



Determinants of multiple central-place territory use in wild young-of-the-year Atlantic salmon (*Salmo salar*)

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5 **salmon (*Salmo salar*)**

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16 **Abstract** Patterns of space use provide key insights into how animals exploit local resources,
17 and are linked to both the fitness and distribution of individuals. We studied territory size,
18 mobility and foraging behavior of young-of-the-year Atlantic salmon *Salmo salar* in relation to
19 several key environmental factors in Catamaran Brook, New Brunswick, Canada. The 50 study
20 fish were all multiple central-place foragers (i.e. alternated among several sit-and-wait foraging
21 stations) and showed great variability in territory size and the total distance traveled within the
22 territories. Territory size increased with the mean distance traveled between consecutive foraging
23 stations, the number of stations visited and the mean foraging radius. Fish also varied greatly in
24 how much of the total travel distance was associated with foraging at a station (14.8-91.8%)
25 versus switching among stations (4.6-84.3%). As predicted, fish in slow-flowing waters, where
26 drifting prey were scarce, used larger multiple central-place territories than individuals in faster,
27 more productive waters. Interestingly, however, the most mobile fish did not inhabit slow-
28 running waters as predicted, but were found at intermediate (optimal) water current velocities.
29 Hence, our study suggests that among some multiple central-place foragers, increased mobility
30 may not only serve to increase prey encounter rate, but may reflect an attempt to patrol territories
31 in favourable habitats. Further studies are needed to determine the generality and the ultimate
32 benefits of multiple central-place space use among stream-dwelling fish and other animals.

33

34 **Keywords** foraging mode, home range, invertebrate drift, mobility, stream ecology, water
35 current velocity

36 **Introduction**

37

38 Animals exhibit great variability in local space-use patterns, which in turn provide important
39 insights into how individuals select, exploit and partition habitats and prey resources (Adams
40 2001; Helfman 1990; Sutherland 1996). For example, territories vary in size and the degree to
41 which they are defended (Grant 1997), and thus influence food availability (Stamps 1984;
42 Stamps and Eason 1989), the cost of defending an area (Davies and Houston 1984) and local
43 population density (Patterson 1980). Similarly, at local scales, individuals may vary in foraging
44 mode from sit-and-wait foragers, which search for prey from a stationary position, to cruising
45 foragers, which actively search for food (McLaughlin 1989; Pianka 1966; Schoener 1971). In
46 these situations, foraging mobility may affect prey encounter rate (Grant and Noakes 1987) and
47 the cost of exploiting a particular area (De Kerckhove et al. 2006), which together shape habitat
48 use and population distribution (Sutherland 1996). In summary, territoriality, foraging and
49 mobility play a vital role in shaping individual fitness (e.g. growth) and population structure.

50 Local space-use patterns can be affected by a range of ecological variables (Grant 1997;
51 Helfman 1990). For example, many studies suggest animals occupy smaller and more easily
52 defendable territories when prey is dense and rapidly renewable (Davies and Houston 1984;
53 Grant et al. 1992), the same conditions under which ectothermal animals are expected to adopt a
54 sit-and-wait foraging mode (Helfman 1990; but see Huey and Pianka 1981). In addition, animals
55 are believed to adopt a sit-and-wait foraging mode when prey are mobile or spatially predictable,
56 but cruise for prey when they are sedentary or spatially unpredictable (Helfman 1990; Huey and
57 Pianka 1981). Hence, the literature suggests that territory size and foraging mobility may show a
58 coordinated response to different ecological conditions. However, although cruising foragers are

59 often assumed to travel more widely than sit-and-wait foragers (e.g., Huey and Pianka 1981),
60 surprisingly few studies systematically examine how foraging mobility relates to local space-use
61 patterns and territory size (but see e.g., Ford 1983; Katano 1996).

62 Freshwater fishes and salmonids in particular, are an excellent model system for studying
63 the effects of environmental factors on local space use, because they exhibit great variability in
64 territorial and foraging behavior in the wild (Grant and Noakes 1987; Katano 1996; Nakano et al.
65 1999). In fast-running waters, where drifting invertebrates provide a spatially predictable, rapidly
66 renewing and abundant prey resource, stream-dwelling salmonids typically sit-and-wait and
67 intercept mobile prey from a centrally-placed foraging station (Grant et al. 1989; Kalleberg
68 1958). Intuitively, because the space use of these fish is constrained by repeated returns to the
69 same central-place location, they are often viewed as sedentary and as using small territories (but
70 see Steingrímsson and Grant 2008). In slow-running waters and lakes, however, fish may cruise
71 over large areas, as they specialize on sedentary or patchy food, such as benthic or planktonic
72 invertebrates (Biro et al. 1997; Katano 1996; McLaughlin et al. 1992; Minns 1995). Social status
73 can also influence local space use of stream-salmonids. Dominant individuals adopt sit-and-wait
74 foraging as they defend the best feeding positions where fast water flow provides abundant
75 drifting prey, whereas subordinate fish travel widely where less prey are available (Grant and
76 Noakes 1988; Nakano 1995; but see Martin-Smith and Armstrong 2002).

77 To date, several studies show that salmonid territories tend to be smaller in faster waters
78 where drifting prey is more abundant (Keeley and Grant 1995; McNicol and Noakes 1984; but
79 see Dill et al. 1981). Similarly, foraging mode has been demonstrated to vary between species
80 (Ferguson and Noakes 1983; Nakano et al. 1999), between lake and stream populations of the
81 same species (Biro and Ridgway 1995), and between conspecific individuals found in slow- and

82 faster-running waters of the same stream (Grant and Noakes 1987; McLaughlin et al. 1992). To
83 date, however, studies on salmonids rarely examine how territory size relates to foraging mode
84 and mobility; in part because estimates of territory size are typically confined to sit-and-wait
85 individuals that forage from a single central-place (see Steingrímsson and Grant 2008). This is
86 especially true for young-of-the-year (YOY) fish, which can be difficult to tag and follow in
87 natural settings (see Bachman 1984; Nakano 1995 for studies on older fish).

88 In this paper, we adapt general predictions on how space use relates to water current
89 velocity and prey abundance and apply them to YOY Atlantic salmon, which typically sit-and-
90 wait for prey, but can be defined as multiple central-place (MCP) foragers because they rotate
91 among several foraging stations (Steingrímsson and Grant 2008; see Chapman et al. 1989;
92 Covich 1976; McLaughlin and Montgomerie 1989 for other MCP animals). We predict that fish
93 will (i) use smaller territories, (ii) visit fewer foraging stations, and (iii) be less mobile, as current
94 velocity and the abundance of drifting prey increase. Second, with increasing current velocity
95 and drift abundance, fish will (i) travel shorter distances on each foraging attempt, (ii) forage
96 more frequently, and (iii) be less likely to attack benthic prey. Finally, we expect YOY found at
97 the most preferred current velocity (6-24 cm·s⁻¹; Girard et al. 2004) to be the most aggressive and
98 grow fastest (Grant and Noakes 1988; but see Martin-Smith and Armstrong 2002).

99 To test these predictions, we observed the local space use of 50 tagged YOY Atlantic
100 salmon in a natural stream, and measured habitat features of their territories. Below, we first
101 describe the variability in space use found among our study fish, and then examine whether and
102 how territory size relates to foraging behavior and mobility. Finally, we test if, and how space
103 use is associated with water current velocity, prey availability and other key ecological variables.

104

105 **Materials and methods**

106

107 Study population, sampling surveys, body size and growth

108

109 We studied YOY Atlantic salmon at 10 study sites in Catamaran Brook in New Brunswick in
110 2000 (see Cunjak et al. 1993 and Steingrímsson and Grant 2003 for details on the stream biota
111 and the location of the study sites, respectively). Initially, 90 fish were captured, tagged and
112 measured for fork length (range: 27.3-40.6 mm) in two snorkeling surveys on 25 June to 4 July,
113 and 12-13 July. Once we finished the space-use observations for all focal fish (see below), we
114 measured all tagged fish found in the study sites in two final snorkeling surveys on 20-23 August
115 and 11-12 September. In general, we tried to tag and observe fish in the complete range of
116 habitats used by YOY salmon in terms of water current velocity and depth. We described the
117 patterns of MCP territory size and defense for the same fish in Steingrímsson and Grant (2008).

118 Because we did not measure fish on the exact day of their space-use observation, we
119 estimated fork length of each fish on the day of observation by assuming a linear increase in fork
120 length between the capture surveys closest in time; one preceding and the other subsequent to the
121 observation date (Steingrímsson and Grant 2008). Growth rate was measured as $(\text{Fork length}_{\text{final}} -$
122 $\text{Fork length}_{\text{initial}}) \cdot (\text{Day of year}_{\text{final}} - \text{Day of year}_{\text{initial}})^{-1}$ (unit = $\text{mm} \cdot \text{day}^{-1}$). Because most fish were
123 observed between the second (12-13 July) and the third (20-23 August) survey, and because
124 growth rate varied slightly between different time periods, only fish found in both these surveys
125 were used to test if and how growth changed across current velocities.

126

127 Observations of space use

128
129 We observed the space use of 50 tagged individuals via snorkeling from 3 July to 17 August,
130 2000. Typically, fish were monitored for two 10-min periods in the early afternoon, and another
131 two 10-min periods later that same afternoon, yielding 40-min of data for each fish collected
132 between 1330-1850 h. After identifying the focal fish, we waited at least 5 min before each 10-
133 min period to avoid disturbance. For each territory, we recorded the location of foraging stations,
134 the direction (1-12 o'clock) and the estimated distance (in body lengths) of foraging attempts, the
135 location of aggressive acts, and if the focal fish was chased by an intruder. We estimated various
136 aspects of space use by creating a simple x-y coordinate system for each study site, and mapping
137 each territory using ArcView GIS 3.2 in conjunction with the Animal Movement extension
138 (Hooge and Eichenlaub 2000). Territory size was estimated via the minimum convex polygon
139 method based on all spatial coordinates ($MCP_{100\%}$) (Schoener 1981). More details on the
140 measurement and estimation of space use are reported in Steingrímsson and Grant (2008).

141 Because of rapid changes in the behavior of the study fish, we could not record every
142 behavioral event for all 50 fish. We thus gave priority to recording the location of all foraging
143 stations visited (because these greatly affect estimates of territory size), and the location of all
144 aggressive acts (because these events are rare); these variables were recorded consistently over
145 the 40-min observation. We estimated the distance and direction of as many foraging attempts as
146 possible during the first 30 minutes, whereas during the last 10-min period we only estimated
147 foraging rate. Finally, we counted switches between foraging sites and estimated the mean and
148 total distance allocated toward switching for fish using only those 10-min periods in which we
149 recorded all switches between stations.

150 Movement within territories was associated with four activities; (*i*) foraging at a station,

151 (ii) switching between foraging stations, (iii) attacking intruding fish, and (iv) fleeing from an
152 intruder. First, the distance traveled while foraging at a station was calculated as the number of
153 foraging attempts $\times 2 \times$ the mean foraging radius; hence, each foraging bout included a direct
154 return to the same station. Second, we estimated the distance traveled while switching based on
155 the number of switches \times the mean distance traveled between consecutive stations. Finally, the
156 distance traveled while chasing and fleeing from an intruder was calculated as the frequency of
157 these events $\times 2 \times$ the mean aggressive radius. Because focal fish rarely fled from an intruder and
158 because we did not estimate the mean fleeing distance, we assumed it equaled the mean
159 aggressive radius.

160

161 Habitat and food abundance

162

163 For each fish, current velocity and water column depth were measured at, and averaged across
164 the five stations where most foraging attempts were recorded. If a fish visited fewer than five
165 stations, we measured the habitat at all stations visited. We measured current velocity at 40% of
166 the total depth (measured from the bottom) with a Marsh-McBirney meter (Model 201D; Marsh-
167 McBirney, 4539 Metropolitan Ct., Frederick, MD 21704, U.S.A.). Water temperature was
168 measured before and after the 20 min of observation in the early and late afternoon, respectively.

169 Because of time constraints, we did not sample invertebrate drift at each of the 50
170 territories, but predicted drift abundance at each territory using a multiple regression model
171 established for 30 drift samples, collected in the 10 study sites on three occasions (22-23 July, 8-
172 9 August, and 4-5 September) over the season. We sampled drift by placing a 1-m long drift net
173 (mesh size = 300 μ m) with a metal frame opening (15.2 \times 23 cm), haphazardly at the initial

174 location of one of the 90 tagged YOY salmon; no location was sampled more than once. We
175 varied the sampling time depending on how fast drift accumulated in the net (mean = 49 min,
176 range = 15-120 min). For each sample, we recorded the time and day of sampling, water
177 temperature, current velocity (measured in the center of the net opening) and water depth at the
178 sampling location. Samples were only collected during daylight hours (from 1325h to 1845h).

179 Each drift sample was preserved in 10% buffered formalin and processed at Concordia
180 University. First, we separated intact organisms from other drifting material and counted all
181 organisms within the size range of edible prey (>99% of the total number) for YOY Atlantic
182 salmon (Keeley and Grant 1997). Second, we obtained the dry weight of each sample by placing
183 it in an oven at 50°C for 72 h (Merritt and Cummins 1978), then moving it to a desiccator, and
184 weighing it once on three consecutive days until the weight was stable (± 0.0001 g). The number
185 and dry weight of drifting prey were prorated to the area of the drift net frame (if not completely
186 submerged) and to a fixed time of 20 minutes. Because the numbers and dry weights of drift
187 samples were highly correlated [linear regression: \log_{10} drift dry weight ($\text{mg} \cdot 20\text{min}^{-1}$) = $-1.710 +$
188 $1.032 \log_{10}$ drift number ($\text{no.} \cdot 20\text{min}^{-1}$), $r^2 = 0.881$, $n = 30$, $p < 0.001$], we only report numbers
189 hereafter. Finally, we established a multiple regression model based on the sampling date and
190 measured habitat features to predict the invertebrate drift rate at the 50 territories. Overall, the
191 number of prey increased with current velocity, but decreased as the summer progressed
192 [multiple regression: \log_{10} invertebrate drift ($\text{no. organisms} \cdot \text{area of drift net opening}^{-1} \cdot 20\text{min}^{-1}$) =
193 $4.431 + 1.345 \log_{10}$ current velocity (ms^{-1}) - 0.009 day of year, $r^2 = 0.918$, $n = 30$, $p < 0.001$].
194 Neither water temperature (partial $p = 0.231$), water depth (partial $p = 0.727$), nor time of day
195 (partial $p = 0.300$) added significantly to this model. Hence, we predicted the drift rate at each
196 territory based on the mean current velocity at the territory and the Julian date of the observation.

197

198 Statistical analysis

199

200 To facilitate the analysis, we applied a few general rules. First, because drift rate was derived
201 from, and strongly related to current velocity (see above), and because space use changed in an
202 identical manner in response to both variables, we only report on current velocity as a predictor
203 hereafter. Second, because we did not always expect current velocity to associate with space use
204 in a linear manner, we tested for it's effect both via a simple linear regression, and by adding a
205 quadratic component to the model; the best model (with the lowest AIC_c value) was selected
206 using the Akaike's information criteria (Motulsky and Christopoulos 2004). Third, because water
207 depth, water temperature and fork length may also influence space use, we tested for their effect
208 along with current velocity via multiple regression. Overall, these additional variables had minor
209 effects on the p -value obtained for current velocity, and never altered whether current velocity
210 was better associated with space use in a linear or curvilinear manner. Because we do not put
211 forward a priori hypotheses on the effect of water depth, water temperature and fork length on
212 space use in stream-salmonids, we compared partial p -values for these variables to a Bonferroni
213 corrected significance level (α -value) of 0.005 (unplanned tests for eleven space use variables for
214 each correlate = $0.05/11$). Where necessary, variables were \log_{10} - or square-root transformed.

215

216 Results

217

218 Variability in territory use

219

220 The 50 YOY Atlantic salmon monitored in this study (mean fork length = 4.30 cm, range = 2.99-
221 5.24) exhibited great variability in local space-use patterns. Over the 40-min observation, focal
222 fish used territories ($MCP_{100\%}$), which ranged from 0.268 m² to 4.469 m² (mean, back-
223 transformed from $\log_{10} = 0.932$ m²) (Fig. 1abc), visited as few as 3, and as many as 26 foraging
224 stations (median = 12.5 stations) (Fig. 2 in Steingrímsson and Grant 2008), and traveled within
225 their territory, a total distance ranging from 15.7 to 95.0 m (median = 39.3 m) (Fig. 1def).

226 Further variability is revealed when the distance traveled by each fish is classified into
227 different behavioral activities (Table 1; Fig. 2). The distance traveled during foraging attempts
228 varied 6.0 fold, from 8.2 m to 49.6 m over 40 minutes. More impressively, the distance traveled
229 while switching between stations ranged 33.7 fold from 2.4 m to 79.2 m (Table 1). In terms of
230 frequency, YOY Atlantic salmon foraged, on average, 0.85 to 48 times at each station before
231 switching, which occurred as rarely as once every 10 minutes, and as often as once every 12.9
232 seconds (Table 1). Together, foraging (mean = 48.9%, range = 14.8-91.4%) and switching
233 stations (mean = 47.8%, range = 4.6-84.3%), accounted for 96.6% of the total distance traveled,
234 whereas only limited distances were allocated towards chasing (mean = 3.0%, range = 0-20.3%)
235 or fleeing from (mean = 0.4%, range = 0-1.8%) intruders (Fig. 2).

236 Finally, the focal fish directed most of their foraging attempts toward prey drifting in the
237 water column (mean = 91.2%; range = 75.0-99.1%), and only few attempts towards the benthos
238 (mean = 7.5%; range = 0.0-25.0%) or the water surface (mean = 1.3%; range = 0.0-12.1%).

239

240 Behavioral determinants of territory size

241

242 The size of the multiple central-place territories of YOY Atlantic salmon increased with the

243 mean distance traveled between consecutive foraging stations ($p < 0.001$), the number of
244 stations visited within the territory ($p < 0.001$) and the mean foraging radius around these
245 stations ($p = 0.019$) (Table 2). Neither foraging rate nor the rate at which individuals switched
246 stations was related to territory size (partial $p > 0.05$). Finally, in two univariate analyses,
247 territory size increased with the distance traveled while switching stations (Pearson's $r = 0.308$, n
248 $= 50$, $p = 0.030$; both variables \log_{10} transformed) but not with the total distance traveled
249 (Pearson's $r = 0.206$, $n = 50$, $p = 0.151$; both variables \log_{10} transformed). Hence, whether
250 territory size is significantly associated with fish mobility depends on our measure of mobility.

251

252 Ecological determinants of space use and growth

253

254 The 50 study fish were observed over a wide range of current velocities (mean = $0.159 \text{ m}\cdot\text{s}^{-1}$,
255 range = $0.012\text{-}0.362$) and water depths (mean = 34.4 cm , range = $14.6\text{-}78.7$), but at a narrow
256 range in water temperatures (mean = $19.8 \text{ }^\circ\text{C}$, range = $17.5\text{-}22.5$). Predicted drift rate at the 50
257 territories varied 99.7 fold from 0.9 to 89.7 invertebrates (mean = 30.0) drifting through an area
258 equal to the drift net frame ($15.2 \times 23 \text{ cm} = 349.6 \text{ cm}^2$) in 20 minutes.

259 Water current velocity was related to several components of space use in YOY Atlantic
260 salmon, but not always as expected (Fig. 3). First, as predicted, territory size decreased with
261 increasing current velocity ($\log_{10} \text{ territory size m}^2 = 0.301 - 0.886 \text{ current velocity}^{1/2} \text{ m}\cdot\text{s}^{-1}$, $r^2 =$
262 0.119 , $n = 50$, $p = 0.014$) (Fig. 3a). Second, contrary to predictions, the number of stations visited
263 within a territory did not increase as current velocity decreased (no. of foraging stations = 9.516
264 $+ 8.573 \text{ current velocity}^{1/2} \text{ m}\cdot\text{s}^{-1}$, $r^2 = 0.034$, $n = 50$, $p = 0.202$) (Fig. 3b). Third, the total distance
265 traveled within territories was best described by a curvilinear relationship, where fish traveled

266 most at intermediate water current velocities (\log_{10} total distance traveled $m = 0.547 + 6.010$
267 $\text{current velocity}^{1/2} - 7.907 \text{ current velocity } m \cdot s^{-1}$, $r^2 = 0.298$, $n = 50$, $p < 0.001$) (Fig 3c); this
268 contradicts the prediction that mobility should be greater in slow waters where drifting prey is
269 scarce. Overall, the results above were supported when the effects of current velocity on space
270 use were examined via multiple regression analysis. In no case did the inclusion of water depth,
271 water temperature and fork length, affect whether current velocity was significantly associated
272 with a given space-use component, or whether this relationship was better described in a linear or
273 curvilinear manner. Water depth was the only other correlate that was related to the components
274 of space use; fish in deep waters used significantly larger territories than those found in shallow
275 waters (partial $p = 0.005$). Interestingly, the total distance traveled was not related to the size of
276 the focal fish (partial $p = 0.315$).

277 The influence of current velocity on space use was explored further by examining the
278 foraging and switching behavior of the study fish (Fig. 4). Overall, these two components of
279 behavior showed a similar response to current velocity, although these results were not always
280 predicted from MCP theory. First, as expected from the increased availability of drifting prey
281 and increased swimming costs, the mean foraging radius and the mean distance traveled between
282 consecutive stations decreased as current velocity increased (\log_{10} mean foraging radius $cm =$
283 $0.828 - 0.306 \text{ current velocity}^{1/2} m \cdot s^{-1}$, $r^2 = 0.102$, $n = 50$, $p = 0.023$; \log_{10} mean switching
284 $distance \text{ cm} = 1.916 - 0.804 \text{ current velocity}^{1/2} m \cdot s^{-1}$, $r^2 = 0.370$, $n = 50$, $p < 0.001$) (Fig. 4ad).
285 Second, as current velocity increased, both the foraging rate and the rate at which fish switched
286 between stations, increased initially and then leveled off and decreased slightly (\log_{10} foraging
287 $attempts \text{ no.} \cdot 10 \text{ min}^{-1} = 0.809 + 4.355 \text{ current velocity}^{1/2} - 5.359 \text{ current velocity } m \cdot s^{-1}$, $r^2 =$
288 0.348 , $n = 50$, $p < 0.001$; \log_{10} station switches $\text{no.} \cdot 10 \text{ min}^{-1} = -0.409 + 6.980 \text{ current velocity}^{1/2} -$

289 7.966 current velocity $\text{m}\cdot\text{s}^{-1}$, $r^2 = 0.174$, $n = 50$, $p = 0.011$) (Fig. 4be). These findings were
290 unexpected for the switching frequency because drift-feeding fish are predicted to be less mobile
291 in fast waters where prey is abundant. Third, the distance traveled during foraging attempts was
292 greatest at intermediate current velocities (\log_{10} distance traveled foraging $\text{m}\cdot 40 \text{ min}^{-1} = 0.342 +$
293 $5.215 \text{ current velocity}^{1/2} - 6.928 \text{ current velocity m}\cdot\text{s}^{-1}$, $r^2 = 0.262$, $n = 50$, $p < 0.001$) (Fig. 4c).
294 Similarly, the total distance moved between stations fit better to current velocity in a curvilinear
295 manner, although not significantly (\log_{10} distance traveled switching $\text{m}\cdot 40 \text{ min}^{-1} = 0.251 + 5.323$
296 $\text{current velocity}^{1/2} - 6.752 \text{ current velocity m}\cdot\text{s}^{-1}$, $r^2 = 0.078$, $n = 50$, $p = 0.147$) (Fig. 4f). A
297 multivariate approach did not alter how foraging and switching behavior was associated with
298 current velocity and only revealed one significant association with another potential predictor;
299 i.e., larger fish attacked prey at a greater distance (partial $p < 0.001$). Finally, fish did not switch
300 to benthos in slow running waters as no association, neither linear ($p = 0.780$) nor curvilinear (p
301 $= 0.293$), was detected between the percent of benthic foraging and current velocity.

302 Our results were equivocal regarding the hypothesis that more aggressive individuals,
303 with greater growth potential, inhabit and defend territories in faster waters where drifting prey is
304 more abundant. Based on few aggressive acts per fish, aggression toward intruders was more
305 common at intermediate current velocities than in slow-running waters, but decreased again as
306 current velocity increased further (\log_{10} chase frequency $\text{no.}\cdot 40 \text{ min}^{-1} = -0.390 + 5.843 \text{ current}$
307 $\text{velocity}^{1/2} - 8.189 \text{ current velocity m}\cdot\text{s}^{-1}$, $r^2 = 0.128$, $n = 50$, $p = 0.041$) (Fig. 5a). Interestingly,
308 fish inhabiting fast water grew more slowly than those found in slow water (growth rate $\text{mm}\cdot\text{day}^{-1}$
309 $= 0.448 - 0.184 \text{ current velocity}^{1/2} \text{ m}\cdot\text{s}^{-1}$, $r^2 = 0.191$, $n = 38$, $p = 0.006$) (Fig. 5b). The respective
310 multivariate analyses for aggression and growth found no significant effect of water temperature,
311 water depth and fork length (partial $p > 0.3$ in all cases).

312

313 **Discussion**

314

315 Patterns of territory use

316

317 Many stream fish adopt alternative foraging tactics as they either actively cruise for benthic or
318 patchy prey items (movers), or are relatively sedentary and ambush drifting prey via sit-and-wait
319 foraging tactics (stayers) (Grant and Noakes 1987; Katano 1996; McLaughlin et al. 1999). In this
320 study, however, YOY Atlantic salmon were best described as multiple central-place foragers,
321 which sit-and-wait for prey, rotate among several foraging stations, but rarely attack their prey
322 while moving (Steingrímsson and Grant 2008). Importantly, although our study fish do not
323 appear to be able to switch from sit-and-wait to cruising foraging, they exhibit considerable and
324 often unexpected variability in their territory use patterns.

325 First, YOY Atlantic salmon in Catamaran Brook use MCP territories that are very large
326 compared to typical single central-place territories defended by other YOY stream-dwelling
327 salmonids, and are also highly variable in size (0.268 - 4.469 m²) (see Steingrímsson and Grant
328 2008). Second, our study shows that stream salmonids can vary greatly in the number of foraging
329 stations visited within their territories (3-26 stations) (see Nakano 1995). Finally, in spite of
330 being predominately sit-and-wait foragers, the study fish were very mobile, traveling a total
331 distance of 15.7 to 95.0 m (median = 39.3 m = 914 body lengths·40 min⁻¹), of which 47.8% (4.6-
332 84.3%) was due to switching between foraging stations. In comparison, based on the mean radii
333 and the frequency of aggressive acts and foraging attempts initiated by a territorial stream-fish
334 from one foraging station (*sensu* Materials and methods), we estimate that YOY brook charr

335 (Grant et al. 1989) and YOY rainbow trout (Keeley 2000) traveled on average 501 and 722 body
336 lengths in 40 minutes, respectively. Furthermore, YOY brook charr in two lakes, most of which
337 were cruising foragers, traveled a mean distance of 890 and 1187 body lengths in 40 minutes,
338 while searching for prey (estimated from Biro et al. 1997). Hence, MCP drift-feeding fish are
339 more mobile than single central-place foragers and may even travel similar distances to cruising
340 fish in lakes. Unfortunately, most studies on stream-salmonids focus on the energetic basis of
341 drift-feeding from a single focal point (e.g., Enders et al. 2003; Hughes et al. 2003), and the costs
342 and benefits associated with switching among several stations have received limited attention.

343

344 Ecological determinants of territory use

345

346 Because the use of multiple foraging stations among salmonids has received limited attention
347 (but see e.g. Nakano 1995), this study yields several novel findings on how their space-use
348 patterns relate to ecological conditions. First, in harmony with most single central-place studies
349 (Keeley 2000; McNicol and Noakes 1984; but see Dill et al. 1981), MCP territories decreased in
350 size as current velocity and prey drift rate increased. In MCP territories, this decrease in size is
351 associated with a decrease in the distance traveled between consecutive foraging stations and a
352 shorter foraging radius in faster, more productive waters (Keeley 2000). Interestingly, although
353 fish that visit more foraging stations have larger territories, there is no evidence that they visit
354 fewer stations in faster water where drifting prey is abundant. In contrast, Nakano (1995) found
355 that among masu salmon (*Oncorhynchus masou*) in pools, dominant fish used one or few stations
356 where prey were abundant, while younger subordinate fish switched among several low-quality
357 stations. This discrepancy may be due to Nakano's (1995) fish forming space-related dominance

358 hierarchies across year-classes in a habitat where the best feeding sites (and food resources) are
359 relatively predictable and clumped in space. YOY Atlantic salmon, however, are typically found
360 in a territorial mosaic (Kalleberg 1956), where the input and distribution of drifting prey may
361 play a less obvious role in shaping social status and space use.

362 Unexpectedly, and irrespective of how mobility was measured, YOY Atlantic salmon
363 were not most mobile in slow-running waters where drifting prey is scarce. Instead, the most
364 mobile fish were found at intermediate current velocities; this trend emerged when we examined
365 (i) the total distance traveled, (ii) the rate at which YOY salmon switched between stations (rate
366 of movement, *sensu* Ford 1983), but not significantly so for (iii) the distance traveled while
367 switching. These findings, coupled with the fact that fish in slow waters did not forage more on
368 the benthos, suggest that mobility in YOY salmon was not primarily associated with seeking out
369 alternative prey where drifting invertebrates were rare (but see Armstrong et al. 1999). In this
370 study, however, benthic foraging was greater (7.5%) than in an earlier study on Atlantic salmon
371 in Catamaran Brook (< 1%), where fish used fewer stations (Keeley and Grant 1995). Hence, the
372 link between benthic foraging and multiple central-place space use may warrant further study.

373 Why YOY Atlantic salmon travel more between stations at intermediate water current
374 velocities remains unclear, but habitat selection and territorial behavior may play a role. First,
375 although YOY salmon in Catamaran Brook use a wide range of habitats, they show consistent
376 preferences for current velocities of 6-24 cm·s⁻¹ (Girard et al. 2004; see also Morantz et al. 1987),
377 which match the intermediate current velocities used by the most mobile fish in this study (Fig.
378 4ef). Second, among drift-feeding fish, preferred current velocities generally represent higher
379 quality habitats, e.g. in terms of net energetic gain (Hill and Grossman 1993). Third, Johnsson et
380 al. (2000) showed that brown trout in preferred habitats defend their territories more intensively

381 than those in low quality habitat; a similar trend emerged in this study as aggression is slightly
382 more frequent at intermediate current velocities. Consequently, because our fish rarely attack
383 intruders across their large MCP areas (Steingrímsson and Grant 2008), rapid switches among
384 stations at optimal water currents, may indicate more patrolling of territories. Although patrolling
385 increases travel costs of territory holders, it may also reduce the traffic of intruders immediately
386 upstream of many foraging stations, where a significant portion of the drifting prey may emerge
387 from the benthos (Elliott 2002; McIntosh and Townsend 1998; see Steingrímsson and Grant
388 2008). Importantly, our data suggest that YOY Atlantic salmon occupying preferred current
389 velocities do not grow faster than fish in other habitats (see also Girard et al. 2004). Obviously,
390 the above ideas need to be verified in future studies.

391 Ecological variables other than current velocity and invertebrate drift had limited effects
392 on the space use of YOY salmon. Not surprisingly, foraging radius was positively related to fork
393 length (see e.g. Elliott 1990; Grant et al. 1989), in part because larger fish are better swimmers
394 and may see farther (Dunbrack and Dill 1983). The study fish also used larger territories in
395 deeper water, perhaps because they tend to attack prey at a greater distance, and travel longer
396 distances between consecutive stations. To date, however, any explanations on the ultimate
397 causes for this trend would remain speculative.

398

399 Implications for salmonids and MCP foragers

400

401 Multiple central-place behavior of YOY Atlantic salmon adds a new dimension to the existing
402 literature on how space use relates to environmental conditions, and how these factors combine
403 to shape individual fitness and population dynamics of stream-dwelling salmonids. First, large

404 MCP territories, although not defended as efficiently as smaller territories, suggest that territorial
405 behavior plays an important role during competition for food and space, even at low population
406 densities where habitats appear not to be highly saturated (see discussion in Steingrímsson and
407 Grant 2008). Second, this study shows that salmonid species differ in the foraging mode they
408 typically adopt, and the flexibility they exhibit in response to different ecological conditions. For
409 example, brook charr (*Salvelinus fontinalis*) (Biro and Ridgway 1995; Grant and Noakes 1987;
410 McLaughlin et al. 1999), Dolly Varden charr (*Salvelinus malma*) (Fausch et al. 1997) and coho
411 salmon (*Oncorhynchus kisutch*) (Puckett and Dill 1985) can adopt both a sit-and-wait and an
412 active foraging mode, where the latter is associated with utilizing benthic (Fausch et al. 1997) or
413 pelagic prey (McLaughlin et al 1999) in slow waters where drifting prey is rare. Other species,
414 such as white spotted charr (*Salvelinus leucomaenis*) (Fausch et al. 1997) and Atlantic salmon
415 (Nislow et al. 1998; but see this study), may respond to reduced drift via increased benthic
416 feeding, but without the corresponding switch to active search (but see Armstrong et al. 1999).
417 Although this study indicates that YOY Atlantic salmon are mostly sit-and-wait foragers, it
418 demonstrates that “less flexible” salmonids, may still exhibit great variability in their space-use
419 patterns, e.g. in the number of foraging stations visited and mobility. Finally, this study suggests
420 that YOY salmon may grow faster, or as fast (Girard et al. 2004) in slow waters where drift-
421 feeding is presumably less beneficial, without switching to alternative prey such as benthos.

422 To date, multiple central-place foraging has been primarily viewed as a foraging tactic
423 used among mammals and birds to increase encounter rate with a depletable food supply while
424 minimizing travel costs (Chapman et al. 1989; McLaughlin and Montgomerie 1989). This study,
425 however, differs in two important ways from earlier MCP studies, because YOY Atlantic salmon
426 (i) defend territories and (ii) feed on drifting prey, often viewed as a rapidly-renewing resource

427 (Sutherland 1996). Hence, this study extends MCP theory to situations where foraging from
428 multiple sites does not obviously increase encounter rate or decrease travel costs, and may rather
429 be related to how intensively home ranges are patrolled and defended (*sensu* Mitani and Rodman
430 1979; Paton and Carpenter 1984). The generality and the ultimate causes of multiple central-
431 place foraging among stream-dwelling fish and other animals warrant further study.

432

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578 **Table 1** Variability in space use associated with foraging from a station, switching between
 579 foraging stations, and chasing intruding fish, by 50 young-of-the-year Atlantic salmon in
 580 Catamaran Brook

Variable	Mean	Median	Range	CV
Distance traveled foraging ($\text{m}\cdot 40\text{min}^{-1}$)	19.4	15.6	8.2-49.6	0.507
- Foraging rate ($\text{no. attempts}\cdot 10\text{min}^{-1}$)	44.9	42.3	19.0-93.0	0.349
- Mean foraging radius (cm)	5.3	4.9	3.6-12.2	0.285
Distance traveled switching ($\text{m}\cdot 40\text{min}^{-1}$)	23.5	16.3	2.4-79.2	0.852
- Switching frequency ($\text{no.}\cdot 10\text{min}^{-1}$)	14.4	9.7	1.0-46.5	0.805
- Mean switching distance (cm)	43.0	41.0	22.3-117.0	0.382
Distance traveled during chases ($\text{m}\cdot 40\text{min}^{-1}$)	1.3	1.0	0.0-6.1	1.089
- Aggressive frequency ($\text{chases}\cdot 40\text{min}^{-1}$)	3.4	3.0	0-11	0.886
- Mean aggressive radius	15.9	15.2	1.9-31.8	0.409

Table 2 Multiple regression model^a describing the behavioral correlates of \log_{10} territory size (m^2) in young-of-the-year Atlantic salmon using multiple foraging stations in Catamaran Brook

Correlate	Slope	r^2	p -value
\log_{10} mean switching distance (cm)	1.2407	0.622	< 0.001
Stations visited ($\text{no.} \cdot 40 \text{ min}^{-1}$)	0.0273	+0.171	< 0.001
\log_{10} mean foraging radius (cm)	0.5225	+0.013	0.019
Total number of observations (n)	-0.0007	+0.016	0.047

Full model	--	0.822	<0.001

^aThe model was selected using the Akaike's information criteria; \log_{10} foraging attempts ($\text{no.} \cdot 10 \text{ min}^{-1}$) and \log_{10} station switches ($\text{no.} \cdot 10 \text{ min}^{-1}$) were removed from the model.

Figure legends

Fig. 1 Variability in the space-use patterns of YOY Atlantic salmon in Catamaran Brook. The 100% minimum convex polygon (wide solid line) encircles the location of all aggressive acts and foraging attempts (solid circle), the foraging stations visited (crossed circle), and the travel pattern (thin solid line) of selected individuals. The left column depicts (a) the smallest and (b) the largest territory, and (c) the frequency distribution of territory sizes. The right column depicts the fish that traveled (d) least and (e) most, and (f) the frequency of the total distances traveled in 40 minutes within the 50 territories

Fig. 2 Individual variability in the distance traveled within the territories of 50 YOY Atlantic salmon in Catamaran Brook. Each column shows one fish (1-50, in the order of observation), and indicates the percentage of the total distance traveled in 40 minutes, allocated toward switching between stations (grey), foraging attempts (empty), aggression toward intruding fish (hatched), and fleeing from intruders (dotted)

Fig. 3 The effect of water current velocity on (a) the territory size, (b) the number of foraging stations, and (c) the total distance traveled within territories of 50 YOY Atlantic salmon in Catamaran Brook. The equations best describing these relationships are represented either by a solid (significant) or dashed line (not significant). For visual clarity, transformed values on both axes were replaced with the original, back-transformed values. All dependent variables were estimated over 40 minutes

Fig. 4 The influence of current velocity on foraging behavior (a, b, c) and switching between foraging stations (d, e, f) of 50 YOY Atlantic salmon in Catamaran Brook. The equations best describing these relationships are represented by a solid (significant) or dashed line (not significant).

Fig. 5 The association between current velocity and (a) the number of aggressive acts directed toward intruding fish and (b) the growth rate of YOY Atlantic salmon in Catamaran Brook. The solid lines represent the best fit to the data. Growth rate is measured between 12-13 July and 20-23 August, 2000, and is only reported for fish caught in both surveys









