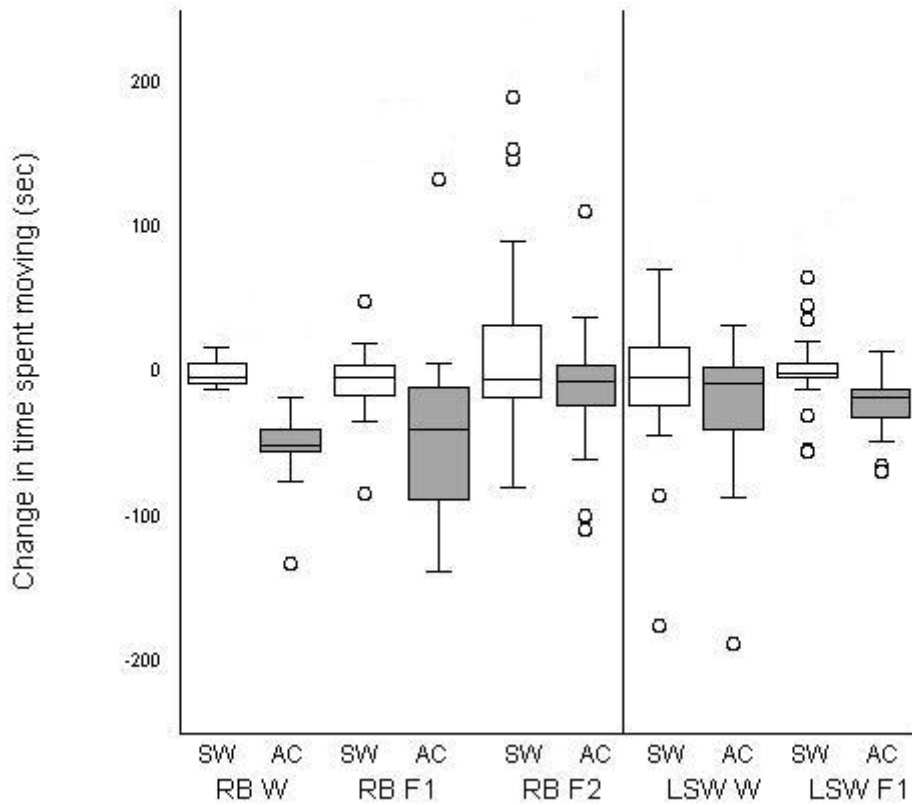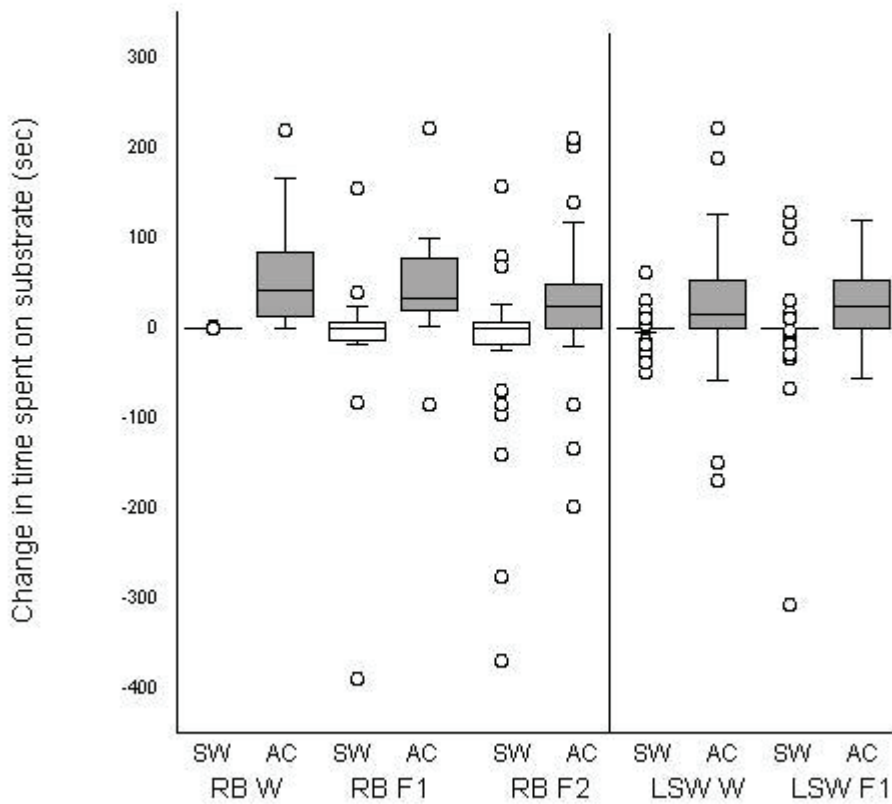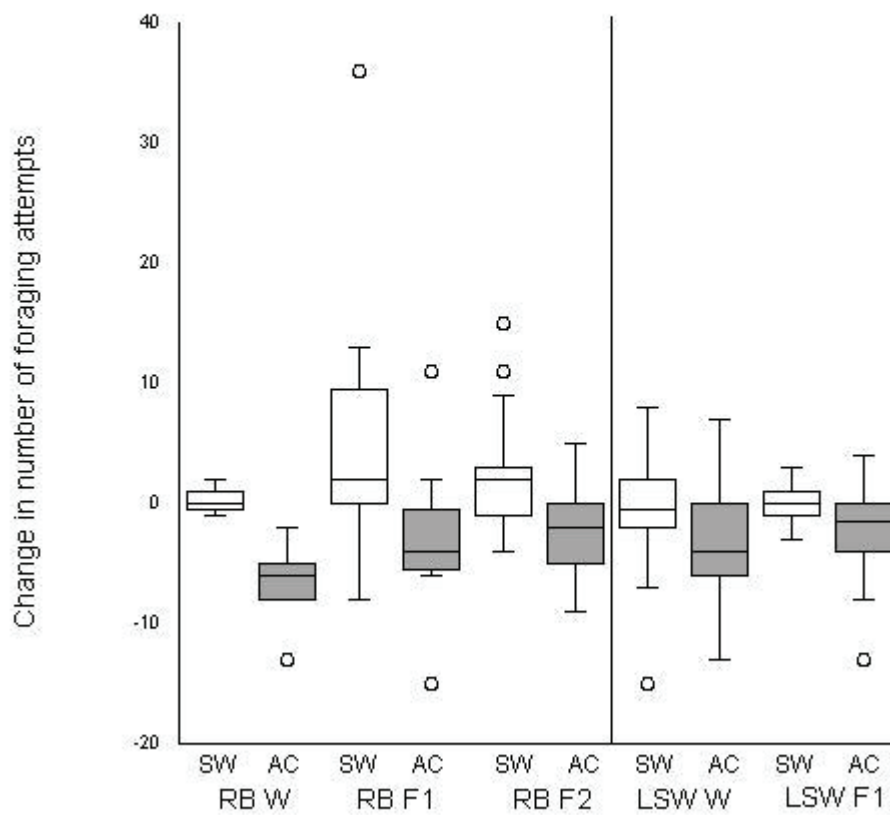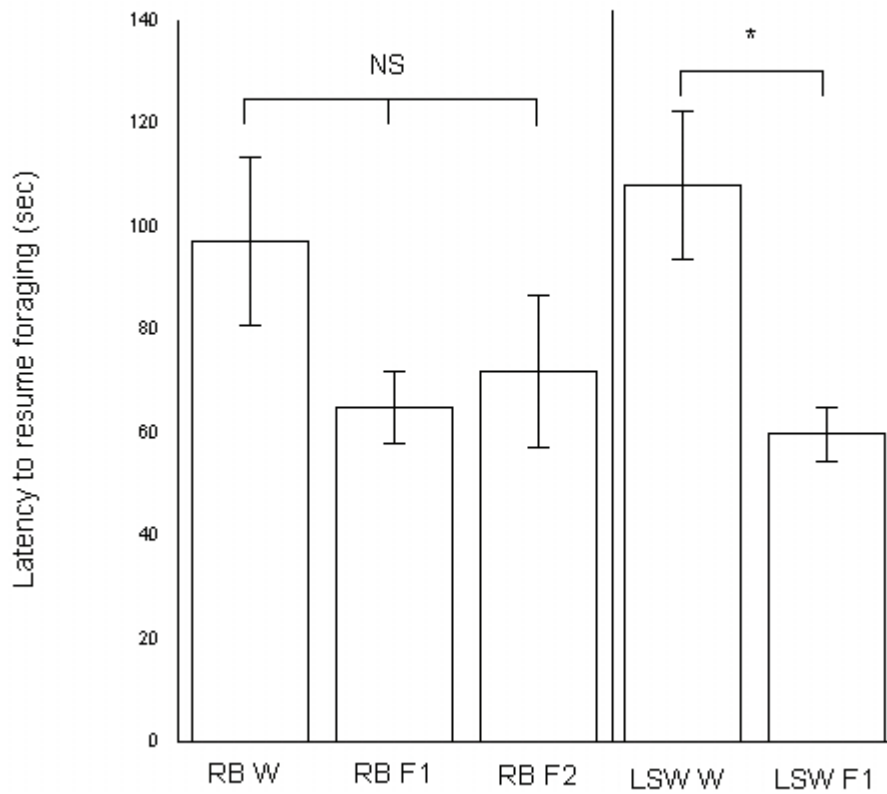of each treatment.

Figure 6.   Mean (± SE) latency to resume foraging (in seconds) for wild (W), first
(F1) and second (F2) generation hatchery-reared juvenile Atlantic salmon
for both Rocky Brook (RB) and Little Southwest (LSW) populations.
Sample sizes: RB W = 11, RB F1 = 15, RB F2 = 27, LSW W = 29, LSW
F1 = 26. * indicates significance, while NS indicates not significant.

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