

1 **Do juvenile Atlantic salmon (*Salmo salar*) use chemosensory cues to detect and avoid**
2 **risky habitats in the wild?**

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4 Jae-Woo Kim¹ · James W.A. Grant · Grant E. Brown

5

6 Department of Biology, Concordia University, 7141 Sherbrooke W., Montreal, Quebec, H4B

7 1R6, Canada

8 Email: J.-W. Kim jaew.kim@utoronto.ca (corresponding author)

9 J. W.A. Grant grant@alcor.concordia.ca

10 G. E. Brown gbrown@alcor.concordia.ca

11

12 Corresponding author: Jae-Woo Kim

13 Department of Ecology and Evolutionary Biology, University of Toronto, 25 Harbord St.

14 Toronto, Ontario, M5S 3G5 Canada

15 Tel.: +1-416-946-7230

16 Fax: +1-416-978-8532

17 Email: jaew.kim@utoronto.ca

18

¹ Jae-Woo Kim is currently a FQRNT Postdoctoral Fellow in the Department of Ecology and Evolutionary Biology at the University of Toronto, 25 Harbord St. Toronto, Ontario, M5S 3G5 Canada, E-mail: jaew.kim@utoronto.ca

19 **Abstract**

20 We examined whether juvenile Atlantic salmon (*Salmo salar*) in the wild adjust their
21 behaviour in response to chemical cues of predator activity during a four-week period after
22 emergence from gravel nests. In each of seven 75 m² sites in Catamaran Brook, New
23 Brunswick, we established three contiguous sections differing in perceived predator activity
24 by releasing stream water in control sections, conspecific alarm cues in risky sections, and
25 nothing in buffer sections in both 2006 and 2007. As predicted, the density of YOY salmon
26 tended to decrease in alarm-cue sections, while increasing in control and buffer sections. After
27 the two week manipulation in 2006, we switched treatments so that buffer sections became
28 alarm-cue sections and alarm-cue sections became buffer sections for an additional two-week
29 period. After the switch, the number of YOY increased least in the new alarm-cue sections
30 and most in control and new buffer sections. In contrast to YOY, the density of age 1+ parr
31 was not affected by the experimental treatments. Our results suggest that YOY salmon can use
32 chemical alarm cues to assess the predator activity of habitats in the wild.

33

34 **Keywords** Habitat selection · Damage-released chemical alarm cue · Long-term

35 perceived predation risk · Population density

36

37

38 **Introduction**

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

48 Prey capable of reliably assessing predation risk at the scale of whole habitats should
49 presumably be at a selective advantage. To assess the safety of habitats, animals in the wild
50 rely on various sources of information, including the direct assessment of the presence or
51 abundance of predators via visual, chemosensory, auditory, and/or tactile cues (Lima and Dill
52 1990; Kelley and Magurran 2003). For example, fathead minnows (*Pimephales promelas*)
53 avoid areas labelled with the faeces of predatory northern pike (*Esox lucius*) (Brown et al.
54 1995), and Hawaiian roof rats (*Rattus rattus*) avoid the fecal odours of their predators, the
55 mongoose (*Herpestes auropunctatus*) and red fox (*Vulpes vulpes*) (Burwash et al. 1998).

56 Animals also use chemosensory cues to assess the level of immediate predation risk

57 (Lima and Dill 1990). Chemosensory cues released from the skin of injured fish provide
58 reliable information about current and past predation events (Smith 1992). Many freshwater
59 fishes, including fathead minnows, avoid areas that have been recently labelled with
60 conspecific alarm cues under laboratory and natural conditions (Mathis and Smith 1992;
61 Chivers and Smith 1998; Brown 2003). Similarly, terrestrial invertebrates avoid areas
62 containing dead congeners (Grostal and Dicke 1999; Dukas 2001; Nilsson and Bengtsson
63 2004).

64 Because it is often difficult to obtain reliable information about predator abundance
65 or activity, animals can use indirect measures such as habitat features to assess predation risk
66 (Lima and Dill 1990; Verdolin 2006). Deer mice (*Peromyscus maniculatus*) and white-
67 throated sparrows (*Zonotrichia albicollis*) prefer feeding stations close to or containing
68 abundant cover (Schneider 1984; Anderson 1986). Similarly, juvenile lingcod (*Ophiodon*
69 *elongatus*) and winter flounder (*Pseudopleuronectes americanus*) prefer habitats with
70 structure (rock, shell, or seagrass) compared to bare sand habitats (Petrie and Ryer 2006;
71 Pappal et al. 2009).

72 In stream-dwelling salmonids, studies of habitat selection typically focus on physical
73 variables, such as current velocity and depth, which affect foraging profitability (Girard et al.
74 2004; Rosenfeld and Taylor 2009). Although juvenile salmon prefer sites with an abundance
75 of cover (Culp et al. 1996; Dolinsek et al. 2007; Venter et al. 2008), little is known about how

76 they actually assess predator abundance or activity when selecting habitats. In the short term,
77 juvenile salmonids exhibit antipredator behaviour when exposed to visual and/or chemical
78 cues indicating the presence or activity of predators under laboratory and field conditions
79 (Leduc et al. 2006; Blanchet et al. 2007; Kim et al. 2009). While the short-term benefits
80 associated with antipredator behaviour are clear, whether and how juvenile Atlantic salmon
81 (*Salmo salar*) in the wild use chemical information to assess the relative predator activity of
82 alternative habitats at larger temporal and spatial scales are unknown.

83 The objectives of this study were to examine (1) whether wild juvenile Atlantic
84 salmon use chemical information to avoid habitats that have a higher perceived predator
85 activity when settling in a new habitat, and (2) how they respond to changes in perceived
86 predator activity after settling in a habitat and establishing a territory. Juvenile Atlantic
87 salmon are ideal subjects for our study because they are relatively sedentary (Steingrímsson
88 and Grant 2003; Breau et al. 2007), which allows us to manipulate the perceived predator
89 activity of small sections of habitat while monitoring abundance during the four weeks after
90 emergence from redds.

91

92 **Materials and methods**

93 **Study site and species**

94 We conducted this study in the lower reach of Catamaran Brook, located in

95 Northumberland County, New Brunswick, Canada (46°52'42"N, 66°06'00"W) from 17 June
96 to 22 July 2006 and 21 June to 25 July 2007. Catamaran Brook is a nursery stream for a
97 naturally reproducing population of anadromous Atlantic salmon (Cunjak et al. 1990). Young-
98 of-the-year (YOY) Atlantic salmon emerge from gravel nests in mid-June at about 2.6 cm in
99 fork length (Randall 1982). Upon emergence, juvenile salmon disperse from redds (gravel
100 nests) and begin defending foraging territories, even at 2-3 cm in length (Keeley and Grant
101 1995).

102 We selected seven sites of relatively shallow depth (< 50 cm) and slow current (0.2 –
103 0.5 m · s⁻¹), which are the preferred habitats for YOY Atlantic salmon in Catamaran Brook
104 (Girard et al. 2004). Within each site (mean width ± *SD* = 8.18 ± 1.60 m), we manipulated the
105 perceived activity of predators in three 5 X 5 m sections as follows: a risky section received
106 conspecific alarm cues; a control section received stream water; and, a buffer section received
107 nothing (Fig. 1a). Sections of this size (25 m²) were chosen as an appropriate scale for our
108 study because YOY salmon typically defend a territory of about 1 m² (Steingrímsson and
109 Grant 2008) and typically move less than 5 m during their growing season (Steingrímsson and
110 Grant 2003). Consequently, YOY salmon respond to changes in habitat quality at spatial
111 scales as small as 6 m² (Dolinsek et al. 2007; Venter et al. 2008). To ensure that chemical
112 alarm cues from the risky section had no effect on the control section (Blanchet et al. 2008),
113 we always assigned the control to the upstream quadrat of the site (Fig. 1a). Furthermore, we

114 added a buffer section between the control and risky sections so that the buffer and risky
115 sections could be switched during late settlement (Fig. 1b) and fish emigrating from the risky
116 section in an upstream direction could settle in habitat other than the control section during
117 early settlement (Fig. 1a). Because there were no barriers or enclosures, each site was also
118 exposed to the ambient risk of predation from potential predators, such as common merganser
119 (*Mergus merganser*), belted kingfisher (*Megaceryle alcyon*), brook charr (*Salvelinus*
120 *fontinalis*), and Atlantic salmon (Scott and Crossman 1973; Dolinsek et al. 2007). To
121 minimize the potential cumulative effects of chemical alarm cues dispersing from upstream to
122 downstream (Dionne and Dodson 2002; Kim et al. 2009), sites were at least 30 m (range: 30 -
123 93 m) apart.

124 To ensure that the three sections within a site were similar in habitat characteristics,
125 we measured the depth and current velocity at 40% of the water column depth, using a Marsh-
126 McBirney meter (Model 201D, Frederickton, MD, U.S.A.) at five locations along a transect
127 across each section. The depth (mean \pm *SD* = 45.75 \pm 13.43 cm) and current velocity (0.40 \pm
128 0.27 m \cdot s⁻¹), the two key variables used in habitat selection (Girard et al. 2004), did not differ
129 significantly among treatments or sites (*P*-values all > 0.18).

130 For the purpose of this study, we defined the early settlement period for YOY Atlantic
131 salmon as June 15 – July 7, the time when salmon typically emerge and disperse from their
132 redds in Catamaran Brook (Randall 1982; Johnston 1997). During this period, YOY salmon

133 select a suitable habitat and begin defending a territory (Armstrong and Nislow 2006). We
134 defined the late settlement period as July 8 – 21. During this late settlement period, fewer
135 YOY Atlantic salmon emerge from redds and more fish have settled into feeding territories
136 for the summer than during the early settlement period (Steingrímsson and Grant 2003).

137 **Collection of alarm cue**

138 Hatchery-reared Atlantic salmon parr (1+) from the Rocky Brook population of the
139 Miramichi watershed (2006, $n = 199$, mean $\pm SD$, standard length = 8.57 ± 0.74 cm; 2007, $n =$
140 163 , fork length = 10.64 ± 0.72 cm) were obtained from the Miramichi Salmon Conservation
141 Centre, South Esk, New Brunswick for use as skin donors. Skin donors were killed with a
142 single blow on the head in accordance with Concordia Animal Care Committee Protocol AC-
143 2005-BROW. Skin fillets from both sides were removed and immediately placed into an ice-
144 chilled container filled with stream water. Skin fillets were homogenized and diluted with
145 stream water. The resulting concentration ($0.09 \text{ cm}^2 \text{ of skin} \cdot \text{ml}^{-1}$) of cue from this population
146 elicits a consistent anti-predator response in juvenile Atlantic salmon in Catamaran Brook
147 under natural conditions (Leduc et al. 2006; Leduc et al. 2007; Kim et al. 2009). Furthermore,
148 alarm cues are equally effective at eliciting anti-predator behaviour in field and laboratory
149 settings for a variety of prey fishes (Brown and Godin 1999; Wisenden et al. 2004; Wisenden
150 et al. 2010). The alarm cue was frozen in 50 ml aliquots at $-20 \text{ }^\circ\text{C}$ until needed, whereas
151 stream water was obtained at the site. The frozen solutions were thawed 60 min prior to use.

152 For this study, 630 and 315 50-ml aliquots of alarm cue were used in 2006 and 2007,
153 sufficient for 30 and 15 days of the experiment, respectively. The remainder of the alarm cue
154 was used in other cognate studies.

155 **Experimental protocol**

156 *Early settlement*

157 We manipulated the long-term perceived predator activity in each site by releasing
158 either the alarm cue or stream water twice a day for 17 and 15 days in 2006 and 2007,
159 respectively (Fig. 1a). To coincide with the peak activity of YOY Atlantic salmon (Breau et al.
160 2007), we released either 50 or 100 ml of the chemical stimuli (alarm cue or stream water) at
161 1100 h (1030-1130) and 1700 h (1630-1730) for a total volume of 150 ml per day per section;
162 the amount released in the morning was alternated each day. Studies simulating a single
163 predation event typically use about 20 ml from 1.8 cm² of skin (Leduc et al. 2006; Kim et al.
164 2009), roughly equivalent to the size of a wound left by a predator (Smith and Lemly 1986).
165 Hence, the release of 150 ml per section per day would be equivalent to about eight predation
166 events, equivalent to the skin of one parr, being released in the 25 m² section per day. The
167 background predation rate in Catamaran Brook is estimated to be lower than 13 predation
168 events per section over eight weeks if fish density is 1 YOY · m⁻² (Girard et al. 2004). We used
169 a 60-ml syringe to release the chemical stimuli continuously within 20 cm of the substrate,
170 while slowly walking across the site. To minimize the potential disturbance when releasing

171 the stimulus (alarm cue or stream water), we always entered the stream upstream of the
172 section receiving the stimulus. Hence, we walked across the stream upstream of the control
173 section to release stream water and across the buffer section to release the alarm cue in risky
174 sections. Furthermore, YOY Atlantic salmon do not seem to react to overhead movements,
175 including a person walking slowly in the stream (personal observation).

176 To determine how long the chemical stimulus remained in a section, we released
177 samples of either milk or salt water ($n = 3$ for milk and $n = 4$ for salt water) in similar stream
178 reaches ($n = 7$; current velocity = $0.70 \text{ m} \cdot \text{s}^{-1}$, depth = 0.44 m). The initial plume of milk or
179 salt water, detected by eye and using a conductivity meter, respectively, took an average of
180 11.5 sec to reach 5 m downstream of the point of release. However, milk could be detected in
181 the 5 m-section for up to 20 sec and the salt water for up to 34 sec after release (J.-W. Kim,
182 unpublished data).

183 Juvenile salmon can minimize their predation risk by either settling in alternative
184 habitats or hiding in the substrate of risky habitats. To estimate both components of avoidance,
185 we recorded the number, age class (only for Atlantic salmon), and species of all visible fishes
186 in each site via snorkelling. Snorkelling is a useful technique for estimating the abundance of
187 active fishes with a minimum of disturbance (Breau et al. 2007), particularly when
188 electrofishing is ineffective, such as in small areas of stream or at night (Gries et al. 1997;
189 Mullner et al. 1998; Dolinsek et al. 2007). In response to an increase in predation risk, salmon

190 parr often become more active at night (Gries et al. 1997; Imre and Boisclair 2004; Breau et al.
191 2007). Hence, we estimated density during both the day and night. For all surveys, the
192 snorkeler moved slowly upstream, completing each 1-m subsection by moving from the left
193 bank to the right bank, taking approximately 30 - 40 min to complete one 15-m site during
194 either the day or night. The daytime surveys of all sites were completed within the same day.
195 For night surveys, we used a waterproof handheld flashlight (20 watt) to illuminate fish,
196 which were typically lethargic and unresponsive when approached. Night surveys of all sites
197 were completed either in one or two consecutive nights.

198 For the initial counts, three density surveys were conducted on day 1 and 2 for each
199 section: two during the day (between 1200 h and 1600 h) and one at night (between 2300 and
200 0300 h). All daytime surveys were conducted at least one hour after or before the release of
201 the chemical stimuli at 1100 and 1700, respectively. For the final counts, we conducted three
202 density surveys on day 17 and 18 in 2006, and on day 14 and 15 in 2007: two during the day
203 and one at night. We had planned to release chemical stimuli for 14 consecutive days during
204 early settlement period. In 2006, however, heavy rain increased the water level and turbidity
205 of all sites on day 14. Hence, to minimize any potential effects of this rainfall, we continued
206 the treatments for a total of 17 days.

207 *Late settlement*

208 To investigate whether juvenile Atlantic salmon that have likely established territories

209 respond to changes in the long-term riskiness of their local habitat, the 17-day experiment was
210 extended for another 13 days in 2006. The treatment protocol was similar to the 17-day
211 experiment except the buffer section during the early settlement now received the alarm cue
212 making it the risky section and the risky section now received nothing making it the buffer
213 section (see Fig. 1b). We expected the density to decrease the most in the new risky sections
214 (formerly the buffer sections), where the perceived predator activity increased the most. All
215 sections received a total of 150 ml of chemical stimulus (alarm cue or stream water) twice
216 daily for 13 days on July 8-21 in 2006 (Fig. 1b). The density survey protocol was similar to
217 that used in early settlement.

218 **Statistical analysis**

219 Because YOY are primarily day-active (Breau et al. 2007), whereas 1+ parr are active
220 during the day and night (Imre and Boisclair 2004; Dolinsek et al. 2007), we analyzed the
221 data separately for each age class. In addition, because of different diel activity patterns of
222 YOY and 1+ parr, we analyzed the YOY data separately for day and night, whereas we used
223 the average of the mean daytime densities and night-time densities for 1+ parr. To test for the
224 effects of perceived predator activity on the population density of YOY and 1+ parr Atlantic
225 salmon during the early settlement periods, a repeated measures two-way ANOVAs (three
226 treatments by two years with the early and late settlement periods as the repeated measure,
227 and site as a block) were used to compare the mean number of salmon per section at the

228 beginning and end of the early settlement periods. After we switched treatment in 2006, the
229 repeated measures analysis compared the numbers at the beginning (i.e. the number at the end
230 of the early settlement period) and end of the late settlement period.

231 For all analyses, only significant interactions between the effects of treatments, years,
232 sites, and time periods were reported, unless a non-significant interaction between the effects
233 of treatments, years, sites, and time periods might appear to be significant to the reader and
234 hence require an explanation. Results of all analyses are also presented in Table S1. To meet
235 the assumptions of parametric analyses, the number of YOY salmon counted during the day
236 and night and of parr salmon at the start and end of the treatment during early and late
237 settlement periods were $\log_{10}(X+1)$ transformed. For visual purposes, all data were back
238 transformed following the analyses and are shown with asymmetric S.E. bars.

239

240 **Results**

241 A total of 3682 fishes was counted in the two years, including six species: Atlantic
242 salmon, blacknose dace (*Rhinichthys atratulus*), lake chub (*Couesius plumbeus*), brook charr,
243 white sucker (*Catostomus commersonii*), and slimy sculpin (*Cottus cognatus*). YOY Atlantic
244 salmon were the most abundant (64.4 % of all observed fishes), followed by 1+ parr Atlantic
245 salmon (14.6 %), blacknose dace (11.4 %), 2+ parr Atlantic salmon (4.8 %), lake chub (2.7 %),
246 brook charr (1.6 %), white sucker (0.6 %), and slimy sculpin (one count).

247 **Early settlement**

248 As expected, the final number of YOY salmon in the 75 m² sites after the early
249 settlement period was higher during the day than at night (repeated measures one-way
250 ANOVA: $F_{1,12} = 130.99$, $P < 0.001$; mean \pm SE = 31.18 ± 4.92 for day and 1.36 ± 0.62 for
251 night). Furthermore, the final number of YOY was higher in 2006 than in 2007 (repeated
252 measures one-way ANOVA: $F_{1,12} = 20.60$, $P < 0.001$; mean \pm SE = 22.75 ± 6.63 for 2006
253 and 9.79 ± 2.89 for 2007). Hence, we analyzed the YOY data separately for day and night.

254 The final number of 1+ parr salmon in the 75 m² sites after the early settlement period
255 was higher in 2007 than in 2006 (repeated measures one-way ANOVA: $F_{1,12} = 54.71$, $P <$
256 0.001 ; mean \pm SE = 2.21 ± 1.50 for 2006 and 12.43 ± 5.58 for 2007), but did not differ
257 significantly between day and night (repeated measures one-way ANOVA: $F_{1,12} = 2.18$, $P =$
258 0.17 ; mean \pm SE = 8.64 ± 2.00 for day and 6.00 ± 1.45 for night). Hence, for the subsequent
259 analyses of parr, we used the average of the mean daytime and night-time densities.

260 As expected, the number of YOY salmon counted during the day increased over the
261 early settlement period (repeated measures two-way ANOVA, with site as block: $F_{1,30} =$
262 40.04 , $P < 0.001$; Fig. 2a). As predicted, there was a significant interaction between the effects
263 of treatments and the time periods on the number of YOY salmon counted during the day
264 (repeated measures two-way ANOVA, with site as block: $F_{2,30} = 5.12$, $P = 0.012$; Fig. 2a).
265 The number of salmon in the alarm-cue sections decreased in 2006 and increased the least in

266 2007 (Fig. 2a). Contrary to our expectations, however, the increase in number of YOY was
267 greatest in the buffer sections rather than control sections. The effect of treatments on the
268 number of YOY per section also appeared stronger in 2006 than in 2007; however, there was
269 no significant interaction among the effects of treatments, years, and time periods (repeated
270 measures two-way ANOVA, with site as block: $F_{2,30} = 1.76$, $P = 0.19$; Fig. 2a). The number
271 of YOY counted during the day was greater in 2006 than in 2007 (repeated measures two-way
272 ANOVA, with site as block: $F_{1,30} = 39.30$, $P < 0.001$; Fig. 2a).

273 Because YOY salmon were absent at night in 19 out of 21 sections in 2007, we only
274 tested the effect of treatments on the number of YOY at night during the early settlement
275 period in 2006. Moreover, because YOY salmon were absent at night in all 21 sections at the
276 start of early settlement period in 2006, we analyzed the data using a one-way ANOVA with a
277 randomized block design on the final number of YOY at night during early settlement. In
278 contrast to the patterns in the daytime data, the number of YOY at night appeared to increase
279 least in the buffer section and most in the alarm-cue and control sections (Fig. 2b), however,
280 this difference was not significant (one-way ANOVA, with site as block: $F_{2,12} = 1.84$, $P =$
281 0.20 ; Fig. 2b). However, the contrasting patterns between the day and night data in 2006 led
282 to a significant interaction among the effects of treatments, time of the day, and time periods
283 (repeated measures two-way ANOVA, with site as block: $F_{2,30} = 8.73$, $P = 0.001$). Hence, the
284 treatments had opposite effects on the number of YOY during the day and at night during the

285 early settlement period in 2006.

286 In contrast to YOY salmon, there was no significant interaction between the effects of
287 treatments and the time periods on the number of 1+ parr (repeated measures two-way
288 ANOVA, with site as block: $F_{2,30} = 2.31$, $P = 0.12$; Fig. 2c). However, there was a significant
289 interaction between the effects of time periods and years on the number of parr (repeated
290 measures two-way ANOVA, with site as block: $F_{1,30} = 17.01$, $P < 0.001$); the number of parr
291 increased over the early settlement period in 2007 (repeated measures one-way ANOVA, with
292 site as block: $F_{1,12} = 38.21$, $P < 0.001$; Fig. 2c), but remained the same in 2006 (repeated
293 measures one-way ANOVA, with site as block: $F_{1,12} = 0.17$, $P = 0.68$; Fig. 2c). Furthermore,
294 the number of parr was greater in 2007 than in 2006 (repeated measures two-way ANOVA,
295 with site as block: $F_{1,30} = 73.12$, $P < 0.001$; Fig. 2c).

296 **Late settlement**

297 As expected, the number of YOY during the day increased over the 13-day late-
298 settlement period (repeated measures one-way ANOVA, with site as block: $F_{1,12} = 45.24$, $P <$
299 0.001 ; Fig. 3a), indicating that some fish were still selecting habitats in which to settle at this
300 time. The number of YOY salmon increased significantly more in control and buffer sections
301 than in risky sections (repeated measures one-way ANOVA, with site as block: $F_{2,12} = 6.26$,
302 $P = 0.014$; Fig. 3a). Perhaps because of alarm cues dispersing downstream, the buffer section
303 had an intermediate final number of YOY (Fig. 3a).

304 At night, the number of YOY per section increased over the 13-day late-settlement
305 period (repeated measures one-way ANOVA, with site as block: $F_{1,12} = 10.80$, $P = 0.007$; Fig.
306 3b), and this increase differed between treatments (interaction between treatments and time
307 periods: $F_{2,12} = 5.84$, $P = 0.017$; Fig. 3b). Again, in contrast to the patterns during the day
308 time, the number of YOY salmon increased more in the risky sections than in the control or
309 buffer sections (Fig. 3a and 3b). Hence, the treatments again had opposite effects on the
310 number of YOY during the day and at night during the late settlement period in 2006.

311 Contrary to the results for YOY, the number of 1+ parr per section did not differ
312 significantly over the 13-day late-settlement period (repeated measures one-way ANOVA,
313 with site as block: $F_{1,12} = 3.82$, $P = 0.074$; Fig. 3c). Furthermore, there was no significant
314 interaction between the effects of the treatments and the time periods on the number of parr
315 per section ($F_{2,12} = 1.70$, $P = 0.22$; Fig. 3c).

316

317 **Discussion**

318 Our results suggest that YOY Atlantic salmon can use chemical information to
319 directly assess the relative activity of predators in different habitats and then avoid
320 particularly dangerous habitats. During the early settlement period, the number of YOY
321 during the day in risky sections decreased or increased less than in the buffer and control
322 sections. The magnitude of increase in density in the buffer sections was not expected and

323 may have been caused by fish moving upstream out of the risky sections. During the late
324 settlement period, the number of YOY salmon increased most in the control and buffer
325 sections and least in the risky sections, where the perceived predator activity increased the
326 most.

327 It is also possible that YOY salmon remained within risky sections but altered their
328 behaviour, by spending more time hidden in the substrate (Leduc et al. 2007), and were not
329 counted during surveys. We think this explanation of our results is unlikely for three reasons.
330 First, the delay between the release of the stimulus and the subsequent density survey (i.e. >
331 one hour) was much longer than the latency to resume feeding in response to the same
332 stimulus (i.e. < 50 sec; Kim et al. 2009). Second, YOY salmon are most active during the day
333 (Breau et al. 2007), so it is unlikely that the decrease in daytime density could be entirely
334 accounted for by more YOY salmon hiding in refuges. Third, if YOY were indeed hiding in
335 the substrate during the day, then we would have presumably detected them during night
336 surveys. While the increase in night densities was greatest in the risky sections, the magnitude
337 of this increase could not account for differences observed during the day. Nevertheless, we
338 cannot rule out the alternate explanation that YOY salmon responded to the alarm cues by
339 hiding in the substrate during the day and night. If true, this result would suggest that YOY
340 salmon hide in the substrate much longer during the summer than previously thought (Breau
341 et al. 2007). Taken together, these results suggest that YOY salmon detect and avoid the sites

342 with alarm cues. Furthermore, our data suggest that alarm cues have longer-lasting effects on
343 the behaviour of YOY salmon at larger spatial scales than is typically measured during short-
344 term anti-predator experiments (Leduc et al. 2006; Kim et al. 2009).

345 Following the switch of treatments in 2006, we found no significant decline in
346 numbers in the alarm-cue sections (formerly the buffer sections), suggesting that once YOY
347 have settled on a foraging territory within a habitat, an increase in predator activity is not
348 sufficient to cause them to relocate to 'safer' habitats. Because the quality of alternative
349 locations is uncertain, the increased energy expenditure and decreased energy intake during a
350 relocation may decrease the net benefits of leaving risky sections (McDougall and Kramer
351 2007). In addition, if most YOY salmon have established their territories, then the prior
352 residency effect (Cutts et al. 1999) may make the costs of relocation outweigh the costs of
353 staying in risky habitats. Alternatively, YOY salmon can defend smaller territories to
354 compensate for the increased risk (Kim 2009; Kim et al. in press). However, the increase was
355 less in the alarm cue than in the other treatments, suggesting that new settlers either avoided
356 risky sites or hid in the substrate.

357 Interestingly, the patterns of YOY abundance at night during early and late settlement
358 periods were significantly different from and opposite to those observed in the day; the
359 increase in density at night was highest in the alarm-cue sections and lowest in the buffer
360 sections. The relatively few YOY found in risky habitats may become more night-active to

361 avoid the higher perceived activity of predators during the day. Furthermore, the few fish in
362 risky habitats may benefit from the reduced competition for food and space, which often leads
363 to an increased growth rate (Imre et al. 2005).

364 Contrary to our results for YOY, 1+ parr did not respond to the experimental
365 treatments. 1+ parr clearly detect and respond to alarm cues in the short term by decreasing
366 their foraging rates and increasing their latency to foraging (Kim et al. 2009). Because 1+ parr
367 already forage primarily at night (Imre and Boisclair 2004; Breau et al. 2007), they may be
368 less influenced by the increased perceived predator activity of alarm-cue sections during the
369 day. Alternatively, 1+ parr may have reached a size that makes them less vulnerable to gape-
370 limited fish predators such as brook charr and Atlantic salmon (Sogard 1997).

371 Overall, our data suggest that YOY Atlantic salmon can use chemical information to
372 assess the quality of habitat in terms of predator activity. Our study suggests that if habitats
373 differ markedly in ambient predator activity, YOY will avoid settling in particularly risky
374 habitats, or hide in the substrate for long periods of time. Whether the differences in perceived
375 predator activity between the treatments in our study represent the degree of spatial variability
376 in actual predation risk in salmon streams is an open question, especially so given that the
377 treatment effect was not strong enough to over-ride the differences in initial density. While
378 our study tested whether the differences in perceived predator activity in each section
379 influence settling decisions, it would be important to examine how the intrinsic riskiness of

380 habitat (Lima and Dill 1990; Verdolin 2006) influence the population density of a given
381 habitat, potentially affecting the relative predation risk of an individual. It would also be
382 interesting to examine whether and how predators redistribute themselves in response to the
383 altered distribution of prey. Moreover, investigating the potential interaction between the
384 effects of predation risk and population density on habitat selection would lead to the better
385 understanding of population consequences at broader spatial and temporal scales (Werner and
386 Peacor 2003; Blanchet et al. 2008). Further research is also needed to determine if YOY
387 salmon use alarm cues to assess the spatial variation in predation risk in an unmanipulated
388 system. Furthermore, given the well known difficulties in studying long-term predation risk in
389 natural populations (Lima and Steury 2005), our current study suggests that chemical alarm
390 cues may provide a valuable tool for future studies examining the ecologically relevant effects
391 of predation.

392

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411

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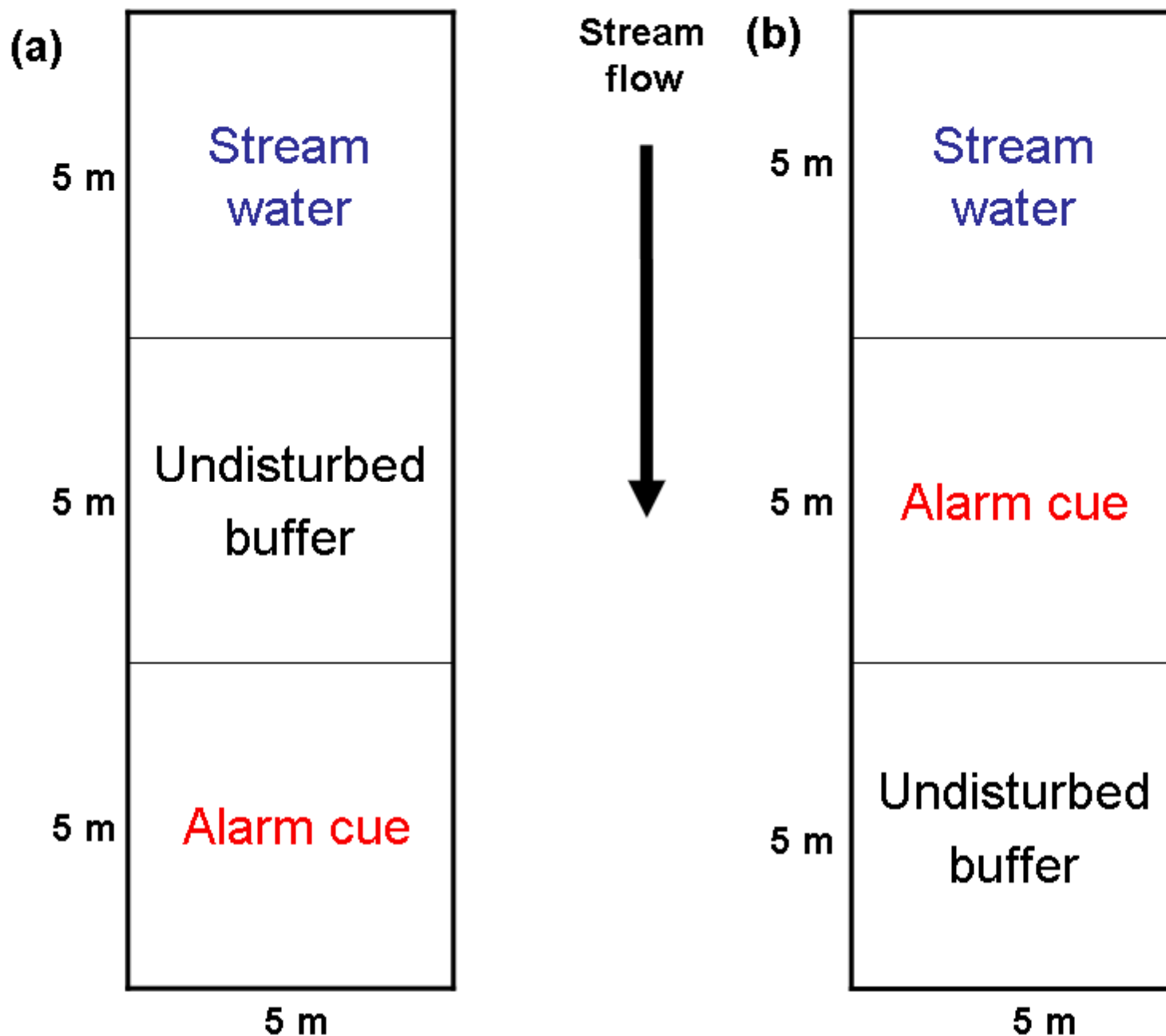
569

570 **Figure legends**

571 Figure 1. Experimental design in one of seven stream sites during the (a) early and (b) late
572 settlement periods of YOY salmon where a risky section received conspecific alarm
573 cues; a control section received stream water; and, a buffer section received nothing,
574 twice a day for 13-17 days in 2006 and 2007.

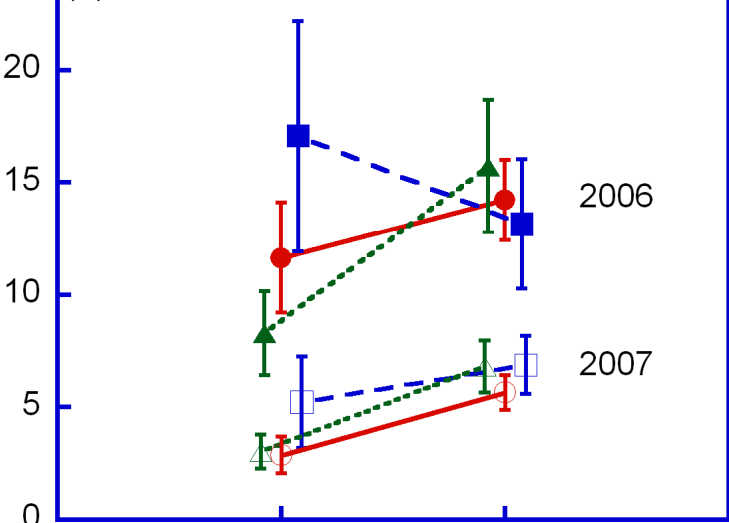
575 Figure 2. Mean number (\pm SE, $n = 7$) of Atlantic salmon exposed to three treatments: stream
576 water (●, solid line), alarm cue (■, dashed line), and a buffer (▲, dotted line) during
577 the early settlement period in 2006 (closed symbols) and 2007 (open symbols) for
578 young-of-the-year (a) during the day, (b) at night, and (c) for parr during the day and
579 night (Note that the results for YOY at night is reported for 2006 only)

580 Figure 3. Mean number (\pm SE, $n = 7$) of Atlantic salmon exposed to three treatments: stream
581 water (●, solid line), alarm cue (■, dashed line), and a buffer (▲, dotted line) during
582 the late settlement period in 2006 for young-of-the-year (a) during the day, (b) at
583 night, and (c) for parr during the day and night

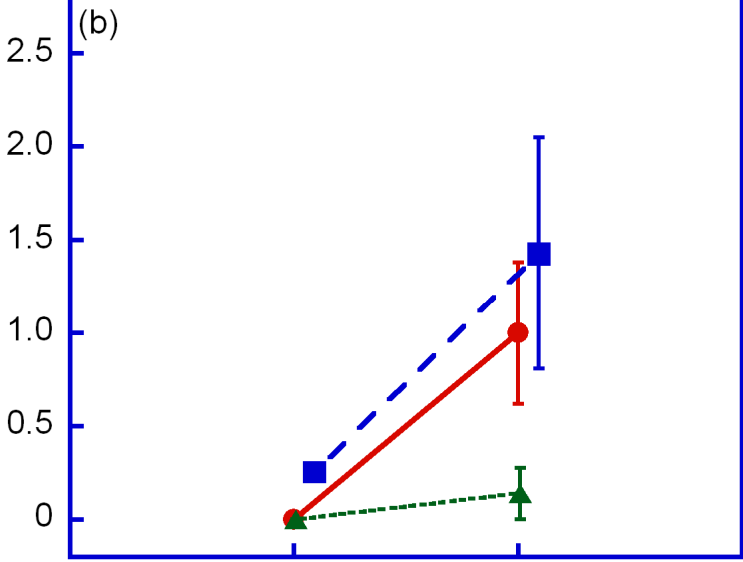


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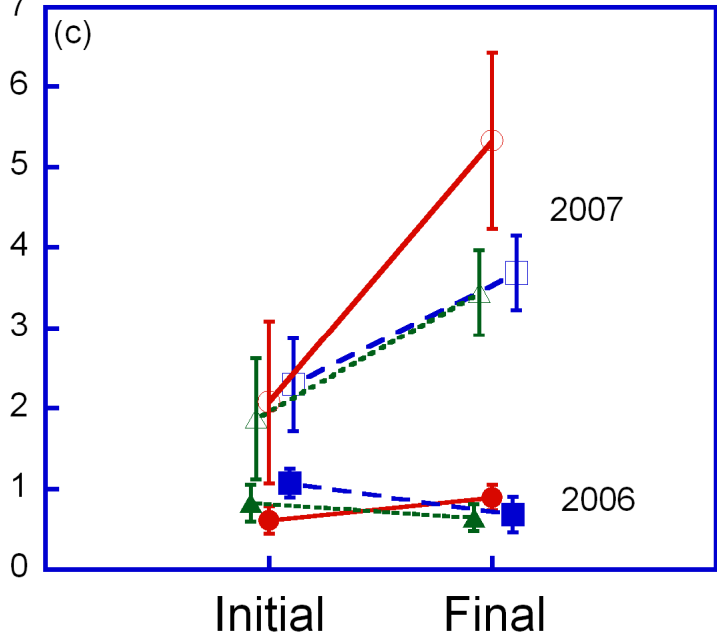
(a)



(b)



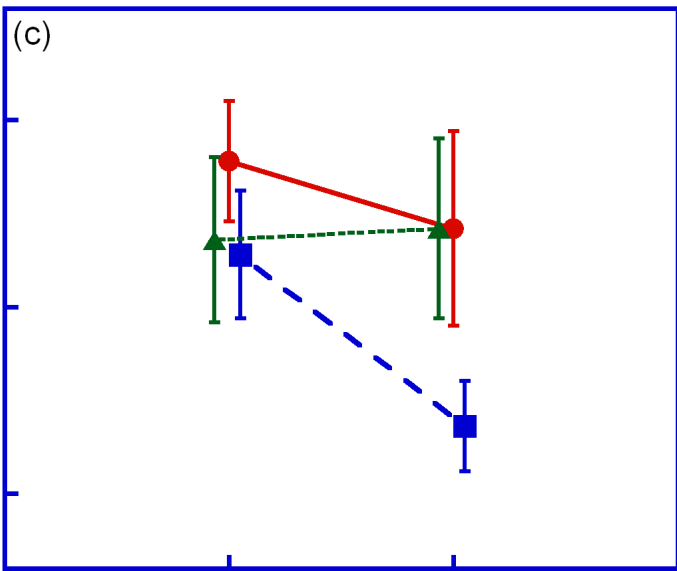
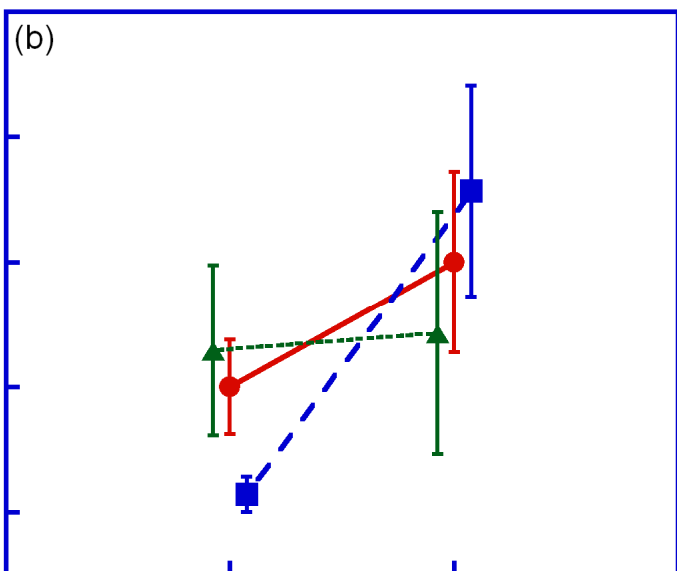
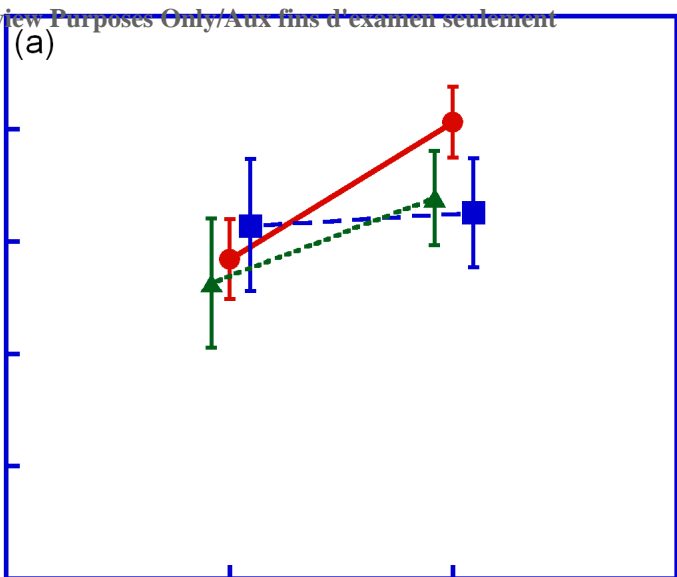
(c)



Number of salmon per section

Initial Final

Number of salmon per section



Initial Final