

**Foraging and territorial decisions by juvenile Atlantic salmon
Salmo salar under chronic predation threat in the wild**

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Abstract

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Most animals are at some point in their development required to perform behaviours under the threat of predation. There is a need to trade off behaviours like foraging and territoriality with anti-predator behaviour in order to maximize survival. Recent studies have shown that Atlantic salmon potentially compensate for chronic predation risk by reducing territory size but maintaining the same growth rate. However, no direct measures of foraging or growth were collected. Here, I tested the hypothesis that juvenile Atlantic salmon can adjust behaviours depending on the perceived risk of predation. I conducted trials under semi natural conditions in which the experimental group was exposed to alarm cue and the control group to stream water over two field seasons in 2010 and 2011. Territory size was recorded on Day 1 and Day 7 while foraging was recorded daily for as many individuals as possible. The change in weight between Day 1 and Day 7 was also recorded for every individual. Overall, I found that territory size reduced over the seven day period for the alarm cue group while foraging and growth did not differ significantly between treatments. However, there were significant differences in results over the two field seasons. These results suggest a behavioural compensation between territory defense and foraging under the effect of chronic predation. The differences in response by year can be explained by looking at the resources dynamics of each year. Future work could examine this influence further.

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This thesis is dedicated to my grandfather David Malka, who would have loved to have heard all about it.

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Introduction

Behavioural trade-offs and non-consumptive effects

Most animals are at some point in their development under the threat of predation and so, must trade investment in behaviours like foraging (Dill & Fraser 1984) and territory defense (Kim *et al.* 2011a), with investment in behaviours intended to decrease the risk of predation (Lima 1998). Prey are forced to make behavioural decisions in order to optimize these conflicting demands while recent models show that predation increases costs by increasing the risk of performing other behaviours (Lima & Dill 1990).

Models of non-consumptive effects of predation (NCEs) suggest considerable lifetime fitness consequences to responding to predation risk (Werner & Peacor 2003, Walsh 2013). NCEs are the long term results of responding to predation that are not death. In many cases, the decrease in lifetime fitness can be as important as direct consumption by a predator (Preisser *et al.* 2005). For example, voles (*Clethrionomys* sp.) intimidated by predators reduce their foraging rate which in turn reduces important early growth (Heikkila *et al.* 1993). Dormant anostracan eggs experience significantly reduced hatch rates when in the presence of the predatory mesostoma species, or their chemical cues (DeRoeck 2005). Both Adelie penguin *Pygoscelis adeliae* and emperor penguin *Aptenodytes forsteri* avoid foraging in darkness due to predation though they have been shown to be capable of foraging effectively at night (Ainley & Ballard 2012). Aversion to darkness due to predation risk in an area of the world that experiences long periods of darkness forces costly migration by both penguin species, often away from more productive waters. Mud crabs *Panopeus herbstii* reduce foraging on oyster prey

when in the presence of a large predator biomass of blue crab *Callinectes sapidus* (Hill & Weissburg 2013). Here, the NCEs of blue crab on mud crab also impact oyster survivorship. These examples illustrate how the sum of the decisions made by prey to avoid being killed combined with the resource dynamics of the environment, such as food or habitat availability, result in the overall NCEs of predation on lifetime fitness of the individual, conspecifics and other species related through trophic interactions (Preisser *et al.* 2009). Peckarsky and several co-authors (2008) suggested that many classic examples of predator-prey interactions are better understood with the incorporation of NCEs (Peckarsky *et al.* 2008) and that a predator's effect on prey density is no longer enough to understand the impact of predation on the community as a whole.

*Territory Defense and the Atlantic salmon *Salmo salar**

Animals may defend territories in order to accrue a variety of benefits. Juvenile Atlantic salmon *Salmo salar* with prior residency of a territory show higher growth and energy density than individuals arriving at a later time and though there is no effect on survival, the accumulated resources of prior residents can result in higher over winter survival rates and earlier maturation (Kvingedal & Einum 2011). Brown trout *Salmo trutta* will defend territories faster and more aggressively when that territory represents their habitat preference of gravel, instead of a uniform bright substrate that would increase their conspicuousness (Johnsson *et al.* 2000). Juvenile coho salmon *Oncorhynchus kisutch* territory holders will on average forage more using less energy than their floating or non-territorial counterparts because holding a territory reduces the search and pursuit costs of foraging as well as limiting defense to invasive conspecifics (Puckett & Dill 1985). By defending a given area, territory holders are attempting to

maximize the benefits offered by that space. Benefits like foraging opportunity, nesting sites and protection. Since a territory is dependent on the holder's ability to defend it, and not all territories are of equal value, the territory's ease of defense is also an important factor (Brown 1964).

Territories are defined by the interactions of the territory holder and neighbouring competitors (Kaufmann 1983). The boundaries, which give the territory size and shape, can be described by the limits of the holder's movement for foraging and aggressive defense (Adams 2001). Optimality models of territory defense predict that territory size should decrease as costs of defense begin to outweigh benefits so territory size should be the product of a cost-benefit balance. (Hixon 1980, Schoener 1983, Grant & Noakes 1987). Some of the costs associated with territory defense include the energy expended during aggressive encounters with competitors, the increased risk of injury during defense, and increased conspicuousness to predators (Martel & Dill 1993).

Various stream dwelling salmonids defend territories using different tactics depending on foraging mode and habitat preference (Armstrong *et al.* 2003, Dolinsek *et al.* 2007, Gunnarsson & Steingrimsson 2011, Steingrimsson & Grant 2011). Atlantic salmon, an anadromous salmonid species found in streams and rivers of eastern and Atlantic Canada as well as the north-eastern United States (Scott & Crossman 1973, Jonsson & Jonsson 2011, Page & Burr 2011), can be aggressively territorial from their emergence. Atlantic salmon spawn in the fall and the young of the year (YOY) emerge in late spring, feeding on drifting invertebrates and defending territories of roughly 1 m² from multiple central placements, the stations within a territory which individuals leave to forage and defend, and subsequently return to (Keenleyside & Yamamoto 1962,

Brannas 1995, Steingrímsson & Grant 2008, Steingrímsson & Grant 2011). By using multiple central placements, territory holders can utilize a larger area as resources deplete within their territories. Territory sizes tend to increase with body size but decrease with higher food density, habitat visibility, dominance rank and competitor density (Imre *et al.* 2004, Schoener 1983, Venter *et al.* 2008, Jonsson & Jonsson 2011, Toobaie & Grant 2013). Along with territory size, growth is also dependent on density (Grant & Imre 2005, Imre *et al.* 2010). Populations at lower densities typically have higher growth rates and during this same period of early growth, a relationship has been shown between size and survival for salmonids over their first winter (Quinn & Peterson 1996) so a premium should be placed on foraging and territory defense despite the number of factors affecting the costs and benefits of the behaviour.

Acute and chronic predation risk

Kim *et al.* (2011a) studied the effects of acute and chronic perceived predation risk on the territorial behaviour of juvenile Atlantic salmon. Territory defense increases foraging but costs of territory defense increase with higher predation risk. As mentioned above, as costs increase, the size of defended area should decrease and with that comes an associated decrease in growth. Kim *et al.* (2011a) predicted that in response to both acute and chronic predation risk, YOY Atlantic salmon would decrease foraging, territory size and the number of switches between central placements. Observations were performed on wild individuals defending territories after having elevated the perceived predation risk. They found that individuals under acute risk only reduced the number of switches between central placements but when revisited after an extended period of time, only territory size had decreased significantly. Territory size was predicted to reduce

over the long term and with that reduction should come a decrease in foraging and number of switches. That associated reduction was not found, suggesting a possible behavioural compensation is taking place in response to the different time scales under the risk of predation. Despite this result, the authors called for future experiments to include a direct comparison between acute and chronic effects of predation risk on territory size and foraging as well as any effects on future fitness indicators like growth or survival.

Salmon fry are prey to a variety of predators during their first few months of development, including most commonly to larger members of their own species (Scott & Crossman 1973, Dolinsek *et al.* 2007), common merganser *Mergus merganser*, belted kingfisher *Megaceryle alcyon* and brook trout *Salvelinus fontinalis*. The ability to respond early to predation conveys an important advantage but assumes that prey are able to reliably recognize predation risks (Ferarri *et al.* 2010a). A variety of sensory modalities including chemical alarm cues released into the environment following mechanical damage of the prey's epidermis have been shown to reliably indicate risk within aquatic environments (Chivers & Smith 1998, Brown *et al.* 2011). A number of salmonid species have been repeatedly shown to respond with typical antipredator behaviour to alarm cues in both field and laboratory experiments (Martel & Dill 1993, Chivers & Smith 1998, Blanchet *et al.* 2007, Kim *et al.* 2009). In addition, chemical alarm cues have also been shown to elicit antipredator response in Ostariophysian species (Wisenden *et al.* 2004), marine fish like the tropical goby *Asterropteryx semipunctatus* (McCormick & Larson 2007), mosquito larvae *Culex restuans* (Ferrari *et al.* 2008), larval newts *Triturus pygmaeus* (Gonzalo *et al.* 2012) and adult salamanders *Ambystoma*

macrodactylum (Chivers *et al.* 1996). In experiments where predation risk needs to be assessed by prey, alarm cues are useful in determining antipredator response without exposing the focal prey species to the actual predator, when antipredator response is of interest while controlling the population's density. Non-consumptive effects tend to be stronger with long term predation in aquatic species because they are better suited to assess their environment's level of risk, and change their behaviour accordingly (Preisser *et al.* 2005).

In this experiment, I hypothesized that juvenile Atlantic salmon can adjust behaviours depending on the perceived risk of predation. From this, several predictions can be made for territory defense and foraging, with regards to predation risk under "chronic" or persistent long term risk. For the purpose of this study, chronic response to predation can be further defined as the response taking place after a week long period of exposure.

I tested the predictions that with chronic exposure to predation risk, territory sizes would decrease and be smaller than that of the control groups unless individuals show compensation for their reduced territory size by maintaining or increasing their foraging rate. The increased cost of territory defense under the risk of predation due to both decreased territory size and foraging should also lead to a decrease in growth unless, again, foraging is maintained and growth continues proportionally. Using growth as a proxy for fitness, we can further predict that reduced territory size has an associated fitness cost (Martel and Dill 1993, Lind & Cresswell 2005, Biro *et al.* 2006) and that reduced growth could be an important non consumptive effect of long term predation risk.

Methods

Study site

Trials were conducted in the lower reach of Catamaran Brook (46°52'N 66°06'W), a tributary of Little Southwest River located in Northumberland County, New Brunswick during the months of July and August 2010 and 2011 (Figure 1). Catamaran brook is a site of long term ecological studies (Cunjak et al 1993). Catamaran brook itself is varied in character with flats, runs, riffles and pools, and the water depth and flow velocity which characterize each, making up the variety of habitat choices available to YOY salmon upon emergence. The stream bed varies in make-up from gravel to cobble sized stones and the canopy cover varies from 100% cover, typically near the stream shores, to complete exposure at the center of the stream and in certain reaches of the brook. Placement of the enclosures was selected to minimize the difference in physical characteristics between enclosures, despite the heterogeneity of the environment.

Preparation of alarm cue

To generate alarm cue used to elevate perceived risk, I collected the skin from the flanks of hatchery reared juvenile salmon killed by cervical dislocation in accordance with Concordia University's Animal Care Protocol (AC-2008-BROW). A running count of the total area of skin collected is recorded in order to achieve the target alarm cue concentration of 0.101 cm² of skin ml⁻¹. This concentration has been shown in previous studies to be effective in eliciting a typical antipredator response among salmonids in the lab and in the field (Brown & Smith 1998, Jackson & Brown 2011, Kim *et al.* 2011b, Leduc *et al.* 2006). Once collected, I homogenized the skin in a recorded quantity of

chilled distilled water then filtered using a funnel and polystyrene wool. The resulting solution was further diluted to achieve the desired concentration then packed in 75 ml quantities and frozen at -20°C until ready to be used.

Experimental Setup

Net enclosures, 4 in 2010 and 6 in 2011, with a 3 mm mesh size measuring 6m x 1m x 0.75m were placed and anchored directly into the stream in staggered pairs. Each pair consisted of a downstream experimental and upstream control enclosure. The bottom of each was covered with a gravel substrate from the stream bed to best resemble the surrounding environment and to offer further structural support. Flagging tape was placed every 25 cm along the bottom edges of the enclosures, creating a grid composed of ninety-six 25 cm² squares to aid in visualizing and recording territory data. These 96 squares were then each divided into 16 squares on the weather proof data sheets. To simplify observations, all territory data (i.e. central placements, foraging attempts, aggressive defense) were recorded at this resolution (Figure 2). Catamaran brook contains a population of wild YOY Atlantic salmon which were used as the sole test species in this field experiment. Before the start of the 7 day observation period, YOY salmon were captured directly from the brook via snorkeling.

Day 0

For each active enclosure, 6 YOY salmon were measured for weight (to the closest 0.01g) and length (to the closest 0.1 cm) then tagged using visible implant elastomer injected either into the tail or dorsal fin for future identification. After being placed in the enclosure, the salmon were left to acclimate for a minimum of 24 hours.

Placing 6 individuals in a contained area of 6 m² mimics a natural density of 1 individual m⁻² (Steingrímsson & Grant 2008). This method allows for a control of the competitive effects of high density on territory size (Grant & Kramer 1990).

Day 1 and 7

On Day 1, 15 minute territory and foraging observations were conducted for at least two individuals per enclosure, once in the morning (between 11:00 and 14:00, AM) and once in the evening (between 15:00 and 18:00, PM). 30 minutes before morning testing, each enclosure was dosed at the upstream end with either 75 ml of alarm cue (AC) or 75 ml of the stream water control (SW) using a syringe at 40% of the water column height. The same dose was administered in the evening after the day's testing so that every enclosure received a total of 150 ml per day of either AC or SW.

Territory size was recorded on a grid representing the bottom of each enclosure. Foraging stations as well as foraging attempts and aggression away from those central placements were recorded to give territory data for a single, identified individual at a time. The relevant aggressive behaviours which were recorded as single data points on the grid where the event occurred are charges, nips and chases (as described by Keeleyside & Yamamoto 1962). The number of foraging attempts during the 15 minute period was also noted.

On Day 7, the same procedure as Day 1 was followed but instead of injecting alarm cue into the enclosures at the end of the day, the fish were retrieved, measured and released back into the stream. Since each fish was tagged, measurements could be compared before and after the experimental period.

Day 2 through 6

On Day 2 through Day 6, the same schedule for both dosing and testing was maintained but no territory data was collected. For as many individuals as possible per enclosure, the number of foraging attempts over a 5 minute period was recorded.

Statistical analysis

Territory data were recorded as X,Y coordinates on the grid. These coordinates were analyzed to a 95% confidence interval using Arc GIS version 3.2 software. The result is a number representing the area of the Minimum Convex Polygon (MCP) which when multiplied by the physical area of a single square unit of the grid (625 cm²), gives us the final area of an individual's territory. Foraging data were collected in either 5 or 15 minute periods depending on the day so for analytical purposes, all foraging numbers were calculated as number of foraging attempts per fish per minute.

The design of this experiment was such that multiple observations are taken on a single individual at different times during the 7 day testing period. In this case, the resulting data of an observation on a single individual or "replicate" is the average result of the collected observations taken on the six individuals in an enclosure. In other words, each enclosure is a single replicate. Each replicate only received a single treatment but it is important to remember that each observation taken on a single replicate cannot be treated independently so the repeated measures ANOVA design is best suited for this analysis. Foraging and territory size are the dependent variables and treatment (AC and SW), time (AM and PM) and year (2010 and 2011) are the between subject factors.

Growth is a commonly used proxy for fitness in scenarios where future reproductive and survival data cannot be collected (Westerberg 2004, Conrad 2011). Over the relatively short testing period of one week, weight is more relevant than length as growth data since length is typically used as a measure over longer experimental periods (Imre *et al.* 2010, Jonsson & Jonsson 2011). Growth was analyzed by converting the collected weight data to Specific Growth Rate (SGR), a measure of growth in body weight percentage day⁻¹ which accounts for initial differences in size (Jobling 1983):

$$SGR = \left(\frac{(\ln W2 - \ln W1)}{(T2 - T1)} \right) \times 100$$

where W2 is the weight of the individual on day 7, W1 is the weight of the individual on day 0, T2 is day 7 and T1 is day 0. The resulting values were then analyzed using an analysis of variance (ANOVA) with year and treatment as between subject factors.

Results

For the high risk treatment group, I found a decrease in territory size in 2010 over the 7 day period but an increase in 2011. I predicted that territory size would decrease under chronic predation risk and that foraging would decrease along with it. In other words, as size of territory decreases, so should opportunity to forage. However, I did not observe such a relationship between size of territory and foraging effort. In 2010, territory size reduced for the alarm cue group and increased slightly for the stream water group while foraging and growth increased similarly for both groups over the 7 day period. In 2011, both groups increased their mean territory size although the alarm cue

group's increased by less. Despite this difference in territory size by year, foraging and growth remained consistent with the previous year's result. Territory size varying according to perceived predation risk and year while foraging and growth remain the same suggests that a possible behavioural compensation is taking place.

It should be noted that the time of day the data was recorded, either morning or afternoon, was insignificant across the board in repeated measures analysis of territory size and foraging and so was removed from further analysis and presentation of results. Morning and afternoon values were combined and presented here as overall data.

Weather Conditions

I conducted my research between July 12th, and August 25th, 2010 and July 8th, and August 8th, 2011. As can and should be expected with a study conducted in the wild, the physical conditions differed between the two periods. Overall, the 2010 field season was warmer and drier than the 2011 season which characterized the flow of the stream as lower in water column height, slower and containing less visible drift in 2010 than in 2011 (P. Malka, personal observation). Data on the physical characteristics like water column height, flow velocity and water temperature were not quantitatively collected. Placement of the enclosures was selected to control for physical characteristics since the physical variables of the environment were not considered in this study. Personal observations are supplemented with data on daily temperature and precipitation from Environment Canada's Miramichi RCS weather station located 54.12 km away (47°01'N 65°47'W). Average daily temperature did not differ significantly between years (T-test: $t_{75} = 1.15$, $P = 0.13$) but precipitation did (T-test: $t_{75} = -1.70$, $P = 0.046$), totalling 88.2

mm over a 45 day period (an average of 0.6 mm day^{-1}) in 2010 and 143.4 mm in a 32 day period (an average of 4.48 mm day^{-1}) in 2011.

Territory Size

Overall, territory size decreased over the seven day testing period for the alarm cue group but differences between the two field seasons of 2010 (AC n = 13; SW n = 11) and 2011 (AC n = 13; SW n = 10) were addressed. Territory size was not found to be significantly different between Day 1 and Day 7 (RM-ANOVA: $F_{1,39} = 0.760$, $P = 0.785$) but there was a significant effect of treatment (RM-ANOVA: $F_{1,39} = 4.831$, $P = 0.034$) and year the research was conducted (RM-ANOVA: $F_{1,39} = 9.551$, $P = 0.004$). As a result, I analyzed the data separately by year and found that repeated measures analysis was significant for both 2010 and 2011 (RM-ANOVA: $F_{1,20} = 4.525$, $P = 0.046$ and $F_{1,19} = 4.987$, $P = 0.038$ respectively) and significant for treatment effect in 2010 (RM-ANOVA: $F_{1,20} = 6.070$, $P = 0.023$) but not in 2011 (RM-ANOVA: $F_{1,19} = 0.567$, $P = 0.461$) (Figure 3). These results show that there is a difference in territory size between treatment groups but that the response appears different depending on the year the data was collected. However, what remains consistent throughout is that the alarm cue group's territory sizes exhibit a trend of being smaller than the control group's territory sizes.

Foraging and Growth

Foraging (2010 AC n = 13, SW n = 11; 2011 AC n = 12, SW n = 11) did not differ for the two groups over the seven day testing period but there were significant differences between the two experimental groups. Overall, foraging repeated measures analysis was shown to be significantly different between Day 1 and Day 7 (RM-

ANOVA: $F_{1,39} = 7.292$, $P = 0.010$) but treatment and year were not found to be significant (Figure 4). However, the between subject effects, which represent the differences between the groups, were found to be significant for treatment ($F_{1,39} = 4.992$, $p = 0.032$) and year ($F_{1,39} = 14.986$, $p = 0.005$), as well as treatment and year ($F_{1,39} = 4.605$, $p = 0.038$).

Likewise, growth (2010 AC $n = 38$, SW $n = 37$; 2011 AC $n = 35$, SW $n = 43$) did not differ between treatments (ANOVA: $F_{1,153} = 2.232$, $P = 0.137$) or treatment and year (ANOVA: $F_{1,153} = 0.313$, $P = 0.577$) but was found to be significant between years (ANOVA: $F_{1,153} = 173.287$, $P = 0.000$) (Figure 5). In other words, both the stream water and alarm cue experimental groups grew at similar rates during the test period but that this growth differed in 2010 and 2011. It should be noted that though not significantly different in growth rate between Day 0 and Day 7, Table 1 shows that the mean length was different between years for both treatment groups, despite all individuals having been collected during the same time period. This difference may be attributed to weather and therefore emergence time and provides context and reason for having analyzed the data using specific growth rate (Jonsson & Jonsson 2011).

Discussion

The goal of this study was to determine the influence of chronic predation risk on the foraging and territorial defense patterns of YOY Atlantic salmon. The results show that depending on level of perceived risk, prey can compensate by reducing the size of defended territory. The trend is that of smaller territory size when under chronic risk

over a period of one week , while over that same time period, there is increased foraging regardless of treatment. One of the major benefits of defending a territory to its holder is access to resources and although a larger territory means a larger area to defend, it also means more opportunity to forage with reduced costs associated to searching for food (Both & Visser 2003). The semi-natural setting of the trials addressed the need to record whether or not growth was affected by chronic predation risk's potential effect on territory size (Kim *et al.* 2011a).

Behavioural Compensation

Models of behavioural compensation suggest that decisions are made to adjust the performance of a particular behaviour in order to offset the costs of another one (Elvidge *et al.* 2013, Elvidge *et al.* in press). These behavioural decisions can be influenced by internal and external factors such as predation. Almost all animals are at some point in their development vulnerable to predation, but the threat of predation is one that can vary in intensity as well as varying in both space and time (Lima & Bednekoff 1999, Sih & McCarthy 2002, Ferrari *et al.* 2009, Ferrari *et al.* 2010b) so there are benefits to flexible anti-predator behavioural responses (Lima 1998). In this experiment, there was variability in territory defense between the stream water control group and the group exposed to chronic predation risk but over the course of the same week, I did not see the same variability in foraging or growth.

The impact of predation on behaviour and the resulting compensation that can occur has been shown across multiple species and contexts. Crickets *Grillus integer* with extravagant songs, a mating display which greatly increases vulnerability to predation,

have been shown to increase vigilance by hiding for longer periods of time after a disturbance as well as waiting longer periods to resume calling (Hedrick 2000). Specifically, males with longer songs were shown to be the ones compensating. But noise reception can be a method of detecting predators as well. When chaffinches *Fringilla coelebs* are exposed to a high level of background noise, effectively eliminating a method of risk detection, they became more vigilant during foraging, spending less time in the “head down” position and increasing time spent scanning (Quinn et al 2006). Scorpions *Centruroides vittatus* show post natal parental care by carrying their young and it has been shown that although typical antipredator behaviour is to flee to the nearest shelter, due to decreased escape speed, females will aggressively defend themselves from attack, a potentially riskier but necessary compensation in behaviour (Shaffer & Formanowicz Jr. 1996). When conflict arises over a food source, great tits *Parus major* respond with threat displays but under riskier conditions, subordinate individuals reduce the frequency of their displays (Lange & Leimar 2006). Prolonged exposure to northern pike *Esox lucius* predator cues over an 11 day period can cause crucian carp *Carassius carassius* to alter their diel activity pattern from nocturnal to aperiodic and switch habitat preference for vegetation cover (Pettersson et al. 2001). Examples of foraging and mating behavioural compensation under the risk of predation tend to be more common while studies providing a direct test of the effect of chronic predation risk on territory size, foraging and growth as a combined study are far less frequent.

The risk allocation hypothesis

Over acute time frames of minutes to hours, typical anti-predator behaviour for juvenile Atlantic salmon involves reducing movement and foraging (Chivers & Smith

1998, Leduc *et al.* 2007). This reaction to acute predation threat represents time taken away from increasing energy stores. Territory defense seems as though it would fall in this category as well but by defending a territory, and gaining exclusive access to both its energetic and safety resources, territorial salmonids can have faster growth rates than non-territorial fish (Martel 1996). Like with all behaviour, territory defense appears to be a chosen strategy as long as the benefits outweigh the costs. This is predicted by optimality models of territory defense and in this case, holds true for the observed reduced territory, the response to the extra cost imposed by predation risk.

The risk allocation hypothesis states that during periods of low predation risk, prey should devote more energy to responding proportionally to threat, but during periods of high risk, prey should choose to trade anti-predator behaviour for foraging (Lima & Bednekoff 1999, Ferrari *et al.* 2009). In other words, if an individual is under a high or chronic threat of being preyed upon, lost foraging opportunities represent just as important a risk as continuing to do so under acute predation threats. Behaviour should be optimized to benefit future fitness or to be more specific, foraging should be optimized to benefit growth (Blanchet *et al.* 2007). For example, convict cichlids *Archocentrus nigrofasciatus* exposed to high levels of background risk over a 3 day period exhibited a low intensity antipredator response when subsequently exposed to a variety of alarm cue concentrations (Brown *et al.* 2006). The threshold alarm cue concentration which elicited a response was also higher in the group with the high risk pre-exposure period.

I looked at two extremes of predation risk in a natural setting: high risk and ambient risk. Strictly speaking, because no low risk group above ambient levels is represented in this experiment, this is not a test of the risk allocation hypothesis,

however, its influence is found in our results. This experiment's chronic threat of predation as mimicked by twice daily doses of alarm cue over a 7 day period represents a temporally stable high risk situation, one similar to that described by the risk allocation hypothesis and my results hold true to its predictions. Though predation risk was high, individuals continued to forage at a rate not significantly different than the stream water control group. Where this study differs is in its analysis of a related behaviour and the trade-off made there in order to optimize foraging. Reducing territory size as an anti-predation strategy could signify a reduction in energy devoted to defense and as a consequence, I could predict a decrease in foraging. That this was not seen provides evidence for the idea that anti-predator behaviours are plastic, can be treated independently, and that trade-offs and behavioural decisions can be made under this level of chronic risk.

Non-consumptive effects and resource dynamics

This experiment was conducted over two field seasons which differed in environmental conditions and therefore, also differed in resource dynamics. In 2010, conditions were warmer and precipitation less abundant than in 2011. Territory size for the alarm cue treatment group decreased over the 7 day period in 2010 but increased in 2011, though on average they remained smaller than the control group. A possible answer for these results could come from the weather's effects on resources. When resources are in persistent flux, like in 2010, non-consumptive effects are stronger than when resources are stable (Preisser *et al.* 2009). Non-consumptive effects of predation are the long term results of predation other than death. In a season like 2010 where there is low flow and drift, individuals should show higher compensation and therefore higher

non-consumptive effects. Even if YOY salmon attempted to compensate for decreased territory size, the resources were not there to reward the effort. Conversely, stable conditions like those of high flow and high drift in 2011 should show lower compensation and lower non-consumptive effects. This unpredictable but natural flux in conditions and its effects on behaviour exposes yet another important reason for this work being conducted in the wild. No growth difference was detected between treatment groups between 2010 and 2011 despite this difference in territorial response and environmental conditions. It is possible that a 1 week period is not enough to detect a difference and so, further research extending the test period would be required.

In summary, I found that chronic perceived predation risk over a seven day period can affect territory size in a semi natural setting without affecting related behaviours like foraging effort. Over this period of time, I also found no difference in growth, suggesting that juvenile Atlantic salmon under chronic risk compensate for changes in territory size by maintaining a similar foraging effort to individuals under ambient risk. In addition, I also found that the year the trials were completed affected territorial behavioural, a response which could be due to the difference in resource dynamics of the two field seasons. Future work would need to address the roles of resources and competition, including dominance rank, in behavioural decision making under chronic predation pressure. This could be achieved by increasing the density of individuals being tested. Increasing the length of the chronic testing period could address the need to verify that one week is enough to measure a difference in growth between groups as well as extending the test for future fitness beyond growth to include survival over winter.

Figure 1. Map of Catamaran Brook adapted from Leduc *et al.* 2006. Bold arrow indicates the lower reach of the brook where the study sites were located.

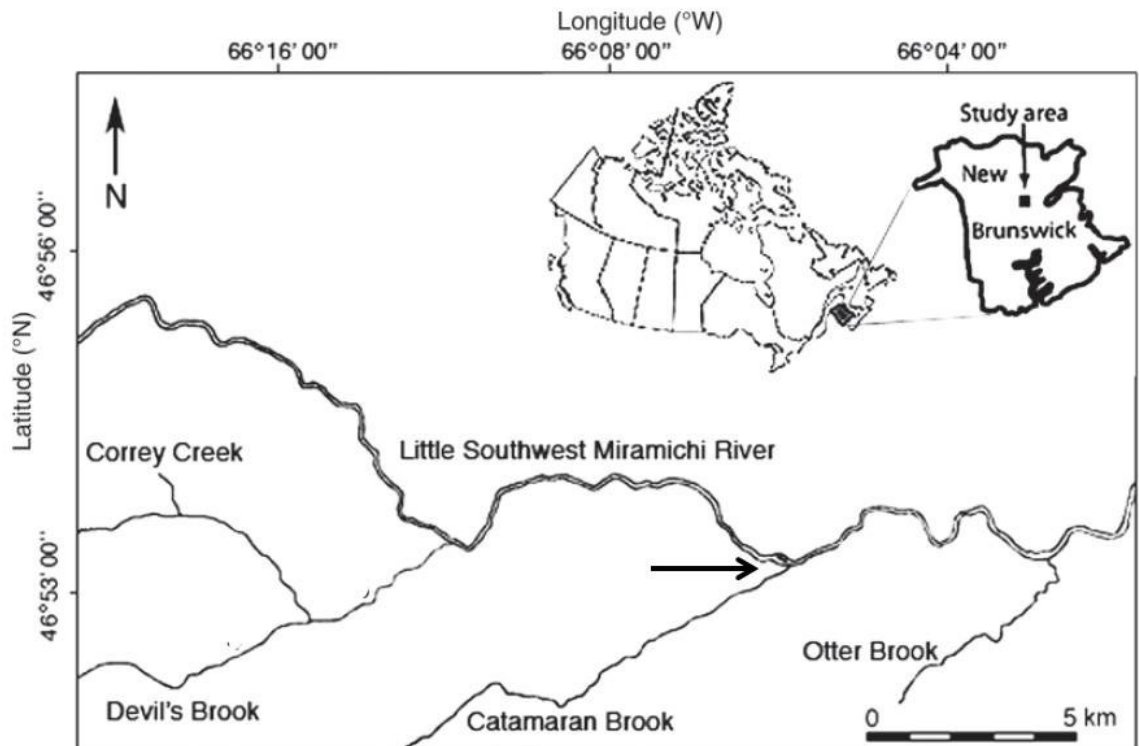
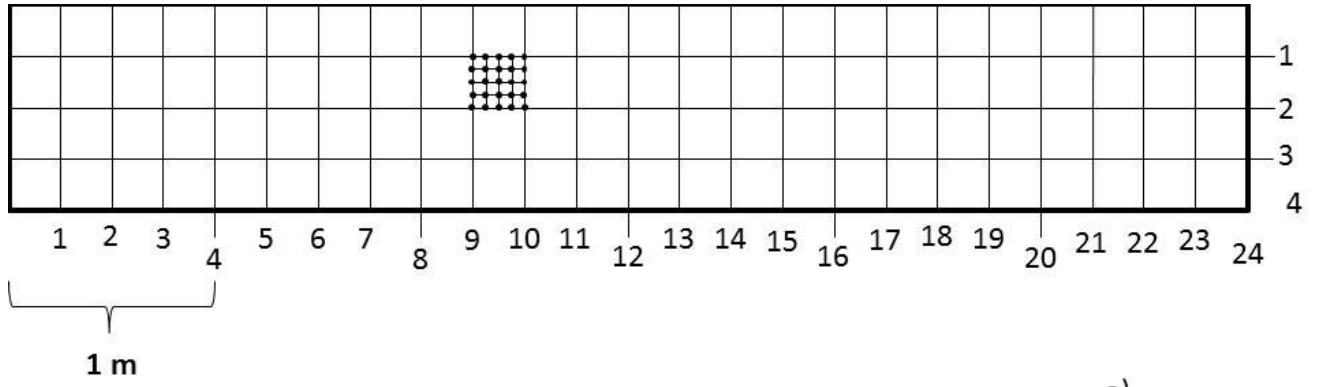


Figure 2 . a) Representation of the grid used for territory size analysis. For every 25 X 25cm square, the focal fish was marked as being at the closest of one of 20 locations judged by the observer. b) Picture of the enclosure with markers every 25 cm along the bottom edge. Taken July 2010.



a)



b)

Figure 3. Mean \pm SE. Territory size for the 2010 and 2011 field seasons separated by treatment (Alarm Cue and Stream Water Control) and day (1 and 7).

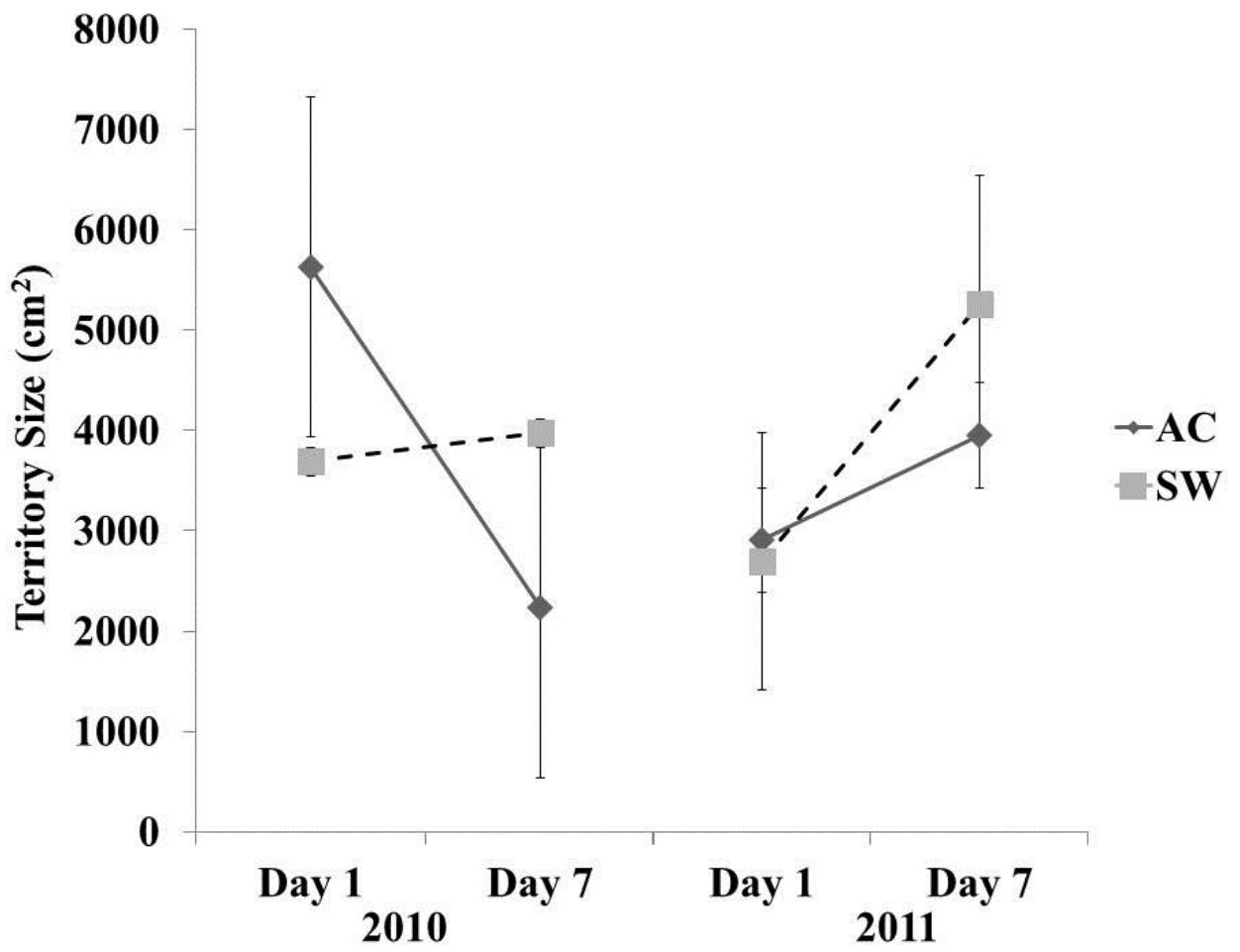


Figure 4. Mean \pm SE. Foraging for the 2010 and 2011 field seasons separated by treatment (Alarm Cue and Stream Water Control) and day (1 and 7).

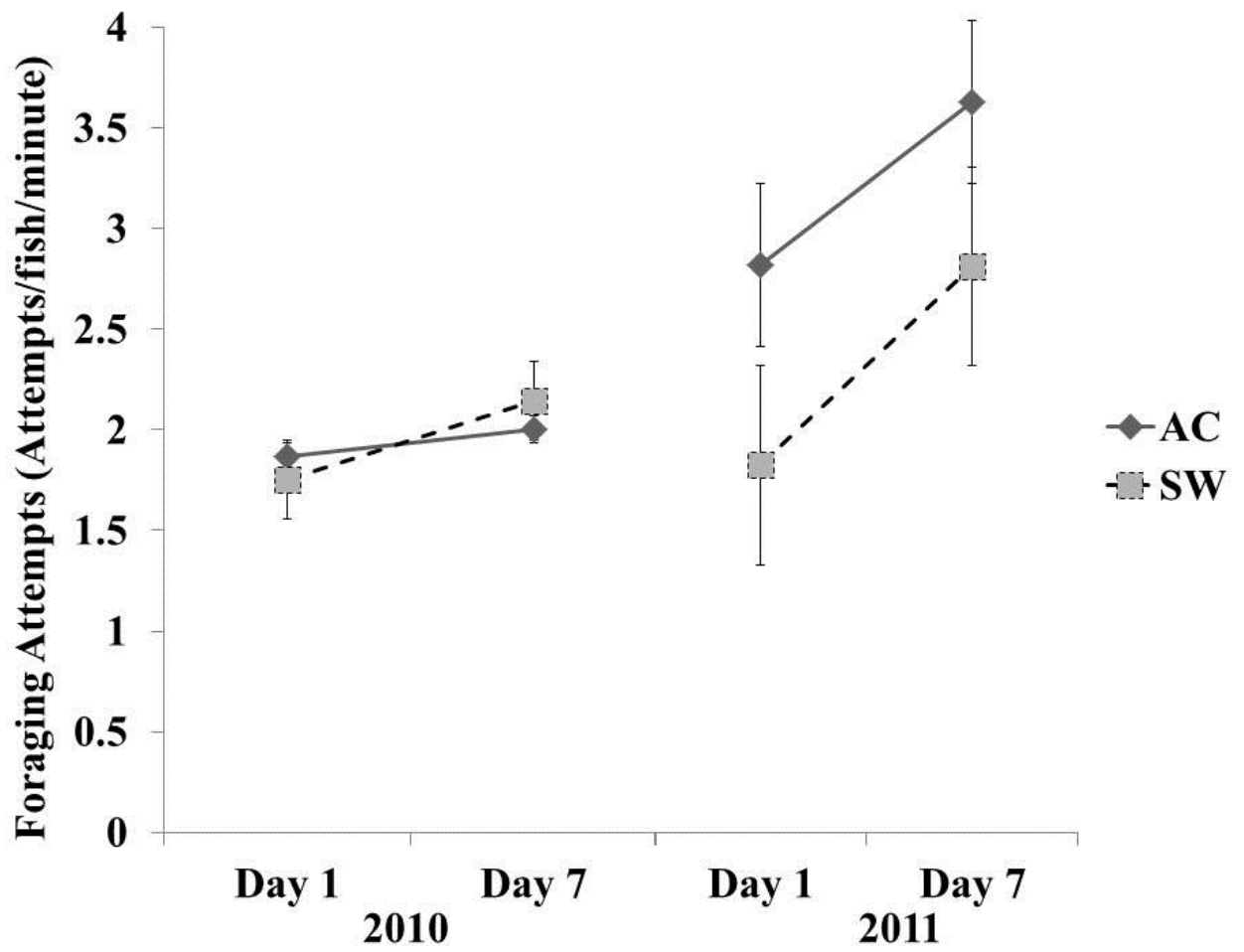


Table 1. Mean weight \pm SE. Between treatment groups, the mean weight did not vary significantly, either within the 7 day period or between years but the difference in weight of individuals in 2010 and 2011 is worthy of note and may be explained by the difference in weather between years.

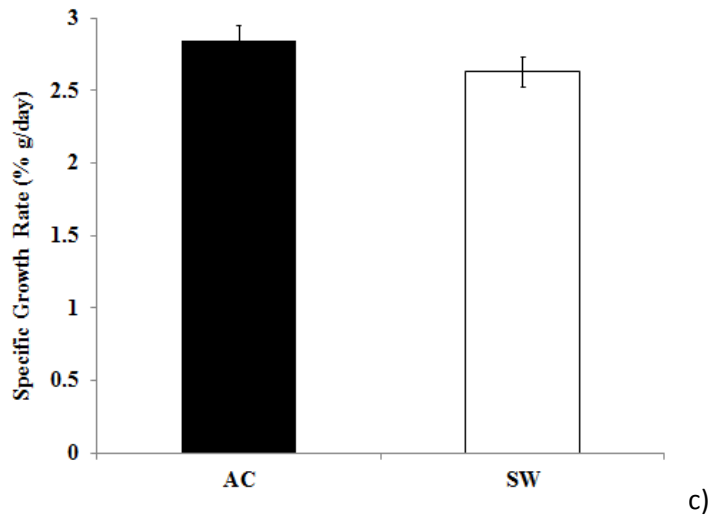
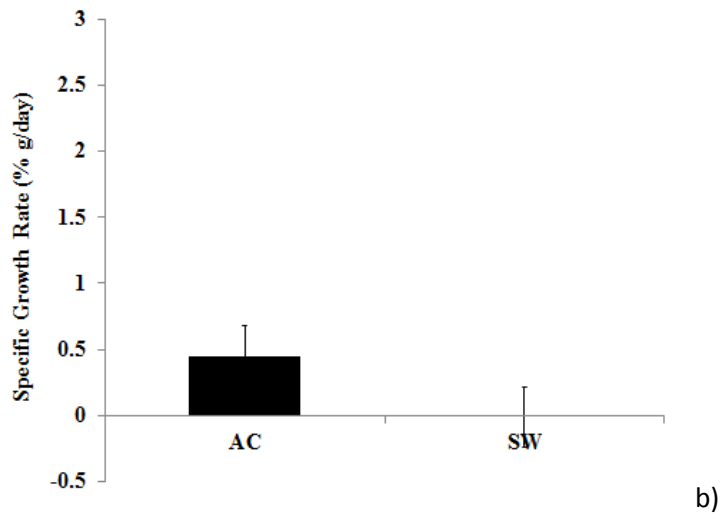
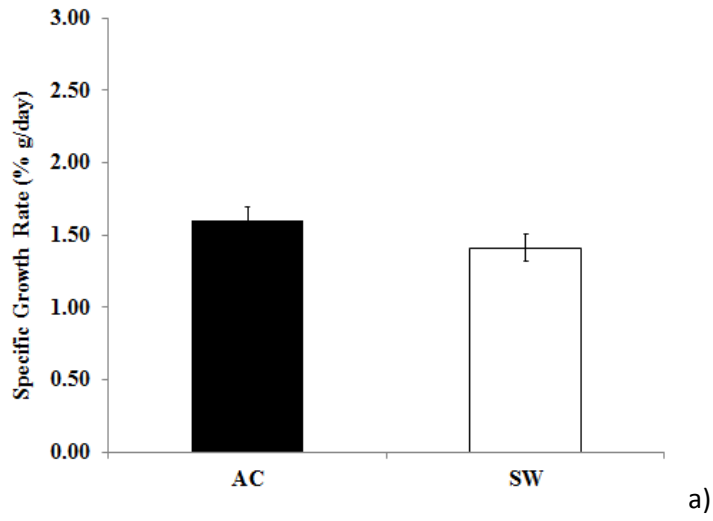
Alarm Cue Treatment Group

		Mean Weight \pm SE (g)	
	n	Day 0	Day 7
2010	7	1.16 \pm 0.05	1.20 \pm 0.07
2011	8	0.73 \pm 0.06	0.90 \pm 0.04

Stream Water (Control) Treatment Group

		Mean Weight \pm SE (g)	
	n	Day 0	Day 7
2010	7	1.22 \pm 0.06	1.22 \pm 0.05
2011	8	0.60 \pm 0.05	0.73 \pm 0.05

Figure 5. Mean \pm SE. Specific Growth Rate results for a) overall, b) 2010 and c) 2011, for both treatment groups.



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