Behavioural and Ecological Implications of Predation Risk in Juvenile Atlantic Salmon (*Salmo salar*)

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Abstract

Behavioural and Ecological Implications of Predation Risk in Juvenile Atlantic Salmon (*Salmo salar*)

Jae-Woo Kim, Ph.D.

Concordia University, 2009.

Despite the wealth of laboratory studies, the effects of local predation risk on the behaviour and ecology of a prey species under natural conditions have rarely been examined. In Chapter 1, I tested the hypothesis that juvenile Atlantic salmon (*Salmo salar*) use both chemical and visual information to assess predation risk under natural conditions. Both young-of-the-year (YOY) and parr salmon exhibited antipredator responses when exposed to a chemical alarm cue and exposure to alarm cues influenced their response to a visual threat. While YOY and parr differed in the type and intensity of antipredator responses, both chemical and visual cues are used in an additive manner. In Chapter 2, I tested the prediction that YOY use chemical alarm cues to assess the predation risk of alternative habitats and decide where to settle over a two-week period following emergence. In seven similar reaches of Catamaran Brook, New Brunswick, I established three contiguous sections where I manipulated the perceived predation risk by releasing alarm cues versus a stream water control.

The density of YOY decreased in risky sections and increased in control and untreated buffer sections, whereas the density of parr was not affected. Clearly, YOY salmon can assess and select habitats based on the perceived level of predation risk. If one assumes that predation risk is a cost, optimality models predict that territory size will decrease with increasing predation risk. In Chapter 3, I examined whether both acute and chronic predation risk influences the territorial behaviour of YOY. When exposed to a single dose of chemical alarm cue, YOY salmon decreased the number of switches between foraging stations, but did not change their territory size or foraging rate. When exposed to chemical alarm cue over a two week period, YOY salmon reduced the size of their territories, but did not change their foraging rate or number of switches. Clearly, YOY adjusted their territorial behaviour in response to both acute and chronic increases in perceived predation risk, but in different ways. Together, my results suggest that predation risk influences not only short-term (immediate) anti-predator behaviour, but is also an important component of habitat selection and shapes territorial behaviour over longer periods.

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Contribution of Authors

The Chapters of this thesis were prepared as manuscripts for submission to peer-reviewed journals. I contributed to the planning, collection of data, data analyses, and writing of all manuscripts. Dr. J.W.A. Grant and Dr. G.E. Brown contributed to the planning, data analyses, and editing of all manuscripts. I.J. Dolinsek, N.N. Brodeur, and Dr. A.O.H.C Leduc contributed to the planning, collection of data, and editing of the first paper. J.L.A. Wood contributed to the planning, collection of data, data analysis, and editing of the third paper.

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General Introduction

Predation is a major selective force shaping the evolution of morphological adaptations such as cryptic and aposematic colouration, protective armour, and chemical defences (Harvey and Greenwood 1978; Sih 1987; Lima and Dill 1990). Predation has also been implicated in the evolution of life history traits such as sociality in both the breeding and nonbreeding seasons (Pulliam and Caraco 1984) and reproductive strategies, such as male displays, male-male agonistic interactions, and female sexual responsiveness (Burk 1982; Kelly et al. 1999; Kelly and Godin 2001). More importantly, predation has produced an incredible degree of plasticity in the behaviour of prey organisms (Lima and Dill 1990).

Failure to detect and avoid predators typically means death or a serious injury (Lima and Dill 1990; Lima and Steury 2005). Conversely, unnecessary or maladaptive predator avoidance behaviour wastes energy and time, decreasing the fitness of prey (Werner and Peacor 2003; Sih et al. 2004). Thus, prey should adjust the type and/or intensity of their behavioural responses to the degree of perceived threat of a predation event (Ydenberg and Dill 1986; Helfman 1989). Over time, individuals capable of optimizing these threat-sensitive trade-offs between the conflicting demands of successful detection and avoidance of potential predators and a suite of other fitness related activities such as foraging and mating should be favoured by natural selection (Lima and Bednekoff 1999).

In order to respond appropriately to the threat of predation, it is important to assess the degree of risk accurately. Sensory information used to determine the presence of a potential predator may be visual (e.g. movement, shadows), chemical (e.g. odours, kairomones), tactile (e.g. contact with a predator), or mechanical/acoustic (e.g. near-field air motion, substrate vibration, vocalization) (Lima and Dill 1990; Kats and Dill 1997; Tollrian and Harvell 1999; Relyea 2003; Turner 2008). Among vertebrates, examples include responses to predator visual cues by birds (Kenward 1978; Elgar 1989; Lima 1994), mammals (Caro 1986; Stankowich and Coss 2007), lizards (Burger and Gochfeld 1990; Cooper 2008), and fish (Grant and Noakes 1987) and changes in activity levels or avoidance behaviour in fish and mammals in response to the presence of chemosensory cues (von Frisch 1941; Rehnberg and Schreck 1987; Smith 1992; Engelhart and Müller-Schwarze 1995; Burwash et al. 1998).

Animals, however, likely rely on multiple sources of sensory information to assess the degree of predation risk. Animals may use the information in a complementary (Helfman 1989; Smith and Belk 2001; Brown and Magnavacca 2003) or compensatory (Hartman and Abrahams 2000; Chivers et al. 2001; Lima and Steury 2005) manner. For example, glowlight tetras (*Hemigrammus erythrozonus*) exposed to the odour of cichlids fed tetras exhibited a greater latency to inspect, fewer inspections and a higher minimum approach distance under high light conditions than those under low light conditions (Brown and Magnavacca 2003). However in some situations, animals may rely primarily on one sensory modality to compensate for the lack of or inaccurate information from other sensory modalities about local predation risk. For example, fathead minnows (*Pimephales promelas*) in turbid water rely more on their chemical senses than on their impaired visual sense (Hartman and Abrahams 2000). Alternatively, animals may exhibit non-graded antipredator responses. For example, singleton juvenile convict cichlids (*Amatitlania nigrofasciata*) reduced their time spent moving and foraging rate when exposed to conspecific alarm cue, regardless of the stimulus concentrations (Brown et al. 2006). How prey integrate multiple sensory cues may depend on the availability and quality (e.g. accuracy and reliability) of information about predation risk (Hartman and Abrahams 2000; Smith and Belk 2001; Blanchet et al. 2007).

Particularly within aquatic systems, damage-released chemical alarm cues are a reliable source of information about local predation risk because they are released from the skin of an injured animal during a predation event (Smith 1992; Chivers and Smith 1998; Brown 2003). When alarm cues are released into the water column, they elicit short-term predator avoidance behaviour such as decreased movement or foraging (Smith 1992; Chivers and Smith 1998) across a range of taxa, including gastropods (Dalesman et al. 2007), crustaceans (Peacor and Hazlett 2007), amphibians (Chivers et al. 1996), and fishes (Lawrence and Smith 1989; Dupuch et al. 2004).

Conversely, some studies suggest that alarm cues may be detected but ignored under natural conditions, which may be perceived as safer than laboratory conditions (Magurran et al. 1996; Irving and Magurran 1997). Laboratory conditions may also lack the ecological complexity of the wild, where prey acquire and assess information about predation risk. Hence, while field tests of how prey integrate information are becoming increasingly important, few field studies have been completed due to the difficulty of quantifying or manipulating predation risk under natural conditions (Wisenden et al. 2004; Leduc et al. 2007). In addition, the fitness benefits and costs of threat-sensitive trade-offs have rarely been examined - most studies assume and rarely test that the animals exposed to increased risk suffer in terms of long-term fitness (Mirza and Chivers 2003; Kim et al. 2004). Hence, there is a lack of conclusive evidence demonstrating a link between short-term behavioural responses and the long-term fitness benefits of prey organisms.

The defence of foraging territories provides the owner with relatively exclusive access to resources (Puckett and Dill 1985; Theimer 1987; Grant 1997), but is costly in terms of time and energy spent on defence (Puckett and Dill 1985; Ydenberg and Houston 1986). Because territorial defence is a conspicuous activity, the cost of holding a territory increases under increased risk of predation (Lima and Dill 1990), so that territory size will be subject to balancing these conflicting demands. Optimality models (e.g. Hixon 1980; Schoener 1983) predict that territory size will decrease with increasing benefits or costs. While many studies support these predictions (Grant 1997; Adams 2001), whether the 'optimal' size of a territory will decrease with increasing predation risk is not clear. Furthermore, how predation risk, particularly the long-term risk, influences fitness-related activities such as foraging and habitat selection, and its potential impacts on population dynamics is not known (Werner and Peacor 2003; Blanchet et al. 2008).

Worldwide, salmonids provide important ecosystem services, because they continue to generate a wide range of economic, social, and cultural benefits. However, four species in Canada are considered endangered or threatened (COSEWIC) and their numbers are declining along with 700 other North American freshwater fishes due to anthropogenic influences such as habitat loss, pollution, exploitation, and climate change (Boisclair 2004; Jelks et al. 2008). Hence, the need for conservation and restoration efforts for salmonids and their habitats continues to increase. Moreover, it is becoming increasingly important to understand the mechanisms/causes explaining the declining numbers of salmon in the wild.

Predation is considered as one of the major sources of mortality for juvenile salmonids (Sogard 1997). Juvenile Atlantic salmon (*Salmo salar*) are vulnerable to predation by fishes (Symons 1974; Brannas 1995; Pepper et al. 1985), birds (Scott and Crossman 1973; Wood 1987; Ruggerone 1986), and mammals (Heggenes and Borgstrom 1988; Carss et al. 1990). Despite the potential importance of predation, relatively little is known about the population consequences of predation (Mather 1998). However, between 4 and 60 % of stocked Atlantic salmon fry are eaten by brook trout (*Salvelinus fontinalis*, Henderson and Letcher 2003). Furthermore, controlling the number of potential avian predators, such as common mergansers (*Mergus merganser*) and belted kingfishers (*Megaceryle alcyon*) increases the total number of Atlantic salmon smolts (Elson 1962, 1975).

Stream-dwelling salmonids have been popular model systems for investigating territoriality because they defend feeding territories (Slaney and Northcote 1974; Elliott 1990; Keeley 2000; Steingrímsson and Grant 2008). Furthermore, territoriality may limit the density and size of salmon because of the availability and quality of suitable habitats (Grant and Kramer 1990; Steingrímsson and Grant 1999).

Physical variables, such as current velocity and depth, which affect the foraging profitability of habitats, influence habitat selection in salmonids (Guay et al. 2000; Girard et al. 2004; Rosenfeld and Taylor 2009). While juvenile salmon prefer habitats with abundant cover from predators (Kalleberg 1958; Culp et al. 1996; Venter et al. 2008), it is not clear how they actually assess predator abundance or activity. When exposed to chemical cues indicating the presence or activity of predators, juvenile salmon exhibit short-term antipredator behaviour (Leduc et al. 2006). However, whether juvenile Atlantic salmon in the wild use chemical information to assess and respond to the relative predation risk of alternative habitats when settling in a stream is unknown.

In addition, only a few studies have examined threat-sensitive predator avoidance behaviour in salmonids under natural conditions (Leduc et al. 2006). In contrast, many studies have shown that salmonids exhibit anti-predator behaviour in response to a short-term increase in predation risk under laboratory conditions or in semi-natural enclosures (Brown 2003; Blanchet et al. 2007). For example, juvenile coho salmon (*Oncorhynchus kisutch*) reduce their attack distances on drifting prey when exposed to odour of common mergansers (Martel and Dill 1993). Similarly, Atlantic salmon parr are less likely to orientate to passing food particles and to attack them after a brief exposure to a model trout predator (Metcalfe et al. 1987). However, the long-term consequences of anti-predator behaviour or responses to long-term predation risk in salmonids as well as potential impacts at broader scales are unclear (Blanchet et al. 2008).

The purpose of my thesis is to address the behavioural and ecological implications of predation risk by quantifying the costs and the benefits associated with anti-predator behaviour using wild juvenile Atlantic salmon under natural conditions. In Chapter 1, I examined how juvenile salmon assess and respond to short term predation threats based on the combination of visual and chemical cues. I tested the prediction that juvenile salmon will use the information in a complementary manner when exposed to the combination of chemical and visual cues indicating an elevated level of perceived predation risk.

In Chapter 2, I investigated whether juvenile salmon use chemical information to assess perceived predation risk when settling in a new habitat, and how they respond to changes in perceived predation risk after settling and establishing a territory within a habitat. I tested the prediction that the number of juvenile salmon settling will be greater in control than in risky sites during the settlement period. In addition, juvenile salmon with established territories will detect and respond to changes in perceived predation risk by moving away from areas of high risk.

Finally, in Chapter 3, I examined how both acute and chronic increases in perceived predation risk influence the territorial behaviour of juvenile salmon. I tested the prediction that juvenile salmon will decrease their territory size, foraging rate, and number of switches between foraging stations when exposed to both acute and chronic increases in perceived predation risk. Moreover, the intensity of response will be greater to a chronic increase in perceived predation risk than to a one-time increase in predation risk.

Chapter 1. Combined effects of chemical and visual information in eliciting antipredator behaviour in juvenile Atlantic salmon *Salmo salar* [*]

Introduction

The most widely studied sources of information about predators used by aquatic vertebrates are visual (Metcalfe et al. 1987; Helfman 1989; Dionne and Dodson 2002) and chemical (Brown et al. 1995; Chivers and Smith 1998; Smith 1999) cues. According to the threat-sensitive predator avoidance hypothesis (Helfman 1989), multiple cues about predators should be complementary, contributing in an additive way to threat assessment (Smith and Belk 2001; Brown and Magnavacca 2003; Lima and Steury 2005). For example, mosquitofish *Gambusia affinis* (Baird and Girard) maintained the greatest distance from a potential predator, hungry mosquitofish-fed green sunfish *Lepomis cyanellus* Rafinesque, an intermediate distance from hungry green sunfish fed on chironomids or satiated green sunfish fed on mosquitofish, and the shortest distance from satiated, chironomid-fed green sunfish (Smith and Belk 2001). Similar additive effects of chemical and visual cues on antipredator behaviour have been observed in glowlight tetras *Hemigrammus*

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[*] Kim, J.-W., Brown, G.E., Dolinsek, I.J., Brodeur, N.N., Leduc, A.O.H.C. & Grant, J.W.A. (2009) *Journal of Fish Biology*, **74**, 1280-1290.

erythrozonus Durbin (Brown and Magnavacca 2003) and juvenile Atlantic salmon (Blanchet et al. 2007). In some situations, however, animals may rely primarily on one sensory mode to compensate for the lack of or inaccurate information from other sensory modalities about local predation risk (Hartman and Abrahams 2000; Lima and Steury 2005). For example, fathead minnows *Pimephales promelas* Rafinesque in turbid water rely more on chemical information than on their impaired sense of vision, whereas in clear water they rely more on visual than on chemical information (Hartman and Abrahams 2000). Alternatively, animals may sometimes exhibit non-graded antipredator responses regardless of perceived predation risk. For example, the juvenile bicolor damselfish *Pomacentrus partitus* (Poey) respond strongly to all predator models regardless of the level of perceived threat (Helfman and Winkelman 1997).

Whether or not animals use multiple sensory modes in either an additive or compensatory manner may depend on the availability and quality (e.g. accuracy and certainty) of information about predation risk. The few studies (Hartman and Abrahams 2000; Smith and Belk 2001; Blanchet et al. 2007) addressing this issue have been conducted under laboratory conditions, which may lack the ecological complexity in which prey may require multiple sources of information. Furthermore, some authors suspect that alarm cues may be detected but ignored under natural conditions, which may be perceived as safer than laboratory conditions (Magurran et al. 1996; Irving and Magurran 1997). Therefore, it is important to examine how prey integrate information from multiple cues while assessing predation risk under fully natural conditions (Wisenden et al. 2004; Leduc et al. 2007).

The strength of a predator avoidance response also depends on the 'state' (e.g. hunger level, size, prior experience, and social status) of the prey organism. Larger (older) fish take fewer risks with predators by taking longer to resume foraging after an encounter (Grant and Noakes 1987; Reinhardt and Healey 1999; Dowling and Godin 2002; Brown and Braithwaite 2004), presumably because the relative benefits of growing quickly decrease with size. While different diel activity patterns suggest that parr (age 1+ year) are more risk averse than young-of-the-year (YOY; 0+ year) Atlantic salmon (Gries et al. 1997; Imre and Boisclair 2004; Breau et al. 2007), few studies have yet addressed specifically whether or how age influences risk assessment and predator avoidance in wild juvenile Atlantic salmon (Dionne and Dodson 2002).

In the present study, the combined effects of chemical and visual cues in eliciting antipredator behaviour were examined in two age classes of juvenile Atlantic salmon under natural conditions. The predictions of the study were that: (1) individuals exposed to a chemical alarm cue (i.e. increased perceived predation risk) will exhibit antipredator behaviour by taking longer to resume foraging and decreasing foraging, (2) further exposure to a visual cue will enhance this predator avoidance response (i.e. combined effects of chemical and visual cues) and (3) the intensities of this predator avoidance behaviour will be greater in parr than in YOY.

Materials and methods

Study site and species

This study was conducted in two streams (Catamaran Brook and the Little Southwest Miramichi River), located in Northumberland County, New Brunswick, Canada (46°52'42"N, 66°06'00"W) from 12-16 July, 18-21 August 2005 and 1-18 July 2006. In Catamaran Brook, study sites were located in a 200 m reach upstream of the mouth, whereas in Little Southwest Miramichi River, they were located in a 200 m reach downstream from the mouth of Catamaran Brook.

Collection of alarm cue

Atlantic salmon parr to be used as skin donors were collected by electrofishing in July of 2005 ($n = 23$, mean ± S.D., standard length (L_S) = 64·8 ± 4·8 mm) and June of 2006 ($n = 18$, mean ± S.D., $L_S = 76{\cdot}9 \pm 5{\cdot}1$ mm) from Little Southwest Miramichi River. Skin donors were killed with a single blow on the head (in accordance with Concordia Animal Care Committee Protocol AC-2005-BROW) and skin fillets from both sides were removed and immediately placed into an ice-chilled container filled with stream water. Skin fillets were homogenized and diluted into a solution with stream water. The resulting concentration (9 mm^2 ml^{-1}) elicits a consistent antipredator response in salmonids (Leduc et al. 2006). The standard solution was frozen in 20 ml aliquots at -20°C until needed. For this study, 800 ml of alarm cue (*c.* 72 cm^2 of skin), equivalent to eight donor fish, was used; the remainder was used in other ongoing studies. As a control, 20 ml aliquots of stream water were also frozen. The frozen solutions were thawed 10 min prior to use.

Experimental protocol

The juvenile Atlantic salmon (focal fish) were located by snorkelling the test site. Focal fish were either YOY [Fork length (L_F) < 50 mm] or parr (L_F > 50 mm). Once a focal fish was located, observations were conducted for at least five min to ensure that the fish was foraging normally prior to the quantification of behaviour (Leduc et al. 2006; Steingrímsson and Grant 2008). The observer was *c.* 1·5 m downstream of the focal fish to ensure a clear view and to reduce interference with drifting items and the stream current. Trials of 15 min in duration were divided into three blocks of five min: baseline, post-chemical stimulus and post-visual stimulus. After 5 min of observation (i.e. the end of baseline observation), an assistant randomly selected either chemical alarm cue or stream water and released the stimulus (20 ml) in the water column with a 60 ml syringe from 1 to 1·5 m upstream of the focal fish. At the end of post-chemical stimulus observation, a novel (visual) stimulus (a fluorescent orange ball 40 mm in diameter attached to the end of a 2 m long, metal rod of 10 mm in diameter) was presented to the focal fish. The focal fish was approached with the visual stimulus by sliding the rod and ball towards the fish at a constant speed (0·3 m s^{-1}) from either '3' or '9' o'clock, with '12' o'clock as the direction the fish was facing. As soon as the fish moved from its foraging position, the rod was halted and lowered to the streambed for measurement of reactive distance to the visual stimulus (Grant and Noakes 1987). After each observation, all YOY were captured using dip-nets and measured (± 1 mm) with a calliper or ruler; parr were more wary and were not captured. All control and experimental trials were conducted over similar habitats (Dolinsek et al. 2007).

A total of 83 (39 alarm cue and 44 stream-water control) trials were completed: 30 YOY (15 alarm cue and 15 control) and 31 parr (14 alarm cue and 17 control) in 2005, and 22 YOY (10 alarm cue and 12 control) in 2006. All the observations were made between 1000 and 1900 hours to coincide with the peak activity level of YOY Atlantic salmon (Breau et al. 2007) and to ensure good visibility for snorkelling. To avoid observing the same fish twice and to minimize the effects of the chemical stimulus from previous trials, subsequent trials were conducted 4-5 m upstream of the previous trial (Dionne and Dodson 2002).

To examine the potential effects of alarm cue on food availability, 20 1 h drift samples were collected using a drift net (152 wide X 230 high X 1000 mm long, mesh-size 300 μm) before and after an injection of chemical alarm cue (released 1-1·5 m upstream of the net) from 19-20 July to 16-17 August, 2006. Each drift sample was preserved in 70% ethanol. Intact prey items in the drift were counted using a dissecting microscope. Inedible material, such as decomposing leaves and insect exuviae, was removed.

Behavioural measures

To assess the intensity of antipredator responses to the chemical and visual stimuli, four behaviour patterns were quantified: the latency to resume foraging after the exposure to the chemical stimulus, the rate of foraging attempts (foraging rate), the latency to resume foraging after the exposure to the visual stimulus and the reactive distance to the visual stimulus. A foraging attempt was defined as a movement of at least half a body length toward a drifting particle or a particle on the substratum. The foraging rate (min^{-1}) was calculated for the entire 5 min for each of the three observation periods. The reactive distance (± 5 mm) to the visual stimulus was measured as the distance from the visual stimulus (e.g. tip of the orange ball) to the focal fish's position at the time of flight following the exposure to the visual stimulus (Grant and Noakes 1987; Wisenden and Harter 2001).

Eighty three observations out of 104 attempts were completed. Parr were more wary of the observer than YOY; seven of 59 YOY and 12 of 43 parr disappeared from view during the baseline observation period (G-test, d.f. = 1, $P < 0{\cdot}05$) and one YOY (stream-water control) and one parr (alarm cue) disappeared immediately after the release of the chemical stimulus and were not included in the analyses. Foraging behaviour during the post-visual stimulus period was measured for 29 parr in 2005 and 22 YOY in 2006 due to a modification of the original experimental design. Partial data were obtained for 10 of 83 completed observations, because five YOY (three control and two alarm cue) and two parr (one control and one alarm cue) did not return after presentation of the visual stimulus (i.e. latency to resume foraging data are missing), and three parr (control) disappeared from view 143, 270, and 295 s after the exposure to the visual stimulus; foraging rates were calculated using the total time of 143, 270, and 295 s. All other available data were included in the analyses.

Statistical analysis

To examine the intensity and frequency of antipredator responses, four dependent variables were analyzed: foraging rates during the three observation periods, latency to resume foraging after both the chemical and visual stimuli, and reactive distance to the visual stimulus (mm). To ensure that the variables were independent of one another, Pearson's correlation coefficients for all pairs of variables were calculated; none were > than 0·90 (range 0·18-0·61), so multicollinearity was not likely a problem (Tabachnick and Fidell 2001).

Because the observations for YOY were conducted in both 2005 and 2006, differences between years were tested for all dependent variables using L_F as a covariate. None of the dependent variables differed significantly ($P > 0{\cdot}05$) between years (latency to resume foraging after the exposure to the chemical stimulus, foraging rate during the baseline observation period, foraging rate during the post-chemical stimulus observation period, reactive distance to the visual stimulus and latency to resume foraging after the exposure to the visual stimulus). While there were small quantitative differences between years, the overall patterns of the treatment effects were similar for both 2005 and 2006. Therefore, the data for 2005 and 2006 were pooled and used in all subsequent analyses.

To examine the relationship between the effects of treatment and age on foraging rates, repeated measures two-way ANOVAs (two treatments X two age classes and the foraging rates during the three periods) were used to compare the foraging rates among three periods. Only significant interactions between the effects of repeated measures and the main factors (treatment and age) were reported, unless a non-significant interaction between the effects of repeated measures and the main factors appeared to be significant and hence required explanation. For the three other dependent variables (latency to resume foraging after the exposure to the chemical stimulus, reactive distance to the visual stimulus and latency to resume foraging after the exposure to the visual stimulus), two-way ANOVAs (two treatments X two age classes) were used.

Three of four dependent variables were not normally distributed (Kolmogorov-Smirnov: latency to resume foraging after the chemical stimulus, reactive distance to the visual stimulus and latency to resume foraging after the visual stimulus). To meet the assumption of parametric tests, these variables were $\log_{10}$ transformed. For visual purposes, all data presented in the figures are back transformed following analysis and are shown with asymmetric S.E. bars.

Results

Effect of the chemical alarm cue

Both YOY and parr exposed to alarm cues took longer to resume foraging than individuals exposed to stream water (two-way ANOVA, d.f. = 1, 75, $P < 0{\cdot}001$;

Fig. 1.1). In addition, parr took longer to resume foraging than YOY (two-way ANOVA, d.f. = 1, 75, $P < 0{\cdot}001$; Fig. 1.1).

As predicted, there was a significant interaction between the effects of the chemical stimulus treatment and the changes in the foraging rates for both YOY and parr during the baseline and post-chemical observations (repeated measures two-way ANOVA, d.f. = 1, 79, $P < 0{\cdot}001$; Fig. 1.2). When exposed to a chemical alarm cue, both YOY and parr decreased their foraging rate compared to the baseline (repeated measures one-way ANOVA, d.f. = 1, 37, $P < 0{\cdot}01$; Fig. 1.2), whereas they increased their foraging rate following the exposure to control (repeated measures one-way ANOVA, d.f. = 1, 42, $P < 0{\cdot}01$; Fig. 1.2). Furthermore, YOY foraged at a higher rate than parr regardless of treatment in all three observations (repeated measures two-way ANOVA, d.f. = 1, 45, $P < 0{\cdot}001$; Fig. 1.2).

To examine the potential effect of alarm cue on the potential prey items of juvenile Atlantic salmon, 20 1 h drift samples were collected before and after the injection of alarm cue. The number of organisms in the drift samples did not differ significantly before ($n = 10$, mean ± S.D., 19·0 ± 10·4) and after ($n = 10$, mean ± S.D., 23·8 ± 19·2) the injection of alarm cue (paired t-test, d.f. = 9, $P > 0{\cdot}05$).

Combined effects of chemical and visual cues

There was a significant interaction between the type of chemical stimulus the fish was previously exposed to and age on reactive distance to the visual stimulus (two-way ANOVA, d.f. = 1, 77, $P < 0{\cdot}05$; Fig. 1.3). Parr had a longer reactive distance to the visual stimulus after a previous exposure to an alarm cue compared to the control (t-test, d.f. = 27, $P < 0{\cdot}001$), whereas YOY did not (t-test, d.f. = 50, $P > 0{\cdot}025$; Fig. 1.3). Despite the significant interaction, parr had a greater reactive distance than YOY (two-way ANOVA, d.f. = 1, 77, $P < 0{\cdot}001$; Fig. 1.3).

As predicted, individuals took longer to resume foraging following the visual stimulus if previously exposed to a chemical alarm cue than to stream water (two-way ANOVA, d.f. = 1, 63, $P < 0{\cdot}05$; Fig. 1.4). Although this increase appeared to be stronger for YOY than parr, there was no significant interaction between the effects of treatment and the age (two-way ANOVA, d.f. = 1, 63, $P > 0{\cdot}05$). In addition, parr took longer than YOY to resume foraging after the exposure to a visual stimulus (two-way ANOVA, d.f. = 1, 63, $P < 0{\cdot}01$; Fig. 1.4).

As expected, the foraging rates for both age classes during the post-chemical and post-visual observations were lower when previously exposed to alarm cue than when previously exposed to control (repeated measures two-way ANOVA, d.f. = 1, 45, $P < 0{\cdot}05$; Fig. 1.2). Contrary to the prediction, however, there was no significant interaction between the effects of type of chemical stimulus on the foraging rates for both age classes during post-chemical and post-visual observations periods (repeated measures two-way ANOVA, d.f. = 1, 45, $P > 0{\cdot}05$). Furthermore, the visual stimulus had no overall effect on changes in the foraging rates of both age classes between the post-chemical and post-visual observations (repeated measure two-way ANOVA, d.f. = 1, 45, $P > 0{\cdot}05$).

Discussion

The present results demonstrated that juvenile Atlantic salmon exhibit short-term antipredator responses to chemical alarm cues under natural conditions, supporting earlier findings by Leduc et al. (2004, 2006). Both YOY and parr foraged at a lower rate and took longer to resume foraging following exposure to an alarm cue than to stream water. Interestingly, juvenile fish actually increased their foraging rate after the exposure to control. This increase in foraging rate did not result from a short-term increase in the drift rate of prey items in response to the alarm cue, as reported by McIntosh et al. (1999). More likely, the upstream snorkeler may have dislodged organisms into the drift when releasing the control stimulus. This potential positive effect on foraging rate, however, should have occurred equally in both treatments.

The results also demonstrated that the response to a visual cue depends on their prior exposure to a chemical cue. Parr had a greater reactive distance to the visual stimulus after exposure to a chemical alarm cue than control groups. Furthermore, both YOY and parr took longer to resume foraging after the visual stimulus if they were previously exposed to an alarm cue, indicating that juvenile Atlantic salmon rely on both chemical and visual information for the assessment of predation risk. As far as is known, this is the first demonstration of the combined use of multiple cues to assess the risk of predation under fully natural conditions.

The data also suggested that age or size influences how fish assess and respond to an increased perceived predation risk (Dionne and Dodson 2002; Brown and Braithwaite 2004). Compared to YOY, parr had a greater reactive distance to a visual stimulus and generally took longer to resume foraging after exposure to both the chemical and visual stimuli. In addition, more observations of parr were incomplete due to focal fish disappearing during the baseline observation period compared to YOY. These results are consistent with the 'asset protection principle' (Clark 1994); parr should be more risk averse than YOY (Brown and Braithwaite 2004) due to their greater body size and shorter latency to smolting. A similar explanation has been advanced to explain why YOY are primarily diurnal when foraging efficiency and predation risk are high whereas parr are active at night (Gries et al. 1997; Imre and Boisclair 2004, Breau et al. 2007). Alternatively, the stronger antipredator response of parr compared to YOY may be attributed to the use of alarm cue (i.e. skin extract) from parr. Both small and large brook charr *Salvelinus fontinalis* (Mitchill) respond stronger to the skin of their own size class than the other size class (Mirza and Chivers 2002).

In summary, the present study demonstrated that juvenile Atlantic salmon rely on both chemical and visual information in a combined manner to assess and respond to an increased risk of predation under natural conditions. Moreover, the study showed that juvenile Atlantic salmon exhibit fine-tuned antipredator responses by varying the type and intensity of their response. In addition, fitness-related behaviour such as foraging rate may be less affected when there is an increase in perceived predation risk (Blanchet et al. 2007). Further research is needed, however, to quantify the benefits and costs associated with predator avoidance behaviour and its potential long term effects on individual's growth and fitness (Lima 1998).

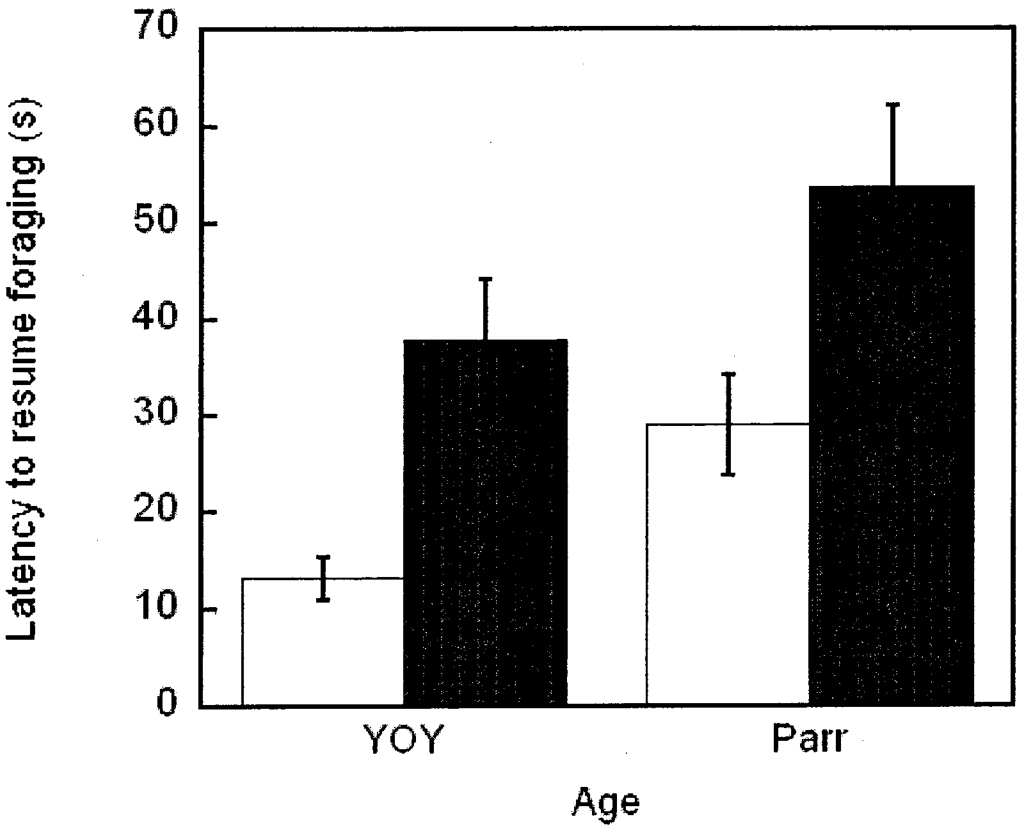

Figure 1.1. Mean ± SE latency to resume foraging for young-of-the-year (YOY) (*n* = 25 for stream water and *n* = 23 for alarm cue) and parr (*n* = 17 for stream water and *n* = 14 for alarm cue) Atlantic salmon either exposed to stream water (☐) or alarm cue (■).

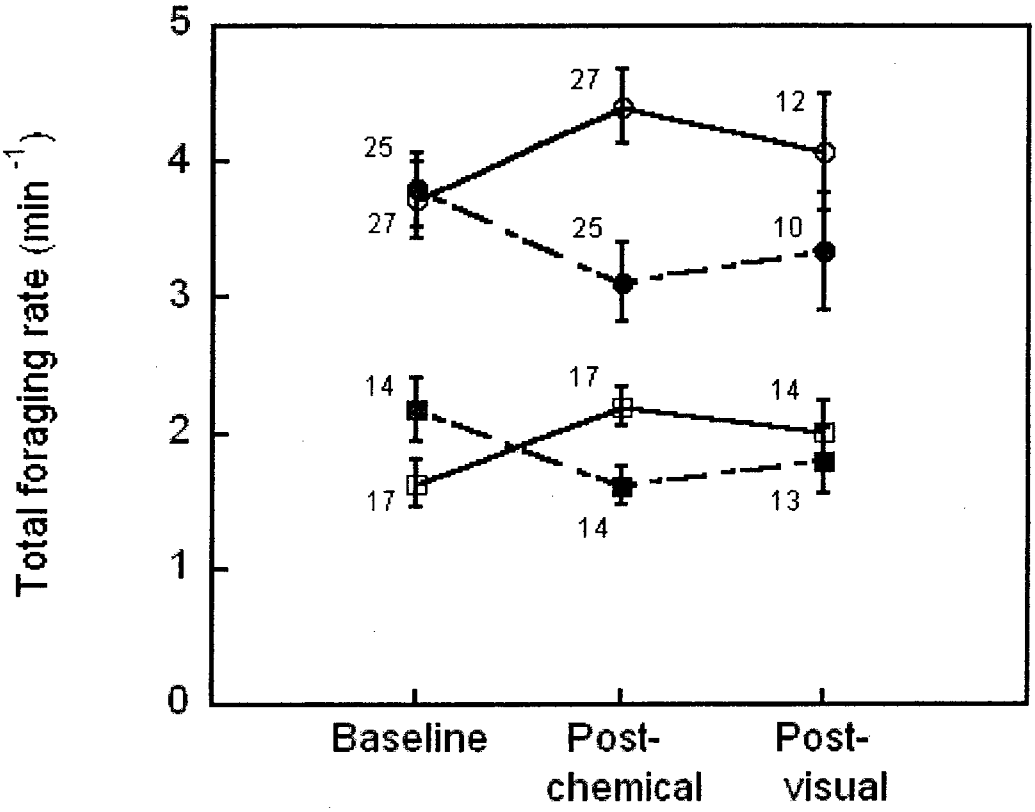

Figure 1.2. Mean ± SE foraging rate for young-of-the-year (○, ●) and parr (□, ■) Atlantic salmon exposed either to stream water (○, □) or alarm cue (●, ■) during the baseline, post-chemical stimulus and post-visual stimulus periods (*n* shown next to symbol).

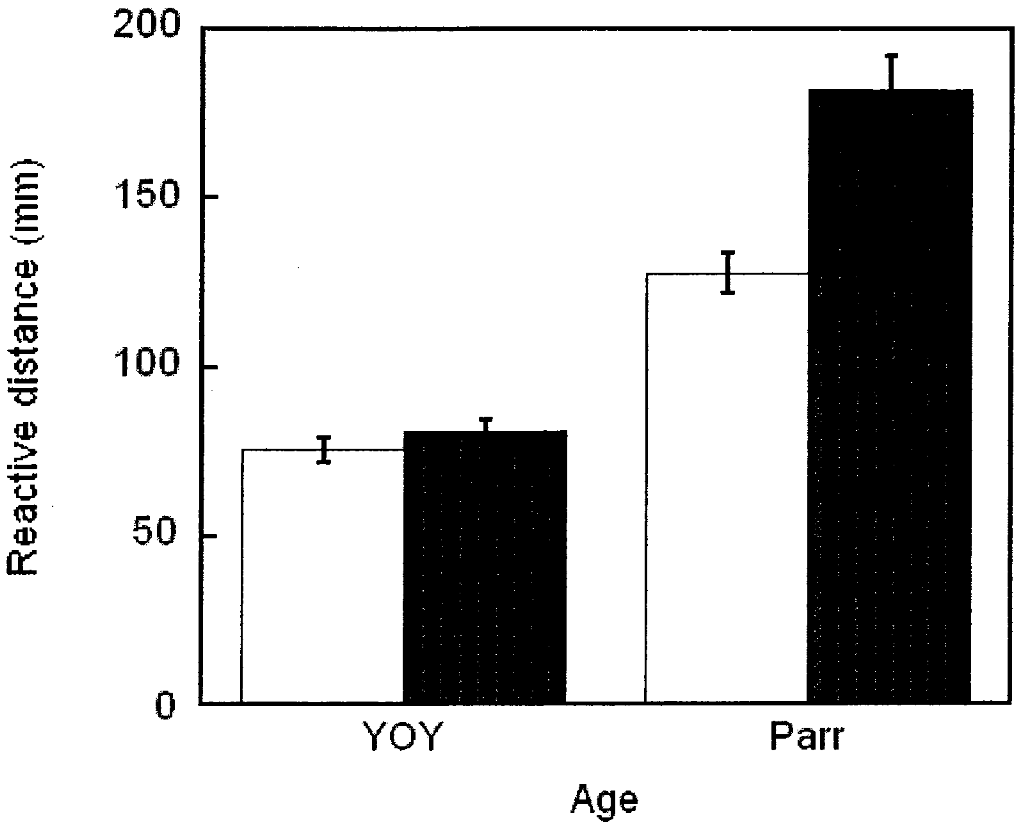

Figure 1.3. Mean ± SE reactive distance to the visual stimulus for young-of-the-year (*n* = 27 for stream water and *n* = 25 for alarm cue) and parr (*n* = 15 for stream water and *n* = 14 for alarm cue) Atlantic salmon previously exposed either to stream water (□) or alarm cue (■).

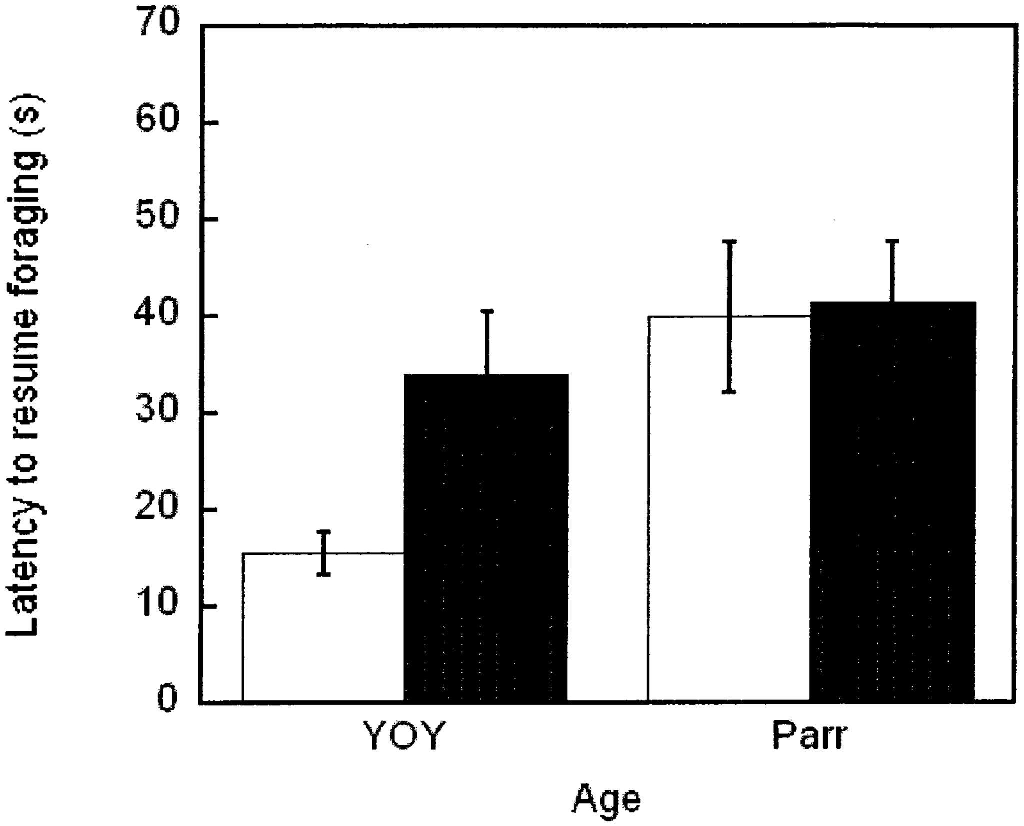

Figure 1.4. Mean ± SE latency to resume foraging after the exposure to visual stimulus for young-of-the-year (*n* = 20 for each) and parr (*n* = 14 for stream water and *n* = 13 for alarm cue) Atlantic salmon previously exposed either to stream water (☐) or alarm cue (■).

Connecting statement

Chapter 1 showed that both YOY and parr Atlantic salmon exhibited anti-predator behaviour after a single episode of increased perceived predation risk under natural conditions. These results indicate that a local increase in predation risk has striking effects on their short-term predator avoidance behaviour. However, the long-term consequences of an increase in perceived predation risk, particularly its effects on habitat selection, remain unclear. Chapter 2 will examine whether the repeated exposure to episodes of alarm cue over a two-week period affects where young fish settle and how fast they grow.

Chapter 2. Do juvenile Atlantic salmon (*Salmo salar*) detect and avoid risky habitats in the wild?

Introduction

Habitat selection has a profound influence on a number of vital processes including population regulation, species interactions, the assembly of ecological communities, and the origin and maintenance of biodiversity (Morris 2003). Given that habitats differ in quality such as growth potential or risk of predation, animals should prefer the habitat that maximizes their fitness (Dill 1978). However, the best areas for foraging are often the most dangerous, forcing the foragers to trade off energy gain against the safety from predators when deciding where to feed (Lima and Dill 1990). In perhaps the most elegant demonstration of this trade-off, Abrahams and Dill (1989) titrated the extra energy required to induce guppies (*Poecilia reticulata*) to forage in a more dangerous patch.

Prey that are capable of reliably assessing predation risk at the scale of whole habitats should presumably be at a selective advantage. To assess the safety of habitats, animals in the wild rely on various sources of information, including the direct assessment of the presence or abundance of predators via visual, chemosensory, auditory, and/or tactile cues (Lima and Dill 1990; Kelley and Magurran 2003). For example, fathead minnows avoid areas labelled with the faeces of predatory northern pike (*Esox lucius*, Brown et al. 1995), and Hawaiian roof rats (*Rattus rattus*) avoid the fecal odours of their predators, the mongoose (*Herpestes auropunctatus*) and red fox (*Vulpes vulpes,* Burwash et al. 1998).

Alternatively, animals use information about current predator activity to assess the level of immediate predation risk (Lima and Dill 1990). Particularly in aquatic environments, alarm cues released from the skin of injured fish provide reliable information about current and past predation events (Smith 1992). Many freshwater fishes avoid areas that have been recently labelled with conspecific alarm cues under laboratory and natural conditions (Chivers and Smith 1998; Brown 2003). Fewer fathead minnows were caught in minnow traps labelled with alarm cue than in control traps (Mathis and Smith 1992). Similarly, terrestrial invertebrates avoid areas containing dead congeners (Grostal and Dicke 1999; Dukas 2001; Nilsson and Bengtsson 2004).

It is often difficult to obtain reliable information about predator abundance or activity. As a result, animals can use indirect measures such as habitat features to assess the riskiness of a given habitat (Lima and Dill 1990; Verdolin 2006). Deer mice (*Peromyscus maniculatus*) and white-throated sparrows (*Zonotrichia albicollis*) prefer feeding stations in areas close to or containing abundant cover (Schneider 1984;

Anderson 1986). Similarly, juvenile lingcod (*Ophiodon elongatus*) and winter flounder (*Pseudopleuronectes americanus*) prefer habitats with structure (rock, shell, or seagrass) compared to bare sand habitats (Petrie and Ryer 2006; Pappal et al. 2009).

In stream-dwelling salmonids, studies of habitat selection typically focus on physical variables, such as current velocity and depth, which affect the foraging profitability of habitats (Girard et al. 2004; Rosenfeld and Taylor 2009). While juvenile salmon prefer sites with an abundance of cover (Culp et al. 1996; Dolinsek et al. 2007; Venter et al. 2008), little is known about how they actually assess predator abundance or activity. In the short term, juvenile salmonids exhibit antipredator behaviour when exposed to visual and/or chemical cues indicating the presence or activity of predators (Leduc et al. 2006; Chapter 1). While the short-term benefits associated with antipredator behaviour are clear, whether and how juvenile Atlantic salmon in the wild use chemical information to assess the relative predation risk of alternative habitats when settling in a stream are unknown.

The objectives of this study were to examine (1) whether wild juvenile Atlantic salmon can use chemical information to avoid habitats that have a higher perceived predation risk when settling in a new habitat, and (2) how they respond to changes in perceived risk of predation after settling in a habitat and establishing a territory. Juvenile Atlantic salmon are ideal subjects for our study because they are relatively sedentary (Steingrímsson and Grant 2003), which allows us to manipulate the perceived predation risk of small sections of habitat while monitoring abundance during and after the settling period.

Materials and methods

Study site and species

This study was conducted in the lower reach of Catamaran Brook, located in Northumberland County, New Brunswick, Canada (46°52’42”N, 66°06’00”W) from 17 June to 22 July 2006, 21 June to 25 July 2007, and 23 June to 16 July 2008. Catamaran Brook is a nursery stream for a naturally reproducing population of anadromous Atlantic salmon (Cunjak et al. 1990). Young-of-the-year (referred to as YOY hereafter) Atlantic salmon emerge from gravel nests in mid-June the following year at about 2.6 cm in fork length (Randall 1982). Upon emergence, juvenile salmon disperse from redds (i.e. gravel nests) and then begin defending foraging territories, even at 2-3 cm in length (Keeley and Grant 1995).

We selected seven sites of relatively shallow depth (i.e. < 50 cm) and slow current (range: $0.2 - 0.5 \text{ m} \cdot \text{s}^{-1}$), which are the preferred habitats for YOY Atlantic salmon in Catamaran Brook (Girard et al. 2004). Within each site (mean width ± *SD* = 8.18 ± 1.60 m), we manipulated the perceived risk of predation in three 5 X 5 m sections as follows: a high predation risk treatment received chemical alarm cues from conspecifics; a low predation risk treatment received stream water as a control; and, a buffer was left undisturbed (Fig. 2.1a). To ensure that chemical alarm cues from the high predation risk treatment had no effect on the low predation risk treatment, we always assigned the latter to the most-upstream quadrat of the site (Fig. 2.1a). Furthermore, we added a buffer treatment between the high and low predation risk treatments so that we could switch treatments between the buffer and high predation risk treatment after settlement (Fig. 2.1b) and fish emigrating from high predation risk treatment would not settle in an adjacent low predation risk treatment during settlement (Fig. 2.1a). Because there were no barriers or enclosures, each site was also exposed to the ambient risk of predation from potential predators, such as common merganser, belted kingfisher, brook charr, Atlantic salmon parr, and otters (*Lontra canadensis*) (Scott and Crossman 1973; Dolinsek et al. 2007). To minimize the potential cumulative effects of chemical alarm cues dispersing from upstream to downstream, sites were at least 30 m (range: 30 - 93 m) apart.

To ensure that sections within a site were similar in habitat characteristics, we measured the depth and current velocity at 40% of the water column depth, using a Marsh-McBirney meter (Model 201D, Fredericton, MD, U.S.A.) five times along a transect across each section. The depth (mean ± *SD* = 44.41 ± 14.05 cm) and current velocity (0.35 ± 0.24 $m \cdot s^{-1}$), the two key variables used in habitat selection (Girard et al. 2004), did not differ significantly among treatments (P-values all > 0.19).

For the purpose of this study, we defined the settlement period for YOY Atlantic salmon as June 15 – July 7, the time when salmon typically emerge and disperse from their redds in Catamaran Brook (Randall 1982; Johnston 1997). During this period, YOY salmon select a suitable habitat and begin defending a territory (Armstrong and Nislow 2006).

Collection of alarm cue

Hatchery-reared Atlantic salmon parr (1+) from the Rocky Brook population of the Miramichi watershed (2006, $n = 199$, mean ± *SD*, standard length = 8.57 ± 0.74 cm; 2007, $n = 163$, fork length = 10.64 ± 0.72 cm; 2008, $n = 141$, fork length = 9.55 ± 0.89 cm) were obtained from the Miramichi Salmon Conservation Centre, South Esk, New Brunswick for use as skin donors. Skin donors were killed with a single blow on the head in accordance with Concordia Animal Care Committee Protocol AC-2005-BROW. Skin fillets from both sides were removed and immediately placed into an ice-chilled container filled with stream water. Skin fillets were homogenized and diluted with stream water. The resulting concentration (0.09 $cm^2 \cdot ml^{-1}$) elicits a consistent anti-predator response in juvenile Atlantic salmon under natural conditions

(Leduc et al. 2006; Chapter 1). The alarm cue was frozen in 50 ml aliquots at -20 °C until needed, whereas stream water was obtained at the site. The frozen solutions were thawed 60 min prior to use. For this study, 630, 315, and 315 50-ml aliquots of alarm cue were used in 2006, 2007, and 2008, sufficient for 30, 15, and 15 days of the experiment, respectively; the remainder of the alarm cue was used in other ongoing studies.

Experimental protocol

During settlement

We attempted to manipulate the long-term perceived predation risk in each site by releasing either the alarm cue or stream water twice a day for 17, 15, and 15 days in 2006, 2007, and 2008, respectively (Fig. 2.1a). To coincide with the peak activity of YOY Atlantic salmon (Breau et al. 2007), we injected the chemical stimuli (alarm cue or stream water) at 1100 h and 1700 h for a total volume of 150 ml per day per section. Studies examining antipredator responses of a focal fish to chemical alarm cue (Leduc et al. 2006; Chapter 1) typically use about 20 ml for a single injection to simulate a single predation event. Hence, the injection of 150 ml per section per day would be equivalent to about eight predation events, equivalent to the skin of one parr, being released in the 25 m^2 section per day. We used a 60-ml syringe to release the chemical stimuli continuously within 20 cm of the substrate, while slowly walking across the site. To minimize the potential disturbance when releasing the stimulus (alarm cue or stream water), we always entered the stream upstream of the section receiving the chemical stimulus. Furthermore, YOY Atlantic salmon do not seem to react to overhead movements, including a person walking slowly in the stream (personal observation).

To determine how long the chemical stimulus remained in a section, we released samples of either milk or salt water (n = 3 for milk and n = 4 for salt water) in similar stream reaches (n = 7; current velocity = $0.70\ \mathrm{m} \cdot \mathrm{s}^{-1}$, depth = 0.44 m). The initial plume of milk or salt water, detected by eye and using a conductivity meter, respectively, took an average of 11.5 sec to reach 5 m downstream of the point of injection. However, milk could be detected in the 5m-site for up to 20 sec and the salt water for up to 34 sec after release (J.-W. Kim, unpublished data).

To estimate the local population density, we recorded the number, age class (only for Atlantic salmon), and species of all visible fishes in each site via snorkelling. For all surveys, the snorkeler moved slowly upstream, completing each 1-m subsection by moving from the left bank to right bank, taking approximately 30 - 40 min to complete one 15-m site during either the day or night. The daytime surveys of all sites were completed within the same day. For night surveys, we used a waterproof handheld flashlight (20 watts) to illuminate fish, which were typically lethargic and unresponsive when approached. Night surveys of all sites were completed either in one or two consecutive nights.

For the initial counts, three density surveys were conducted on day 1 and 2 for each section: two during the day (between 1100 h and 1900 h) and one at night (between 2300 and 0300 h). For the final counts, we conducted three density surveys on day 17 and 18 in 2006, and on day 14 and 15 in 2007 and 2008: two during the day and one at night. Night-density surveys were conducted only in 2006 and 2007. We had planned to inject chemical stimuli for 14 consecutive days during the settlement period. In 2006, however, heavy rain increased the water level and turbidity of all sites on day 14. Hence, to minimize any potential effects of this rainfall, we continued the injections for a total of 17 days.

After settlement

To investigate whether juvenile Atlantic salmon with established territories respond to changes in the long-term perceived predation risk of their local habitat, the 17-day experiment was extended for another 13 days in 2006. The injection protocol was similar to the 17-day experiment except that the undisturbed buffer during settlement now received the chemical alarm cue making it the high predation risk treatment and the high predation risk treatment was left undisturbed making it the undisturbed buffer (see Fig. 2.1b). We expected the density to decrease the most in the alarm-cue sites (formerly the buffer sites), where the perceived predation risk increased the most. In contrast, we did not expect the greatest increase in density in the buffer sites, formerly the alarm-cue sites, because these sites were downstream of the new alarm-cue sites (Fig. 2.1b). All sites received a total of 150 ml of chemical stimulus (alarm cue or stream water) twice daily for 13 days on July 8-21 in 2006 (Fig. 2.1b). The density survey protocol was similar to that used during settlement.

Statistical analysis

Because YOY are primarily day-active (Breau et al. 2007), whereas parr are active during the day and night (Imre and Boisclair 2004; Dolinsek et al. 2007), we analyzed the data separately for each age class. In addition, because of different diel activity patterns of YOY and parr, we analyzed the YOY data separately for day and night, whereas we used the average of the mean daytime densities and night-time densities for parr. To test for the effects of perceived predation risk on the population density of YOY and parr Atlantic salmon during the settlement phase, a two-way ANOVA was used to test the main effect of treatments (control, undisturbed buffer, and alarm cue) and years on the change in number per section (final number - initial number separately for each age class). Because we switched treatments during and after the settlement period, we analyzed the data after the switch in treatments (i.e. after settlement) using an ANCOVA with the final number of juvenile salmon at the end of the post-settlement period as a datum in the analysis and the final number of juvenile salmon before the switch in treatments as a covariate.

For all analyses, only significant interactions between the effects of treatments and years were reported, unless a non-significant interaction between the effects of treatments and years appeared to be significant and hence required an explanation.

Results

During settlement

As expected, the final number of YOY salmon in the 75 m^2 sites after the settlement period was higher during the day than at night (two-way ANOVA: $F_{1,30} = 168.57$, $P < 0.001$; Fig. 2.2a). Furthermore, the final number of YOY was extremely low in 2008 (two-way ANOVA: $F_{2,30} = 57.02$, $P < 0.001$; Fig. 2.2a). Hence, we excluded the data for 2008 from subsequent analyses and analyzed the YOY data separately for day and night.

The final number of salmon parr in the 75 m^2 sites after the settlement period differed significantly among years (two-way ANOVA: $F_{2,30} = 31.10$, $P < 0.001$; Fig.

2.2b), but did not differ significantly between day and night (two-way ANOVA: $F_{1,30} = 1.95$, $P = 0.17$; Fig. 2.2b). Hence, for the subsequent analyses of parr, we used the average of the mean daytime and night-time densities.

As predicted, the change in number of YOY salmon counted during the day differed significantly among treatments (two-way ANOVA: $F_{2,36} = 5.19$, $P = 0.01$; Fig. 2.3a). The number of salmon in the alarm-cue sections decreased in 2006 and increased the least in 2007. Contrary to our expectations, however, the increase in number of YOY was greatest in the buffer rather than control sections. While the increase in number of YOY was greater in the control than the alarm-cue sections, this difference was not significant (a priori contrast: 3.85 ± 2.10, $n = 28$, $P = 0.075$; Fig. 2.3a). The effect of treatments on the change in number of YOY per section appeared stronger in 2006 than in 2007; however, there was no significant interaction between the effects of treatments and years (two-way ANOVA: $F_{2,36} = 2.43$, $P = 0.10$; Fig. 2.3a). Furthermore, the change in number of YOY did not differ between years (two-way ANOVA: $F_{1,36} = 0.16$, $P = 0.69$; Fig. 2.3a).

Because YOY salmon were absent at night in 19 out of 21 sections in 2007 (Fig. 2.2b), we only tested the effect of treatments on the change in number of YOY at night in 2006. In contrast to the patterns in the daytime data, the increase in YOY at night appeared to be lowest in the buffer section and higher in the alarm cue and control sections (Fig. 2.3b). While this difference between treatments were not significant in the night-time data (one-way ANOVA: $F_{2, 18} = 1.70$, $P = 0.21$), the contrasting patterns between the day and night data in 2006 led to a significant interaction between the effects of treatments and time of the day (two-way ANOVA: $F_{2, 36} = 5.54$, $P = 0.008$). Hence, the treatments had opposite effects on the change in number of YOY during the day and at night in 2006.

In contrast to YOY, the change in number of parr did not differ significantly among treatments (two-way ANOVA: $F_{2, 36} = 1.85$, $P = 0.17$; Fig. 2.3c). However, the increase in number of parr was greater in 2007 than in 2006 (two-way ANOVA: $F_{1, 36} = 14.02$, $P < 0.001$; Fig. 2.3c).

After settlement in 2006

Because we switched the treatments that fish were exposed to during and after settlement, we examined the effect of treatments in the post-settlement period using an ANCOVA approach. As expected, during the day the initial number of YOY (i.e. final number at the end of the settlement period) was positively correlated with the final number of YOY 13 days later (initial number as covariate: $F_{1, 17} = 33.75$, $P < 0.001$; Fig. 2.4a). The density of fish in most sites increased during the settlement period indicating that some fish were still selecting habitats in which to settle at this time. After controlling for the number of fish per section at the end of the settlement period, the final number of YOY per section differed among treatments (one-way ANCOVA: $F_{2, 17} = 4.09$, $P = 0.036$; Fig. 2.4a). As expected, the final number was lower in alarm-cue sections than in the control sections (Fig. 2.4a). Despite the potential effect of alarm cues dispersing downstream, the buffer section had an intermediate final number of YOY.

At night, the initial number of YOY per section was also positively correlated with the final number of YOY (initial number as covariate: $F_{1, 17} = 15.01$, $P = 0.001$). After controlling for the initial density, the final number of YOY differed significantly among treatments (one-way ANCOVA: $F_{2, 17} = 3.59$, $P = 0.0499$). However, contrary to the findings during the day, the final number was greater in alarm cue sections than in the buffer and control sections (Fig. 2.4b).

Contrary to the results for YOY, the initial number of parr per section was not positively correlated with the final number of parr (initial number as covariate: $F_{1, 17} = 1.56$, $P = 0.23$). Furthermore, the final number of parr did not differ significantly among treatments (one-way ANCOVA: $F_{2, 17} = 1.73$, $P = 0.21$; Fig. 2.4c).

Discussion

Our results suggest that YOY Atlantic salmon can use chemical information to directly assess the relative risk of predation of different habitats and then avoid particularly dangerous sites. During the settlement period, the number of YOY in risky sections decreased during the day or tended to increase less than those in both the buffer and control sites. The greatest increase in density in the buffer sections was not expected and may have been caused by fish moving upstream of the alarm-cue sections. After the settlement period, the number of YOY salmon increased most in the control sections and least in the alarm-cue sections, where the perceived predation risk increased the most. Instead of leaving the risky sites, YOY may compensate for the increased perceived predation risk by being more night-active or decreasing their territory size during the day (Kim et al. unpublished data). Taken together, these results suggest that alarm cues have longer-lasting effects on the behaviour of YOY salmon than the typical short-term anti-predator responses that have been observed previously (Leduc et al. 2006; Chapter 1).

Interestingly, the patterns of YOY abundance at night were significantly different from and opposite to those observed in the day; the increase in density was highest in the alarm-cue sites and lowest in the buffer sites. The relatively few YOY found in risky sites may become more night-active to avoid the higher perceived risk of predation during the day. Similarly, most fish in sites with a lower perceived risk of predation may have been attempting to maximize their growth by feeding during the day (Fraser and Metcalfe 1997).

Contrary to our results for YOY, parr did not respond to the experimental treatments. Parr clearly detect and respond to alarm cues in the short term by decreasing their foraging rates and increasing their latency to foraging after a visual disturbance (Chapter 1). Because parr are already active during the night (Imre and Boisclair 2004; Breau et al. 2007), they may be less influenced by the increased perceived predation risk of alarm-cue sites during the day. Alternatively, parr may have reached a size that makes them less vulnerable to gape-limited aquatic predators (Sogard 1997).

Overall, our data suggest that YOY Atlantic salmon can use chemical information to assess the quality of habitat in terms of predation risk. Our study suggests that if habitats differ markedly in average predation risk, then YOY will avoid settling in particularly risky sites. Whether the differences in perceived predation risk between the treatments in our study represent the degree of spatial variability in actual predation risk in salmon streams is an open question. Further research is needed to determine if YOY salmon use alarm cues to assess the spatial variation in predation risk in an unmanipulated system.

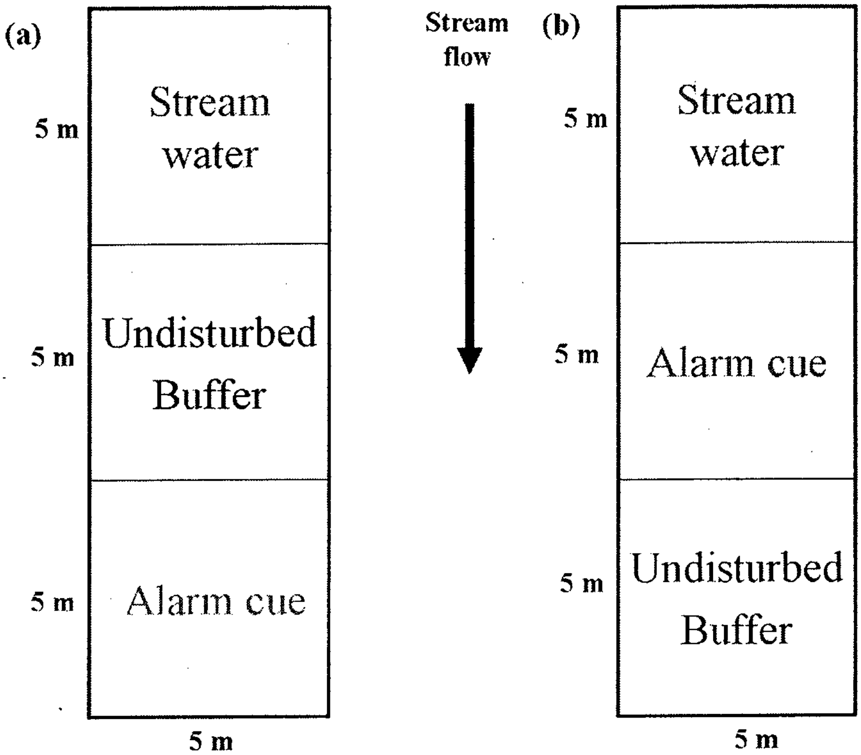

Figure 2.1. Experimental design in one of seven stream sites (a) during and (b) after the settlement of young-of-the-year salmon.

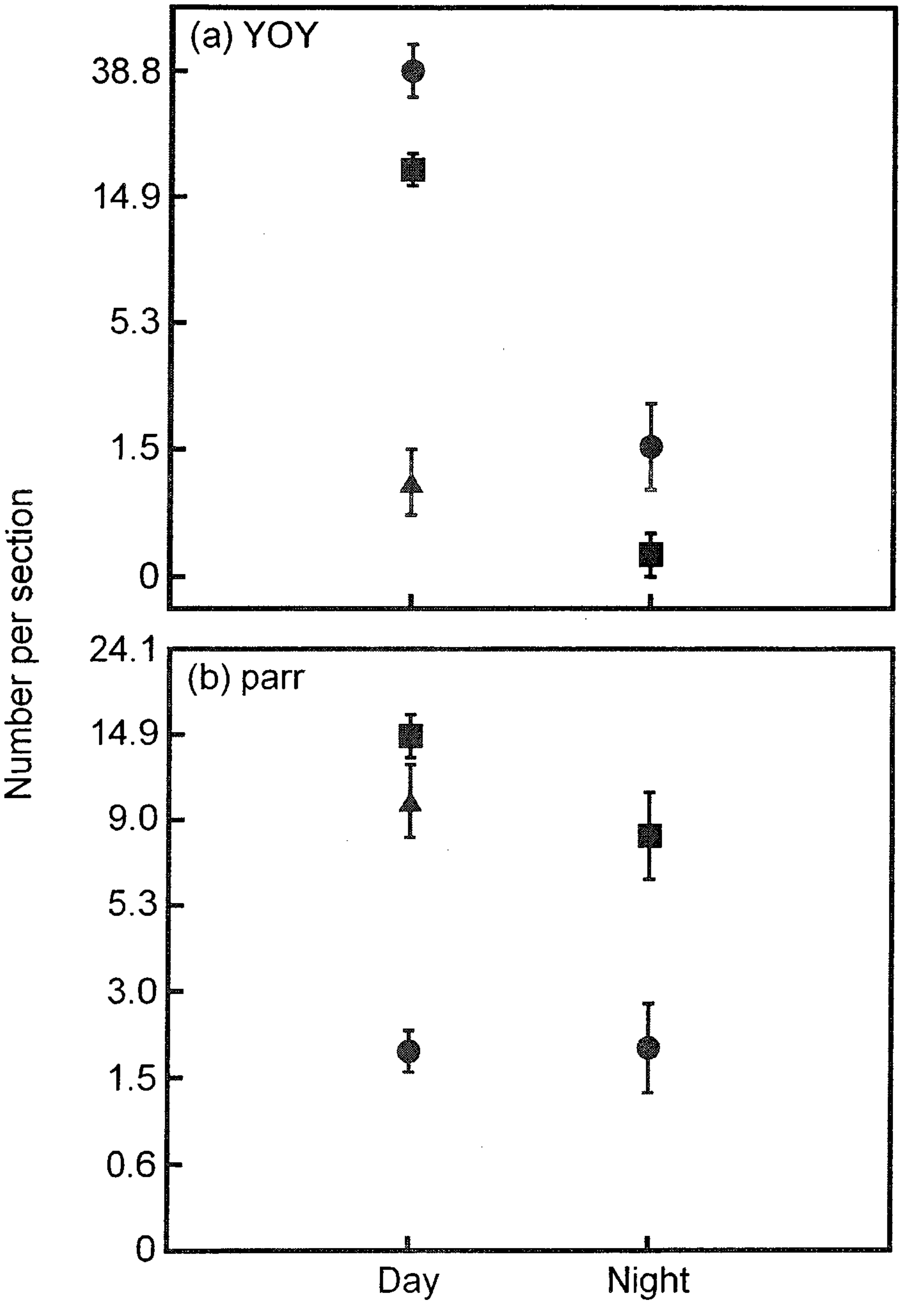

Figure 2.2. Mean (± SE, $n = 7$) final number of (a) young-of-the-year and (b) parr Atlantic salmon per 75 m^2 site during day and night at the end of the settlement period in 2006 (●), 2007 (■), and 2008 (▲). Note that no night-time surveys were conducted in 2008.

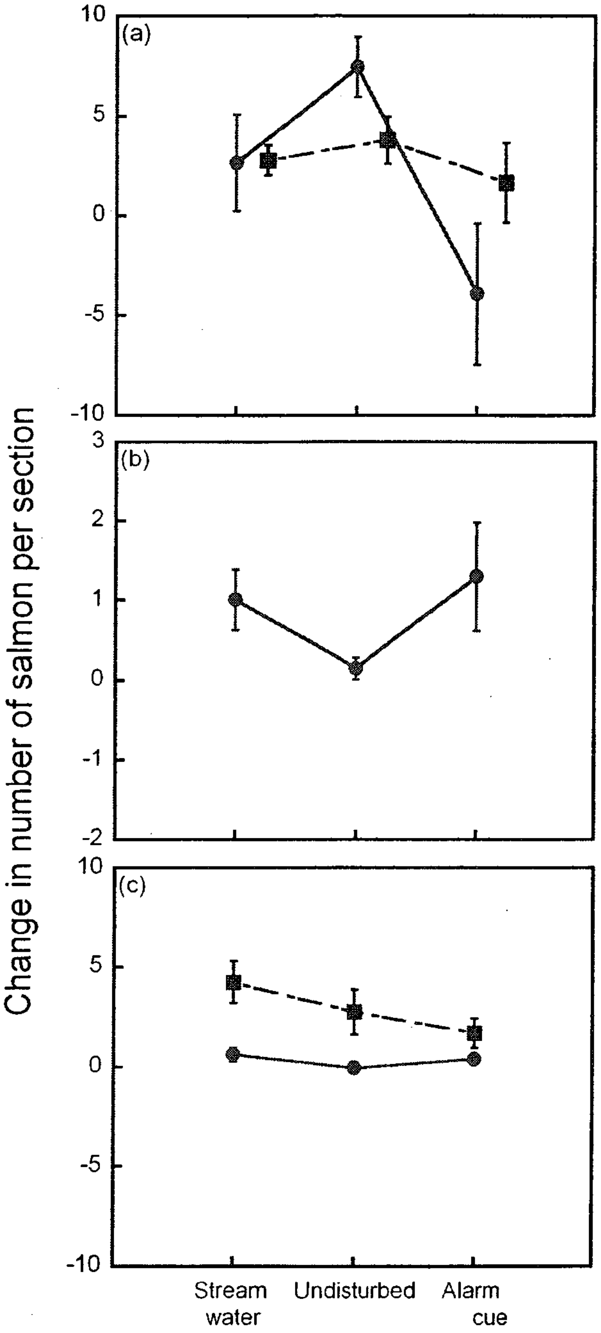

Figure 2.3. Mean change in number (± SE, $n = 7$) of Atlantic salmon exposed to three different treatments during the settlement period in 2006 (●) and 2007 (■) for young-of-the-year (a) during the day, (b) at night, and (c) for parr during the day and night.

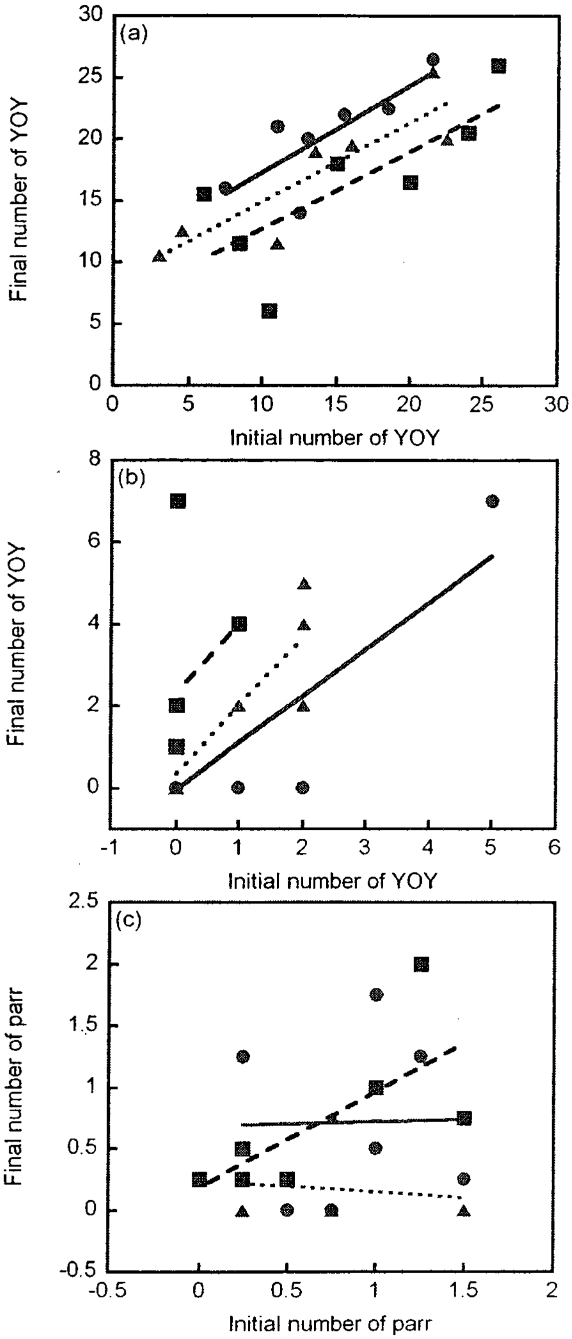

Figure 2.4. Final number of salmon per 25 m^2 section vs. initial number at the end of the settlement period (n = 7), for young-of-the-year (a) during the day, (b) at night and for (c) parr, after 13 days of treatment: stream water (●, solid line), alarm cue (■, dashed line), and an undisturbed buffer (▲, dotted line) in 2006.

Connecting statement

Chapter 2 revealed that YOY avoided settling in risky sites whereas the density of parr was not affected by the experimental treatments. Chapter 2 supports the hypothesis that YOY salmon in the wild use chemical alarm cues to assess the predation risk in different habitats, which influences their habitat selection. While threat-sensitive trade-offs between predation risk and foraging have received much attention in the literature, direct tests on the trade-off between avoiding predators and territorial defence have rarely been conducted. Chapter 3 will examine whether YOY salmon use chemical alarm cues to assess short- and long-term predation risk and adjust their territorial behaviour accordingly.

Chapter 3. Effects of acute and chronic increases in perceived predation risk on the territorial behaviour of juvenile Atlantic salmon (*Salmo salar*) in the wild

Introduction

A territory provides the owner with relatively exclusive access to resources (Puckett and Dill 1985; Theimer 1987; Grant 1997), but is costly in terms of the time and energy spent on defence (Puckett and Dill 1985; Ydenberg and Houston 1986). Thus, territory size should be subject to balancing these conflicting demands. Optimality models (e.g. Hixon 1980; Schoener 1983) predict that territory size will decrease with increasing benefits, such as food abundance, or costs, such as intruder pressure. Numerous field and laboratory studies have verified these predictions in a wide variety of taxa (Grant 1997; Adams 2001), including fishes (Norman and Jones 1984; Grant and Guha 1993), birds (Jones 1983; Johnson et al. 2006), and mammals (Mares et al. 1982; Monaghan and Metcalfe 1985). Presumably, any other factor that affects the benefits and costs of territorial defence may alter this trade-off and influence the 'optimal' size of a territory. One such factor is predation pressure (Eason and Stamps 1992; Kim et al. 2004).

Failure to detect and avoid predators usually means death or serious injury to the prey individual (Lima and Dill 1990; Lima and Steury 2005). Thus, prey should adjust the type and/or intensity of their behavioural responses to a threat of predation in proportion to the level of the perceived threat (Helfman 1989). This threat-sensitive predator avoidance hypothesis has received extensive support across a range of taxa, including invertebrates (Persons and Rypstra 2001), amphibians (Laurila et al. 1997), reptiles (Amo et al. 2004), birds (Edelaar and Wright 2006), and mammals (Swaisgood et al. 1999). Typically, the intensity of an individual's antipredator behaviour is directly proportional to the level of perceived risk and inversely related to the value of its alternative behaviour.

While considerable research has demonstrated that prey exhibit antipredator responses to short term increases in predation risk (Lawrence and Smith 1989; Chivers et al. 2001; Brown 2003; Dupuch et al. 2004), how prey perceive and integrate predation risk over the longer term is one of the key unanswered questions in the field of predator-prey dynamics (Lima and Steury 2005). Furthermore, how long-term patterns of predation risk influence fitness-related behaviour, such as territorial defence, remains unclear.

Territorial aggression may increase the conspicuousness of the defender to local predators, resulting in increased costs associated with holding a territory (Lima and Dill 1990). For example, common mergansers are more likely to attack moving rather than stationary coho salmon (Martel and Dill 1995). Similarly, cutthroat trout (*Salmo clarki*) attack threespine sticklebacks models (*Gasterosteus aculeatus*) that are painted red more than dull ones (Moodie 1972); the redness of the belly indicates the resource holding power of territorial males (Baube 1997). Likewise, animals engaged in aggressive interactions may be less vigilant towards potential predators. For example, animals engaged in aggressive interactions allow predators to approach closer than non-aggressive conspecifics (Jakobsson et al. 1995; Brick 1998; Díaz-Uriarte 1999). Thus, theoretical models predict that aggressive animals under increased predation risk should decrease their territory size to compensate for the increased cost (Schoener 1983; Dubois and Giraldeau 2005).

Similarly, animals engaged in other fitness-enhancing activities such as foraging (Godin and Smith 1988) or mating (Bernal et al. 2007) may also increase their conspicuousness and decrease their vigilance resulting in an increased predation risk. Hence, animals often decrease their foraging rate as an antipredator response. Indeed, the feeding rate of guppies that were captured by predators was higher on average than that of the survivors (Godin and Smith 1988). Hence, animals defending a feeding territory are predicted to decrease their aggressiveness and foraging rate in response to an elevated risk of predation (Helfman 1989; Lima and Dill 1990). For example, juvenile coho salmon reduce their aggressive behaviour directed towards mirrors when exposed to odour of common mergansers (Martel and Dill 1993). Because of the difficulty of manipulating predation risk, there have been few direct tests of this hypothesis under natural conditions.

Stream-dwelling salmonids have been popular model systems for investigating territoriality because they defend feeding territories both in the lab (Slaney and Northcote 1974; Keeley 2000) and the field (Elliott 1990; Steingrímsson and Grant 2008). The territory size of salmonids is inversely related to habitat visibility (Imre et al. 2002; Venter et al. 2008), food abundance (Slaney and Northcote 1974), density of fish (Keeley 2000), and dominance rank (Harwood et al. 2003) and is directly related to body size (Elliott 1990). Young-of-the-year Atlantic salmon defend multiple central-place territories that are much larger than the territories of similar sized stream-dwelling salmonids (Steingrímsson and Grant 2008). Because they move frequently between many foraging stations, multiple central-place foraging salmon may be more conspicuous and exposed to greater predation risk than those with a single-central place territory. When exposed to an acute increase in predation risk under laboratory conditions, juvenile Atlantic salmon reduce their foraging rates or spend more time under refuges (Metcalfe et al. 1987; Blanchet et al. 2007). However, relatively little is known about the threat-sensitive responses of salmon to an acute increase in predation risk under natural conditions. Furthermore, how long-term predation pressure influences the territorial behaviour of juvenile Atlantic salmon is not known.

In this study, we examined the potential effects of both acute and chronic increases in perceived predation risk on the territorial behaviour of juvenile Atlantic salmon in the wild. Specifically, we tested the predictions that in response to both an acute and chronic increase in perceived predation risk juvenile salmon will decrease (1) their territory size; (2) their foraging rate; and (3) the number of switches between foraging stations. Furthermore, we tested the prediction that (4) antipredator responses will be greater in intensity when exposed to chronic as opposed to acute increases in perceived predation risk, (5) which leads to slower growth in the salmon exposed to chronic versus acute increases in perceived predation risk.

Materials and methods

This study was conducted in the lower reach of Catamaran Brook at the sites described in Chapter 2. We conducted the experiment from 12 to 20 July and 14 to 18 August, 2006, from 21 June to 25 July, 2007, and 23 June to 16 July, 2008. Alarm cue was collected and prepared as described in Chapter 2.

Except as noted below, experimental protocols are described in Chapter 1. While waiting for the start of the observation, we sketched a map of the local streambed on a water resistant Mylar sheet. During the observation, we mapped each foraging station (defined as any location where the fish maintained position for at least 5 s), recorded all switches between foraging stations and the direction (1-12 o'clock, with 12 o'clock as directly upstream) and distance (in body lengths) of all foraging attempts and aggressive acts as well as the station from which they were initiated (Steingrímsson and Grant 2008). After each observation, we placed a numbered steel washer at the location of each foraging station.

After each observation, we measured the x and y location (± 5 mm) of each foraging station of a focal fish in relation to the reference point in each site using a meter stick and measuring tape. We used these data to create a digital map using ArcView GIS 3.2 with the Animal Movement extension (Hooge and Eichenlaub 2000). To estimate territory size, we calculated the minimum convex polygon (Schoener 1981) that included 95% and 100% of all events (foraging stations, foraging attempts and aggressive acts). Because the analyses of territory size did not differ qualitatively between the two methods, we present the territory size data based on 100% of events, because the rate of aggressive acts was lower than reported in Steingrímsson and Grant (2008).

We estimated the population density by counting all the visible fish in a 3 m X 3 m quadrat surrounding the focal fish. Using the methods described in Chapter 1 and 2, we also measured the water depth, snout velocity (i.e. current velocity at 3 cm above the substrate) and average current velocity using a Marsh-McBirney meter (Model 201D, Fredericton, MD, U.S.A.), distance to cover, substrate complexity, percentage of canopy and cloud cover, and water temperature.

Acute increase in predation risk

To examine the effects of an acute increase in perceived predation risk, we quantified the territorial behaviour (territory size, foraging rate, and the number of switches between foraging stations) of 18 YOY Atlantic salmon that were exposed first to stream water and then to a chemical alarm cue; 10 were observed from 12 to 20 July and eight from 14 to 18 August, 2006. The observer (J.L.A.W.) conducted each observation via snorkelling between 1200 and 1900h for 45 min, consisting of three 15-min observation periods (baseline, post stream water, and post alarm cue) using the protocol described above. After the 15 min-baseline observation, a second snorkeler (J.-W.K.) moved in slowly from upstream to release 20 ml of stream water from a syringe in the middle of water column approximately 1 m upstream of the focal fish. After the release of the stream water, the post-stream-water observation continued for 15 min. At the end of post-stream-water observation, 20 ml of alarm cue was released as described above, followed by the post-alarm-cue observation for another 15 min.

Statistical analyses

We used a repeated measures ANOVA to detect changes in three dependent variables: territory size, foraging rate, and the number of switches between foraging stations over the three observation periods: baseline, post-stream-water, and post-alarm cue. Because the data were not completely spherical, we used the Hyunh-Feldt correction for the number of switches between foraging stations (Quinn and Keough 2002).

Chronic increase in predation risk

To examine the effects of a chronic increase in perceived predation risk, we manipulated predation risk by releasing either alarm cue or stream water twice a day for 29 and 20 days in 2007 and 2008, respectively. The experimental protocol is described in Chapter 2. We quantified the territorial behaviour (territory size, foraging rate, and the number of switches between foraging stations) of 40 YOY Atlantic salmon, 32 YOY from 12 to 25 July, 2007 and eight YOY from 15 to 16 July, 2008. To ensure that fish in the alarm cue sections experienced the increased perceived risk of predation for as long as possible, we conducted the observations after 16 and 19 days of treatment in 2007 and 2008, respectively. We observed 16 focal fish in each of the risky (i.e. alarm cue) and control treatments in 2007. Because of extremely low densities in 2008, we observed only four fish in the alarm-cue treatment and one in the control treatment. However, we observed three fish in the undisturbed buffer (i.e., no alarm cue) and used them as "control fish" under these extraordinary circumstances.

We observed each focal fish for 30 min via snorkelling between 1200 and 1900h using the experimental protocol described above. We observed at least two fish per section, always starting from downstream to upstream to minimize the potential disturbance to the subsequent focal fish. In 2008, however, we observed fish in only three out of seven sites due to low fish density. In addition, we observed only one fish per section for site 5 and 7. To avoid observing the same fish twice, we completed all observations within a given section without leaving the site. To minimize the variation in environmental variables, we completed observations for each site within one or two consecutive days. At the end of each observation, we captured the focal fish using dipnets and measured their fork length (± 1 mm) and weight (± 0.1 g).

Statistical analyses

We used the average behaviour of each fish in a section as a datum in the analyses. For all statistical tests, we considered each section as a datum (7 control and

7 alarm cue in 2007, 3 control and 2 alarm cue in 2008).

We examined the main effects of treatment (control and buffer versus alarm cue) and years (2007 and 2008) using two-way ANOVAs on five dependent variables: territory size, foraging rate, the number of switches between foraging stations, fork length, and weight. We reported only significant interactions between the effects of treatments and years, unless a non-significant interaction between the effects of treatments and years appeared to be significant and hence required an explanation. To meet the assumptions of parametric tests, we $\log_{10}(X+1)$ transformed the territory size. For visual purposes, all data presented in the figures are back transformed following analysis and are shown with asymmetric S.E. bars.

Results

Acute increase in predation risk

Territory size (ANOVAR: $F_{1, 17} = 1.87$, $P = 0.19$; Fig. 3.1a) and foraging rate (ANOVAR: $F_{1, 17} = 0.06$, $P = 0.82$; Fig. 3.1b) did not differ significantly among the three observation periods. However, the number of switches between foraging stations differed significantly among the three observation periods (ANOVAR, $F_{2, 34} = 5.37$, $P = 0.018$; Fig. 3.1c). The number of switches increased from the baseline to the post-stream water period and then decreased during post-alarm cue period, as indicated by a significant quadratic contrast across three observation periods (quadratic contrast: $F_{1, 17} = 9.78$, $P = 0.006$). To examine changes in the number of switches at a finer temporal scale, we analyzed the data for each of nine 5-min intervals. The number of switches between foraging stations differed significantly among the nine observation periods (ANOVAR, $F_{8, 120} = 2.66$, $P = 0.025$). The number of switches did not change after the addition of stream water (paired t-test, $t_{15} = 0.29$, $P = 0.78$; Fig. 3.2). However, switch rate tended to increase over the first 6 5-min intervals (linear contrast: $F_{1, 15} = 5.38$, $P = 0.035$). The number of switches decreased significantly after the addition of alarm cue (paired t-test: $t_{17} = 2.86$, $P = 0.011$; Fig. 3.2).

Chronic increase in predation risk

As predicted, territories of YOY in risky habitats were significantly smaller than those in control habitats (two-way ANOVA: $F_{1, 15} = 7.93$, $P = 0.013$; Fig. 3.3a). In addition, territories in 2008 were significantly larger than in 2007 (two-way ANOVA: $F_{1, 15} = 6.92$, $P = 0.019$; Fig. 3.3a). While the local density did not differ between treatments (two-way ANOVA: $F_{1, 15} = 0.001$, $P = 0.98$), the local density in 2007 was 0.52 fish $\cdot$ m^{-2} compared to 0.20 fish $\cdot$ m^{-2} in 2008 (two-way ANOVA: $F_{1, 15} = 9.47$, $P = 0.008$). We further analyzed the difference in territory size between treatments with density as a covariate. Although density seemed to be inversely related with territory size, it was not significant (one-way ANCOVA: $F_{1, 16} = 3.80$, $P = 0.069$). To further examine the difference in territory size between treatments, we compared two important components of territory size (Steingrímsson and Grant 2008): the number of foraging stations used and the mean aggressive radius. Fish in the risky sites used fewer foraging stations than those in control sites ($F_{1, 15} = 4.34$, $P = 0.055$; Fig. 3.4a). Because fish in risky sites of 2008 did not engage in aggression, we only analyzed the 2007 data; aggressive radius appeared to be greater in control sites than risky sites (Fig. 3.4b), however this difference was not significant ($t_8 = 1.59$, $P = 0.15$).

Contrary to the prediction, foraging rate did not differ significantly between treatments (two-way ANOVA: $F_{1, 15} = 0.69$, $P = 0.42$; Fig. 3.3b). However, foraging rate was significantly higher in 2008 than in 2007 ($F_{1, 15} = 14.32$, $P = 0.002$; Fig. 3.3b), when the densities were lower. Also, contrary to the prediction, the number of switches between foraging stations did not differ significantly between treatments (two-way ANOVA: $F_{1, 15} = 1.26$, $P = 0.28$; Fig. 3.3c), but was significantly greater in 2007 than in 2008 ($F_{1, 15} = 5.21$, $P = 0.038$; Fig. 3.3c).

Contrary to the prediction, fork length did not differ significantly between treatments (two-way ANOVA: $F_{1, 15} = 0.10$, $P = 0.76$) or years ($F_{1, 15} = 0.56$, $P = 0.47$). Interestingly, there was a significant interaction between the effects of treatments and years on weight (two-way ANOVA: $F_{1,15} = 7.89$, $P = 0.013$); in 2007 fish in risky sites were 0.64 g compared to 0.59 g in control sites whereas in 2008 fish in risky sites were 0.50 g compared to 0.83 g in control sites. However, when we analyzed the main effects of treatments on weight separately for 2007 and 2008, weight did not differ significantly between treatments in 2007 (t-test: $t_{12} = 1.04$, $P = 0.32$) and 2008 ($t_3 = -1.65$, $P = 0.20$).

Discussion

Acute increase in predation risk

Our results suggest that juvenile Atlantic salmon responded to an acute increase in perceived predation risk (i.e. exposure to a single dose of alarm cue) by decreasing their switch rate between foraging stations immediately following the detection of an alarm cue. Salmon may switch foraging stations to increase their encounter rate with benthic prey (Steingrímsson and Grant 2008). If so, decreasing switching between foraging stations may represent a trade-off between decreased predation risk and increased foraging rate (Lima and Dill 1990; Brown 2003). Alternatively, switching between foraging stations may be a type of territorial defence where juvenile salmon move between foraging stations to detect and evict potential intruders in their large multiple central-place territories (Steingrímsson and Grant

2008). If so, a reduction in switch rate may represent a trade-off between increased predation risk and increased vigilance and/or effectiveness of defence (Lima and Dill 1990).

Interestingly, juvenile salmon did not decrease their territory size or foraging rate after detecting a single dose of alarm cue. Perhaps detecting a single dose from somewhere upstream is not threatening enough to cause territory owners to alter their foraging rate or territory size in the short term. After the exhaustion of the yolk sac, a feeding territory is important for the growth and survival of juvenile salmon during this early critical period in which salmonid populations are subject to density-dependent mortality and self-thinning (Martel 1996; Steingrímsson and Grant 1999; Armstrong and Nislow 2006). Thus, juvenile salmon may choose to maintain their territory size even under an increase in predation risk. Furthermore, fitness-related activities such as territorial behaviour and foraging rate may be less affected by a short-term increase in perceived predation risk (Blanchet et al. 2007).

In contrast to previous studies (Leduc et al. 2007; Chapter 1), our study detected no decrease in foraging rate following the exposure to an alarm cue. Because our post-alarm cue observation was longer in duration than in previous studies (Leduc et al. 2007; Chapter 1), 15 min versus 5 min, juvenile salmon in our study may have recovered quickly to baseline foraging levels, diluting the overall treatment effect.

(Steingrímsson and Grant 2008).

Similar to the effects of an acute increase in predation risk, juvenile salmon did not change their foraging rate when exposed to a chronic increase in predation risk. Again, fitness-enhancing behaviour such as foraging may be less affected by an increase in perceived predation risk where fitness advantage of foraging may be at least as important as directly avoiding predators (Martel 1996; Blanchet et al. 2007). Because foraging data were recorded when the risk was relatively low (i.e. during 'safe' periods between the daily releases of alarm cue), an alternative explanation may be that juvenile salmon in risky habitats increased their foraging efforts during safe periods to compensate for the lower foraging rate during times of elevated risk. Such an explanation is consistent with the risk allocation hypothesis (Lima and Bednekoff 1999; Ferrari et al. 2008). Furthermore, there was no difference in fork length or weight between treatments, suggesting that juvenile salmon in risky habitats compensated for the reduced size of their territories, perhaps by foraging at greater intensity during safe periods.

Link between acute and chronic increases in predation risk

How prey perceive and integrate predation risk over multiple time scales is amongst the most important unanswered questions in the field of predator-prey

Moreover, juvenile salmon may forage at a greater rate when they resume feeding to offset any deficit incurred while responding to the predation threat (Talbot et al. 1984; Metcalfe et al. 1987; Gotceitas and Godin 1991). Furthermore, our study design was less powerful at detecting the effects of alarm cues on behaviour because the effect of treatments was confounded by the effects of time. Switch rate tended to increase over time, indicating that focal fish may have been habituating to the presence of observers. Nevertheless, our design should have detected any powerful effects of alarm cues.

Chronic increase in predation risk

Unlike the effects of a single dose of alarm cue, our results suggest that juvenile salmon respond to a chronic increase in perceived predation risk by decreasing their territory size. This result is consistent with the predictions of optimal territory size models, if we assume that predation risk is a cost (Hixon 1980; Schoener 1983). To our knowledge, this is the first demonstration of animals decreasing their territory size in response to an increase in predation risk under natural conditions. This decrease in territory size may have resulted from the cumulative effect of two non-significant behavioural changes. Juvenile salmon in risky habitats appeared to use fewer foraging stations and shorter aggressive distances towards potential intruders, which appears to have led to fish defending a smaller territory in risky habitats dynamics (Lima and Steury 2005). In our study, juvenile Atlantic salmon responded to both acute and chronic increases in perceived predation risk under natural conditions whilst the type and the degree of the antipredator responses differed between the two time scales. This result suggests that both immediate and long-term temporal scale events can influence individual behavioural decisions (Brown et al. 2009) and that prey continually adjust their behavioural responses according to immediate or longer-term patterns of predation risk (Biro et al. 2007; Brown et al. 2009). While the reduction in territory size may influence population density and self-thinning of salmon populations (Grant et al. 1998; Armstrong and Nislow 2006), how these short- and long-term behavioural patterns translate into future fitness such as growth rate (Martel 1996) or survival (Mirza and Chivers 2003) remains to be tested. Moreover, how these behavioural decisions influence population and/or community dynamics (Werner and Peacor 2003; Blanchet et al. 2008) should be addressed in future studies.

In addition, our study suggests that alarm cues can be used to manipulate both the short- and long-term perceived predation risk in natural conditions. Alarm cues may be a valuable tool in the field of predator-prey dynamics, where only few studies have tested the effects of predation risk under natural conditions, due to the difficulty of observing predation risk in the field and to increasing ethical restrictions on live predation studies (Kelley and Magurran 2003). Furthermore, studying how prey perceive predation risk under natural condition is becoming increasingly important (Wisenden et al 2004; Leduc et al. 2006; Chapter 1).

Overall, our study suggests that juvenile Atlantic salmon can respond to both acute and chronic increases in perceived predation risk under natural conditions. An acute increase in predation risk elicited only a decrease in switch rate between foraging stations whereas a chronic increase in predation risk elicited a reduction in territory size of juvenile Atlantic salmon. Future research is needed, however, to examine how animals perceive and respond to actual predators rather than perceived risk at broader spatial and temporal scales (Werner and Peacor 2003; Lima and Steury 2005).

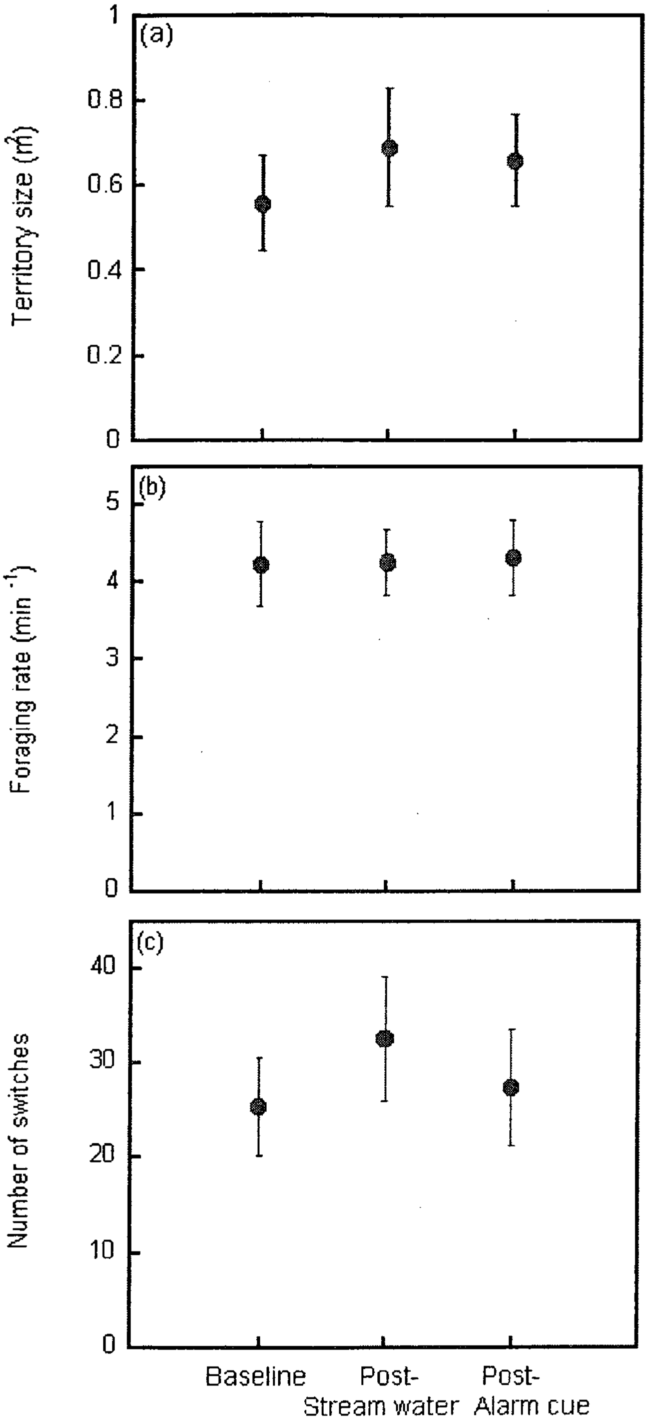

Figure 3.1. Mean (± SE, *n* = 18) (a) territory size, (b) foraging rate, and (c) number of switches between foraging stations of YOY Atlantic salmon during three observation periods: baseline, post-stream water, and post-alarm cue.

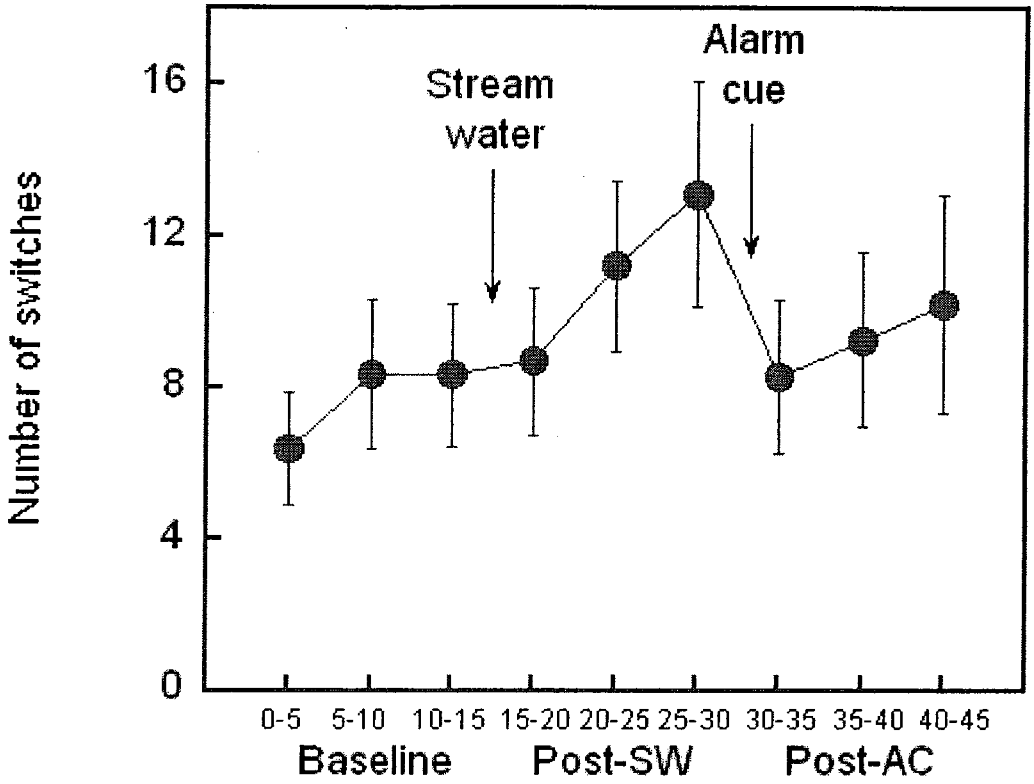

Figure 3.2. Mean (± SE, *n* = 18) number of switches between foraging stations of YOY Atlantic salmon during nine 5-min observation periods.

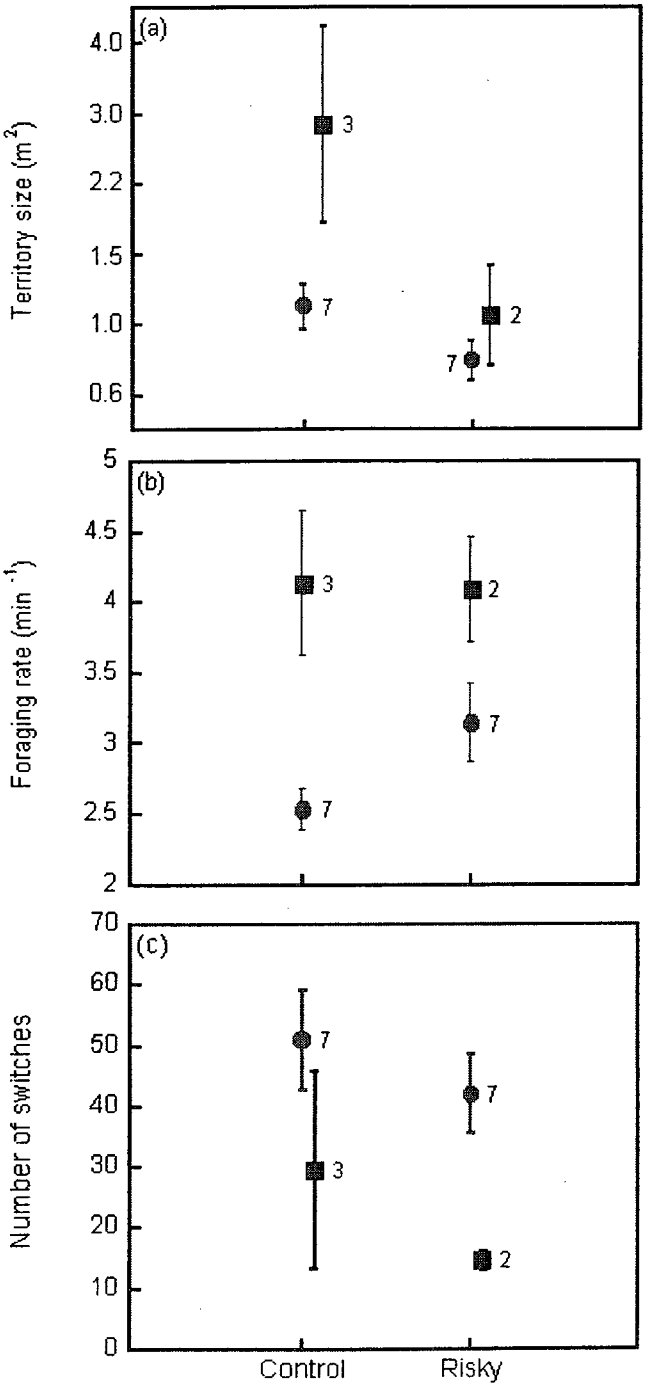

Figure 3.3. Mean (± SE) (a) territory size, (b) foraging rate, and (c) number of switches between foraging stations of YOY Atlantic salmon after 16 and 19 days of treatments in 2007 (●) and 2008 (■) (*n* shown next to the symbols).

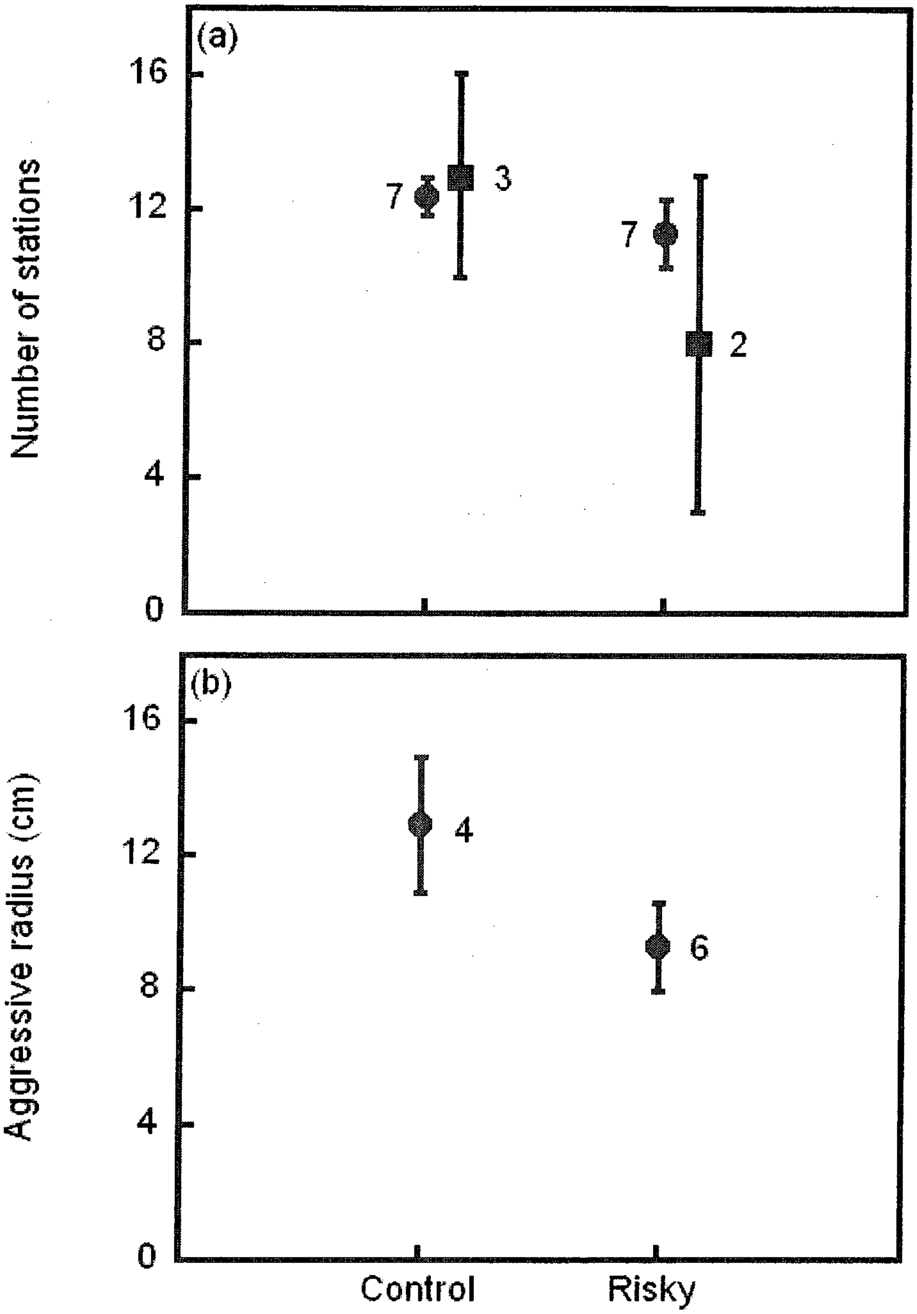

Figure 3.4. Mean (± SE) (a) number of foraging stations used and (b) aggressive radius of YOY Atlantic salmon after 16 and 19 days of treatments in 2007 (●) and 2008 (■). Note that fish in risky sites of 2008 did not engage in aggression (*n* shown next to the symbols).

General Conclusion

My thesis attempts to bridge the gap between short-term behavioural responses to single episodes of heightened predation risk and the longer-term effects of elevated risk on behaviour and population density. Using damage-released chemical alarm cues to manipulate perceived predation threats under natural conditions, my thesis reveals how juvenile salmon assess and respond to perceived predation risk over both the short- (immediate) and long-term (a period of days to weeks). In addition, my thesis provides new insights on how both acute and chronic increases in perceived predation risk influence predator avoidance behaviour, territorial behaviour, habitat selection, and population density of juvenile Atlantic salmon.

Chapter 1 revealed that both YOY and parr Atlantic salmon exhibited anti-predator behaviour in response to short-term increase in predation risk under natural conditions. While YOY and parr differed in the type and intensity of antipredator responses to both chemical and visual stimuli, perhaps due to differential costs and benefits associated with age, both used the chemical and visual information in a complementary manner.

With the results of Chapter 1 and other studies, it is clear that local predation risk has striking effects on short-term predator avoidance behaviour. However, the long-term consequence of perceived predation risk, particularly its effects on habitat selection, is poorly understood. Chapter 2 revealed that the density of YOY salmon decreased in risky sites and increased in control and buffer sites, suggesting that YOY avoided settling in risky sites. In contrast, the density of parr was not affected by the experimental treatments, perhaps because the more night-active parr are less responsive to changes in daytime predation risk than are YOY. Chapter 2 supports the idea that YOY salmon in the wild can use chemical alarm cues to assess the predation risk in different habitats, which influences their habitat selection.

While threat-sensitive trade-offs between predation risk and foraging have received much attention in the literature, direct tests on the trade-off between avoiding predators and territorial defence have rarely been conducted. Chapter 3 revealed that YOY salmon used chemical alarm cues to assess short- and long-term predation risk and adjusted their territorial behaviour accordingly. However, they only reduced the size of their territories when exposed to a chronic increase in predation risk. Chapter 3 provides partial evidence that predation risk may influence how salmonid populations are regulated via territory size.

Overall, these results highlight the importance of predator avoidance behaviour at both the individual and population levels. Furthermore, these results provide a link between two temporal scales: short-term (immediate) behavioural changes to longer term consequences (days to weeks). My results suggest that alarm cues are an effective and practical technique to manipulate the level of perceived predation risk in field settings.

When prey have imperfect information about predation hazard, prey may overestimate or underestimate the risk of predation and are thought to simply deal with 'less optimal' habitats (Abrams 1994). However, my results suggest that they are indeed capable of compensating by adjusting their behaviour patterns in order to better balance threat-sensitive trade-offs. Indeed, juvenile salmon avoided settling in risky habitats. Furthermore, once settled and established territories in risky habitats, juvenile salmon reduced the size of their territories to offset the costs of defending a territory in risky habitats.

Territoriality and habitat selection are important mechanisms of negative density dependent regulation of salmonid populations (Elliott 1990; Grant and Kramer 1990). Hence, predation risk may influence the population dynamics of juvenile salmonids by influencing how juvenile salmon select habitats, forage and defend their territories. While my thesis reveals some of the roles that predation risk may play at the population level, the next logical step would be to examine how juvenile salmon assess and respond to actual predation events rather than just to perceived risk. Removing fish predators from the study site by electrofishing and using field enclosures to keep potential fish, bird, and mammal predators out of the study site would be an effective and practical technique to manipulate actual predation within stream sections. In addition, it would be fruitful to investigate how spatial/temporal distributions of juvenile salmon in relation to local predation risk influences the spatial/temporal distributions of both drifting invertebrate prey, such as mayfly larvae and chironomids, and vertebrate predators, such as common mergansers, kingfishers, brook charr, and otters. This would provide valuable insights on the non-lethal effects of predation risk on population and community dynamics and their processes (Werner and Peacor 2003; Blanchet et al. 2008).

One of the major problems with the viability of restocking programs is the dramatic level of mortality of newly released individuals (Suboski and Templeton 1989; Brown and Laland 2001). On a world-wide basis around 5 billion hatchery reared salmon are released annually but less than 5% survive to adulthood (McNeil 1991). In addition, hatchery-reared fish, including Atlantic salmon, have lower survival rates than wild fish (Heggberget et al. 1992; Dieperink et al. 2001; Jonsson et al. 2003). While the basis for differences in mortality is not clear, predation is considered one of the principal causes of mortality among released hatchery fish (Howell 1994; Henderson and Letcher 2003). It has been suggested that the higher mortality rates experienced by hatchery-reared fish may be due to the fact that they

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had no prior experience of predation and are subsequently easy prey for predators (Brown and Laland 2001). Indeed, predators switch their prey preferences from wild to hatchery-reared smolts as soon as the hatchery fish are released (Thompson and Tufts 1967). However, there is ample evidence demonstrating that repeated exposure to predators improves anti-predator responses in fish including salmonids (Berejikian 1995; Brown and Smith 1996; Mirza and Chivers 2000). Furthermore, pre-exposure to chemical cues has been shown to increase the survival of hatchery-reared chinook salmon smolts post-release (Berejikian et al. 1999). Hence, we should further investigate whether mass conditioning the hatchery-reared salmon to respond appropriately to the presence of visual/chemical cues of predators or the actual predators improves the survival/fitness of these salmon after the release (Brown and Laland 2001; Hawkins et al. 2007). Developing an efficient and cost-effective training method to increase the survival of hatchery-reared salmon would certainly improve the current conservation/restocking programs (Boisclair 2004).

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