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1 **Fish in space: Local variations of home range and habitat use of a stream-**
2 **dwelling fish in relation to predator density**

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4 **FINAL VERSION ACCEPTED BY JOURNAL OF ZOOLOGY**

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16
17 **Page heading:** Variability in space use by stream fishes

18

19 **Abstract**

20 A key response of animals to local environmental variation is altered use of space, but studies
21 simultaneously examining local variation in habitat use and space use are uncommon. We
22 predicted that elevated abundance of avian predators would result in grayling *Thymallus*
23 *thymallus*, a stream-dwelling fish, using mesohabitats containing more cover, superimposed on
24 seasonal changes in use of key resources (and hence space use) for functions such as reproduction.
25 Using radio-telemetry, the pattern of space and habitat use by 40 wild grayling was determined in
26 neighbouring stream sections in relation to season and predator density. Grayling used different
27 habitats between seasons, but displayed similar patterns of habitat use in adjacent sections.
28 Although patterns of habitat use were stable between stream sections, space use was not. In two
29 winter periods, grayling ranged significantly more widely where there were significantly greater
30 densities of avian predators, especially cormorant, *Phalacrocorax carbo*. No such differences
31 were apparent in summer when cormorants were absent, but experimental manipulation of
32 predator densities was not possible, so results are correlative. Support for a predator effect is
33 provided from significantly greater rates of injury, associated with avian beak scar marks, present
34 on grayling from the section with highest avian predator densities, compared to adjacent sections
35 with lower levels of avian predators. Unlike many studies of fish behaviour to elevated predation
36 risk, in which fish make greater use of 'refuge' habitat, grayling exhibited wide-ranging
37 behaviour and high activity, possibly reflecting avoidance behaviour.

38

39

40 **Introduction**

41 One of the key responses of animals to variation in their environment is to alter their use of space.
42 This plasticity in spatial behaviour has been recognised in laboratory and field studies of animals
43 in response to variations in factors such as population density (Schradin *et al.*, 2010), food
44 availability (Brashares & Arcese, 2002; Brodersen *et al.*, 2008; Schradin *et al.*, 2010), sex (Perry
45 & Garland, 2002), preferred physical habitat (Twiss, Thomas & Pomeroy, 2001), reproductive
46 condition (Dahle & Swenson, 2003) and predation risk (Lima & Dill, 1990; Werner, 1991; Eklov
47 & Persson, 1996; Yunger, 2004; Heithaus & Dill, 2006; Willems & Hill, 2009).

48
49 Reported effects of predation risk on behaviour include alterations of levels and timing of
50 foraging activity (Werner, 1991, Railsback *et al.* 2005; Ross *et al.*, 2013), increased vigilance
51 behaviour and grouping (Shulz & Noe, 2002), and increased use of refuge habitat (Grand & Dill,
52 1997, Rangely & Kramer, 1998, Krause *et al.*, 1998; Brodersen *et al.*, 2008; Skov *et al.*, 2013).
53 Fewer studies have sought to examine how the extent of space use and habitat choice vary
54 simultaneously under natural conditions of varying predation risk (e.g. Frair *et al.* 2005; Willems
55 & Hill 2009; Chapman *et al.*, 2013). Frair *et al.* (2005) showed the effects of wolves, *Canis lupus*,
56 on elk, *Cervus elaphus*, movements and space use, while Willems & Hill (2009) demonstrated,
57 for vervet monkeys, *Cercopithecus aethiops*, the interplay between relative avoidance of areas
58 with high predator threat and elevated use of resource-dense habitat. Chapman *et al.* (2013)
59 provide evidence for a predation / growth-potential tradeoff determining winter migration to
60 refuge habitat by cyprinid fishes. There remains a need for a better understanding, through such
61 natural environment experimental approaches, of the spatial behavioural responses of mobile
62 prey in relation to predators and vice versa (Lima 2002).

63
64 In this study, space and habitat use were measured for a stream-dwelling fish, grayling,
65 *Thymallus thymallus*, in adjacent river reaches, where avian predator abundance varied within
66 and across seasons. There has been substantial debate as to the impacts of avian predators,
67 especially cormorant, *Phalacrocorax carbo*, on grayling populations (Suter, 1995; Staub *et al.*,
68 1998). We predicted that elevated predator density would be associated with grayling spending
69 more time in habitats containing more cover and that home range size and daily movement would
70 be unaffected by predator density, but would vary with season due to changes in resource
71 requirements for functions such as reproduction.

72
73

74 **Materials and Methods**

75 **Study area**

76 The study was carried out on the River Rye, the major tributary of the River Derwent (Humber
77 River System), in Northeast England (Whitton & Lucas, 1997). The Rye is typically 10-15m
78 wide, with an average mid-channel depth of 0.7m and mean discharge of $3.5\text{m}^3\text{ s}^{-1}$. The study
79 area (centred on $54^{\circ}12'\text{N}$, $0^{\circ}57'\text{W}$) was separated into three contiguous reaches, bordered by
80 pastureland, and is private, with low human disturbance. The middle section (B), 2.5-km long,
81 was bounded at the downstream limit by a sloping 1.2-m high flow-gauging weir and at the
82 upstream limit by a 1.4-m high sloping mill weir. The lower (A) and upper (C) sections each
83 stretched unobstructed for over 10km downstream and upstream respectively but are defined here
84 as the distance from the boundary with section B to the furthest radio-fix of tracked fish in each
85 section, approximately 4.0km for section A and 5.2km for section C. Although the weirs can be

86 passed, with difficulty, by salmonids (M. Lucas, pers.obs.), in this study no tagged fish passed
87 upstream or downstream from one section to another. The river is characterised by riffle-glide
88 sequences with mostly gravel bed in the former and sandy areas in the latter habitat. In-stream
89 macrophyte growth (mostly *Fontinalis* spp. and *Ranunculus fluitans*) is sparse but substantial
90 riparian tree-cover occurs, principally from *Alnus glutinosa* and *Salix* spp., with the latter more
91 common in the downstream section. In the downstream section, bank regrading has resulted in
92 steeper banks, with less extensive riparian cover.

93
94 The fish community comprises mostly brown trout *Salmo trutta*, some of which are stocked, and
95 wild grayling. Large numbers of the small fish species bullhead, *Cottus gobio*, and minnow
96 *Phoxinus phoxinus*, also occur. The main predators of fish larger than 10cm in the study area are
97 the birds, cormorant, goosander, *Mergus merganser* and grey heron, *Ardea cinerea*. Cormorant
98 and goosander are more abundant on the Rye in winter, most leaving in spring to breed elsewhere,
99 while heron occur all year round. Otter, *Lutra lutra*, and mink, *Mustela vison*, are present at low
100 densities, based upon footprint and scat evidence (M. Lucas, pers. obs.). The piscivorous fish,
101 pike *Esox lucius*, occurs in the river but in over 60h of electric fishing and over 1000h of tracking
102 and habitat surveying no pike were observed; thus within the study area they must be extremely
103 scarce. Although the study area is recreationally fished, fewer than 20 angler visits were observed
104 during the whole study, reflecting a low density of impact and disturbance. Anglers agreed to
105 remove no grayling for the duration of the study.

106

107 **Tagging and recording**

108 Adult grayling for radio-tagging were obtained by electric fishing or rod-and-line. Radio-tracking
109 was carried out in two periods, with a total of 40 fish radio-tracked. In the first period eight

110 grayling were released in each section in late winter (median, 19 February 2004) and tracked
111 until 1 July 2004. In the second period eight fish were released in late autumn (median, 6
112 November 2004) in sections A and B and tracked until 5 January 2005. Mean \pm SE fork length of
113 tagged fish, 318 ± 44 mm, did not vary between experimental groups (ANOVA, $F=1.09$,
114 $P=0.378$). Fish were radio-tagged (173 MHz, biocompatible silicone-potted PIP, Biotrack, UK)
115 by implantation of the tag into the body cavity, with the tag's whip antenna exiting through the
116 body wall and closure of the incision with absorbable sutures (Lucas and Baras, 2000). Tag
117 weight to body weight ratio did not exceed 1%. Tagging was carried out under general
118 anaesthetic (buffered tricaine methansulphonate, 0.1 g L^{-1}) on the bankside under UK Home
119 Office licence PPL60/3260. Fish were released within 10m of the capture site when swimming
120 strongly (< 1 h post-surgery). Fish captured in groups were released together, combining several
121 untagged fish and tagged fish.

122
123 Radio-tracking was carried out on foot using a scanning receiver (Biotrack Sika, UK) and a three-
124 element Yagi antenna, typically at 1-4 day intervals, by day. Fixed-station scanning receiver-
125 loggers (Lotek SRX400, Newmarket, Ontario) were placed at section boundaries to determine the
126 occurrence of movements to section limits, including at night. Fish positions were translated to a
127 field-recording map using a handheld GPS (GARMIN eTrex) and by reference to mapped
128 landmarks, giving a precision of better than or equal to 3m, adequate for quantifying mesohabitat
129 use at the spatial scale of individual bankside trees. During each tracking episode, the number,
130 identity and location of avian piscivores was recorded. Usually the birds flew off and did not
131 appear to land again in the section being walked, or in adjacent sections, although this cannot be

132 discounted. The length of bank walked on each tracking session and river section was recorded
133 and the density of piscivorous birds (number per km of river) of each species was calculated.

134

135 **Home range, activity and habitat use analysis**

136 During summer and winter grayling adopt home ranges (Nykänen, Huusko & Mäki-Petäys,2001;
137 Ovidio *et al.*,2004). Home range use by grayling was expressed in terms of linear range, along
138 the river mid-line. During the prespawning period, in spring, grayling exhibit a breakdown of
139 home range as they prepare to spawn (Nykänen *et al.*,2001; Ovidio *et al.*,2004). In order to
140 analyse space use of grayling tracked during the winter, spawning and summer periods, it was
141 necessary to determine objectively the boundaries of the period associated with spawning. Most
142 grayling tracked exhibited net upstream movement before the period when courtship and
143 spawning was observed (5-18 April 2004) and, to a lesser degree, net downstream movement
144 after the spawning period. Segmented regression analysis (SegRegW) of the mean distance of all
145 fish relative to their release locations against date of location was used to identify the best-fitting
146 function (multiple broken stick) and to generate optimum break points, by maximising the
147 coefficient of explanation. This analysis defined the spawning period, associated with increased
148 mobility and breakdown of home range as, starting on 7 March 2004 (prior to first break point
149 $r^2=0.053$, $P=0.113$, after first break point $r^2=0.905$, $P<0.001$) and ending on 5 May 2004 (prior to
150 second break point $r^2=0.575$, $P=0.001$, after second break point $r^2=0.002$, $P=0.329$). As well as
151 calculating linear home ranges, rates of movement between successive fixes were generated for
152 each fish and expressed as median values by section and season. The interval between position
153 fixes can affect movement estimates (Ovidio, Philippart & Baras, 2000); because most fixes were
154 made at 1-4 day intervals, estimated movement rates are conservative, but because radio-fixes
155 were taken in every section on each tracking date, comparison between sections is legitimate.

156 Data were assessed for normality and homogeneity of variances in determining the use of
157 parametric or non-parametric statistical procedures.

158
159 Habitat along the entire reach was measured at the end of the study at ~Q75 flow by carrying out
160 cross-channel surveys to record habitat availability. Sampling occurred every 10-30m of channel
161 length, covering repeated glides, riffles and transition zone, and at every radio-fix location.

162 Variables measured were riparian cover (scale of 0-5), instream macrophyte cover (0-5), bank
163 slope (0-5), channel width and depth (m), velocity at 60% of depth (ms^{-1}), and substrate
164 composition (percent silt, sand, gravel, pebble, cobble, boulder, bedrock) by visual estimation in
165 quadrats. All in-channel variables were measured at 0.25, 0.5 and 0.75 of river width. Data from
166 a total of 1253 sites (section A, 477; section B, 309; section C, 467) were obtained. Due to the
167 co-linear and highly correlated nature of the habitat variables Principal Components Analysis
168 (PCA) was carried out on the range of habitat variables. Combining all the survey sites, so
169 section-wise PCA of fish habitat use was not compromised, the first two principal components
170 extracted explained 77.8% of variation. Loadings of PC1 (52.6% of variation) were depth 0.575,
171 velocity -0.587 and dominant substrate -0.560 and of PC2 (25.2% of variation) was riparian
172 cover 0.975. Habitat use by grayling in the different sections and seasons were generated from
173 average values for each fish, quantified in terms of the extracted principal components.

174

175 **Frequency of scarring as a measure of long-term predation risk**

176 Grayling ($n=183$) and brown trout ($n=399$) sampled during electric fishing surveys and captured
177 by rod-and-line along the study reaches (Dec 2003 - March 2004; Oct-Nov 2004) were inspected
178 for evidence of healed scars and fresh wounds, indicative of damage from unsuccessful predation

179 attempts, using Carss (1988) as an information source on scar types characteristic of different
180 avian predators.

181

182 **Results**

183 **Predator densities**

184 Densities of piscivorous birds varied between sections and across seasons (Table 1). Cormorant
185 density was significantly greater in the downstream section compared with the middle and
186 upstream sections (Mann-Whitney, $P < 0.001$), but there was no difference between the upper two
187 sections ($P > 0.05$). Cormorants were abundant in the downstream section during winter but began
188 to leave in spring and were less abundant during the grayling spawning season (Table 1). There
189 was no significant difference in median densities of goosander between the three sections
190 (Kruskal-Wallis, $P > 0.05$) but numbers declined in summer (Table 1). Heron were most abundant
191 in spring and summer but occurred at low densities compared to cormorant and goosander.
192 Median densities of heron in the two upstream sections were significantly higher than in the
193 downstream section (Mann-Whitney, $P < 0.001$). River turbidity, expected to affect visual acuity
194 of fishing birds, was significantly higher in winter and spring study periods than in summer
195 (Mann-Whitney, $P < 0.001$).

196

197 Incidence of scarring in grayling and trout was used as an indicator of failed predation attempts.

198 Recent scars included narrow, parallel marks across the fish's flanks, puncture marks and lesions,
199 all associated with scale loss without regrowth. Of 30 such scars greater than 1 cm², 26 fitted the
200 visual characteristics given by Carss (1988) for damage by cormorant (17), sawbill duck (7) and
201 heron (2). Older scars were much more frequent, but it was more difficult to attribute the cause of

202 these because of tissue repair and scale regrowth, but these included patterns typical of bird
203 predation attempts. The frequency of occurrence of fish with scars varied significantly between
204 sections (grayling, $\chi^2 = 11.15$, $P < 0.01$; brown trout, $\chi^2 = 20.56$, $P < 0.001$). The incidence of recent
205 and healed scars larger than 1 cm² was greatest for grayling and trout in the downstream section
206 compared to the middle and upstream sections (Table 2). No radio-tracked fish are known to have
207 been removed by predators during the study, although two tags in the downstream section (A)
208 were lost within 12h of a previous fix, with over half of battery life remaining, and could not be
209 relocated despite extensive searches. The most likely explanation for these losses is from avian
210 predators capturing tagged fish and moving out of detection range.

211

212 **Home range and activity of grayling**

213 In the first radio-tracking experiment (Jan-Jul 2004) there was a significant difference between
214 the median linear ranges of fish tracked in the three sections for winter (Kruskal-Wallis, $P < 0.01$)
215 and spawning periods (Kruskal-Wallis, $P < 0.01$), but not for summer (Kruskal-Wallis, $P > 0.05$)
216 (Fig. 1). Grayling in the downstream section (A) had significantly larger median linear ranges
217 than those in the middle and upstream sections in winter and spawning periods (Mann-Whitney,
218 all $P < 0.05$), but there was no significant difference in range between any sections in summer
219 (both $P > 0.05$). In the second winter radio-tracking experiment, fish in the downstream section A
220 again exhibited larger ranges than in the adjacent section B (Mann-Whitney, $P = 0.002$; Fig. 1).
221 Home ranges for grayling in each of sections A and B, did not differ significantly between winter
222 1 and winter 2 (Mann-Whitney, both $P > 0.05$).

223

224 Rates of movement by grayling differed between sections in the first winter (Kruskal-Wallis,
225 $P = 0.001$), second winter (Mann-Whitney, $P < 0.001$), and the spawning period (Kruskal-Wallis,

226 $P=0.022$) but not in summer (Kruskal-Wallis, $P=0.215$). In the first winter, median rates of
227 movement in section A, were six times greater than in the other sections (Table 3). In the second
228 winter period, median rates of movement in section A, were five times higher than in adjacent
229 section B. In spring, median rates of movement approached three times higher in section A, than
230 the other sections. Because successive fixes were usually 1-4 days apart, these are conservative
231 measures of movement. Winter movement in the lower section was characterised by repeated
232 upstream and downstream movements, rather than movements around one or more core areas as
233 occurred in middle and upstream river sections.

234

235 **Habitat availability and use**

236 The downstream river section had significantly lower average coverage of riparian woody
237 vegetation, but locally dense areas occurred, and trees and bushes provided overhead as well as
238 submerged refuge cover (Table 4). In terms of extracted principal components, availability of in-
239 stream habitats was broadly similar between the study sections, with slightly greater availability
240 of slower water in section B, slightly less deep water in section B and finer substrate in section A
241 (Fig.2). Although the magnitudes of average differences in velocity, depth and substrate were
242 small, large sample sizes showed these differences to be significant between sections (Table 4).
243 Grayling displayed seasonal patterns of habitat use in all sections, with significant differences in
244 mean PC1 value between winter and spawning occurring in all sections, and between winter and
245 summer in sections B and C (ANOVA, with post-hoc Tukey, $P<0.05$). Grayling used deeper,
246 slower water with fine substrate (mostly sand) in winter (higher values of PC1), moved to
247 shallower, faster water with larger substrate (gravel/pebble) in the spawning period (lower values
248 of PC1), and remained in similar PC1 habitat in summer (Fig.3). Greatest use of riparian cover
249 (PC2) occurred in summer, when avian predators were scarcest (Fig.3) but no differences

250 occurred between sections or seasons (ANOVA, $P>0.05$). The only significant difference in
251 mean PC1 use by grayling between sections, within seasons, occurred between fish in sections B
252 and C in winter (ANOVA, with post-hoc Tukey, $P<0.05$).

253

254 **Discussion**

255 Our hypothesis, that fish would display increased use of local ‘refuge’ habitat, with greater cover,
256 when avian predators were abundant was not supported. In contiguous river sections, radio-
257 tagged grayling displayed similar patterns of habitat use within seasons and similar changes in
258 habitat use between seasons. Although riparian (and associated submerged) cover was less
259 abundant in the downstream-most river section where avian predators were most abundant in
260 winter and spawning periods, dense patches of cover were present, but tagged grayling did not
261 accumulate in these or show strong local cover use. Indeed, the opposite was true, with greatest
262 use of riparian cover in summer in all river sections, when avian predator densities were lowest.
263 However, grayling exhibited consistently different spatial behaviour in the downstream-most
264 section when high densities of fish-eating birds, especially cormorants, were present. Grayling
265 and trout in the downstream-most section displayed higher levels of injury, including types
266 characteristic of avian attack (Carss, 1988).

267

268 The home ranges of adult grayling in all three sections in summer and in the middle and upper
269 sections in winter were of similar magnitude to other studies (Nykänen *et al.*, 2001; Nykänen,
270 Huusko & Lahti, 2004; Ovidio *et al.*, 2004), the former two being in a sub-Arctic river, but the
271 latter occurring in a Belgian stream of similar size to the Rye. By contrast, winter home range of
272 grayling in the downstream-most section was 5 (Ovidio *et al.*, 2004) to 20 times (Nykänen *et al.*,

273 2001,2004) greater than published studies, and 3-5 times higher than in adjacent study sections at
274 the same time. Winter-time movement rates in the downstream, predator-rich section were
275 significantly greater in both winter periods. We interpret the clear difference in space use by
276 grayling in the downstream-most section as being a response to avian predators. It was not
277 possible to carry out a predator exclusion experiment in this study; neither have most other
278 studies of predation risk in the natural environment (e.g. Frair *et al.* 2005; Willems & Hill 2009;
279 Skov *et al.*, 2013), so the results are correlative. However, the elevated levels of scarring,
280 including a high proportion characteristic of avian attack, observed in the section with highest
281 predator density provide strong supporting evidence of the role of predation threat there.

282
283 Goosander, heron and cormorant eat grayling where this species is common, but goosander rarely
284 take salmonids longer than 25cm (Marquiss *et al.*, 1998). The grayling tracked are unlikely to
285 have been susceptible to predation by goosander, but foraging goosander might still elicit an
286 evasion response from large grayling. Where grayling are common, they comprise a substantial
287 portion of the cormorant's diet but grayling larger than 40cm are rarely taken (Suter, 1995; Keller
288 1998, Marquiss *et al.*, 1998). Cormorants remain efficient predators even during turbid water
289 conditions, (Grémillet *et al.*, 2012), relevant since, in this study, water turbidity in winter and
290 spring were significantly higher than in summer. Heron predate grayling in some circumstances
291 (Uiblein *et al.*, 2001), but are rarely an important dietary component (Owen, 1955). Based upon
292 the authors' observations of cormorants landing on the study stretches, and the absence of any
293 known cormorant roosts in the immediate vicinity (5km) of the study area, the more open riparian
294 structure of the downstream-most river section may have favoured access to and from the river
295 channel by cormorants. The low density of herons in the downstream river section may have been
296 due to the steeper, regraded banks impeding access for wading.

297
298 The response of most stream-dwelling salmonid fish (the family to which grayling belong) to
299 immediate predation threat is to seek physical cover (Fraser & Huntingford, 1986; Dionne &
300 Dodson, 2002) and this behaviour is shown by cyprinid fishes exposed to avian predation threat
301 (Russell *et al.*, 2008; Orpwood *et al.*, 2010), but no strong evidence of this for grayling was
302 obtained in this study. Unlike many stream-dwelling salmonids, grayling tend to aggregate in
303 small groups (Greenberg, Svendsen & Harby, 1996), especially in winter (Cove, 2004; M. Lucas,
304 pers. obs.), often in open water, and may not utilise refuge habitat in the manner of, for example,
305 brown trout, although Greenberg *et al.* (1996), found that in summer, larger stream-dwelling
306 grayling used overhead cover more than small ones and inferred this as being a likely response to
307 terrestrial predation risk. In the face of frequent, but locally unpredictable, predation threat, an
308 alternative response to taking refuge may be to flee if a predator appears. Since in this study the
309 highly excursive behaviour of tagged grayling in the downstream-most section decreased
310 relatively in spring and summer, this behavioural response appears likely.

311
312 Although high levels of movement associated with leaving localities which predators have
313 entered might be energetically costly, such energy costs would be of low fitness consequence by
314 comparison to continued survival. Moreover, most use of refuge habitats is at the expense of
315 feeding opportunities (Sih, 1997; Chapman *et al.*, 2013) which in grayling continues even at low
316 temperatures (Maitland & Campbell, 1992). Therefore, there may be a balance between the
317 options of grouping and seeking refuges in response to predation threat (Krause *et al.*, 1998;
318 Rangeley & Kramer 1998). This study suggests that for adult grayling in the habitats studied,
319 widespread ranging, rather than strong refuge habitat attachment, is the predominant response to
320 high avian predator density in the natural environment.

321

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325

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432 **Tables**

433 Table 1. Seasonal changes in fish-eating bird densities in contiguous study reaches (downstream:
 434 A, middle: B, upstream: C), given as median (25 percentile, 75 percentile).

		Density of fish-eating birds (no. km ⁻¹ river)		
		Winter	Spawning period	Summer
Section A	cormorant	0.92 (0.1, 1.18)	0.23 (0, 0.5)	0 (0, 0)
	goosander	1.56 (0.51, 1.57)	1.5 (0.63, 2)	0 (0, 0)
	heron	0 (0, 0)	0 (0, 0)	0 (0, 0.5)
Section B	cormorant	0 (0, 0)	0 (0, 0)	0 (0, 0)
	goosander	1.11 (0.33, 1.65)	0.83 (0.21, 1.56)	0.42 (0, 0.42)
	heron	0 (0, 0)	0.21 (0, 0.42)	0.21 (0, 0.42)
Section C	cormorant	0 (0, 0)	0 (0, 0)	0 (0, 0)
	goosander	1.18 (1.11, 1.94)	1.43 (0.88, 1.99)	0.36 (0.09, 0.71)
	heron	0 (0, 0.56)	0.31 (0, 0.36)	0.36 (0.36, 0.63)

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438 Table 2. Incidence of scarring in grayling and brown trout longer than 15 cm sampled in
 439 contiguous study sections (A: downstream, B: middle, C: upstream) during the periods
 440 December 2003 to March 2004 and October to November 2004. In some cases fish classified as
 441 having recent scars also had old, healed scars, counted independently.

Section (<i>n</i>)	Frequency of scarring (%)					
	grayling			trout		
	A (58)	B (60)	C (65)	A (85)	B (147)	C (167)
Recent scarring	12.1	3.3	4.6	7.1	6.1	1.8
Healed scarring	46.5	31.7	26.2	42.3	32.0	18.6
Scarring absent	41.4	65.0	69.2	50.6	63.9	79.6

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447 Table 3. Rates of movement, calculated from distances and elapsed time between successive fixes,
 448 of radio-tagged grayling in contiguous river sections (A: downstream, B: middle, C: upstream)
 449 and between seasons, given as the group median (25 percentile, 75 percentile) of the median rates
 450 of movement by individual fishes. Estimated rates of movement are conservative (see Methods),
 451 but because fixes were made in all sections on each tracking session, comparisons of relative
 452 magnitude between river sections are legitimate.

	Rate of movement (m day ⁻¹)			
	Winter 1	Spawning period	Summer	Winter 2
Section A	117.5 (61.5, 189.5)	48.3 (22.6, 58.1)	20.0 (9.4, 57.8)	48.8 (41.2, 51.9)
Section B	18.5 (13.9, 30.8)	16.1 (13.6, 25.4)	19.3 (4.3, 44.0)	10.6 (9.1, 19.5)
Section C	20.5 (12.2, 26.13)	18.3 (11.9, 29.3)	10.5 (7.5, 14.0)	-

453
 454 Table 4. Comparison of key habitat characteristics between adjacent river sections studied. The
 455 first five categories were measured in the field in downstream section A ($n=477$), middle section
 456 B ($n=309$) and upstream section C ($n=467$). Dominant substrate particle category was recorded
 457 on a scale of 1 (silt) to boulder (6), streambed vegetation and riparian cover were recorded on a
 458 scale of 0 (absent) to 5 (complete cover). Woody riparian cover was quantified as the average
 459 percentage cover of both banks by trees and shrubs from ten 100-m lengths per section, using
 460 Google Earth. Submerged root/shoot area was quantified in the field from 50 randomly chosen
 461 bankside trees per river section. Significance of differences between sections are shown.

Section	Mean (SD)			Significance
	A	B	C	
Depth (m)	0.92 (0.50)	0.84 (0.47)	0.71 (0.40)	<0.001
Flow velocity (m s ⁻¹)	0.46 (0.25)	0.32 (0.22)	0.45 (0.21)	<0.001
Dominant substrate category	3.0 (1.2)	3.3 (1.1)	3.4 (0.9)	<0.001
Streambed vegetation	0.4 (0.9)	0.4 (0.7)	0.6 (0.9)	0.04
Riparian cover	1.8 (1.4)	2.8 (1.3)	2.2 (1.5)	<0.001
Woody riparian cover (%)	39.0 (16.1)	71.2 (24.6)	69.8 (17.7)	<0.001
Submerged root/shoot area per bankside tree (m ²)	2.0 (2.1)	1.7 (1.4)	1.6 (1.5)	0.414

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464 **Figure legends**

465 Figure 1. Variation in linear range of channel use between seasons and contiguous river sections
466 (A: downstream, B: middle; C: upstream) by radio-tagged grayling. Data are given as the median
467 and interquartile range. Home range was significantly greater in section A than the other sections
468 in winter and the spawning period (Kruskal-Wallis, $P < 0.01$) but not during summer (Kruskal-
469 Wallis, $P > 0.05$).

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471 Figure 2. Habitat availability in the three adjacent study reaches (A: downstream, B: middle, C:
472 upstream) analysed by Principal Components Analysis and expressed by PC1 (depth, dominant
473 substrate and current velocity) and PC2 (riparian cover).

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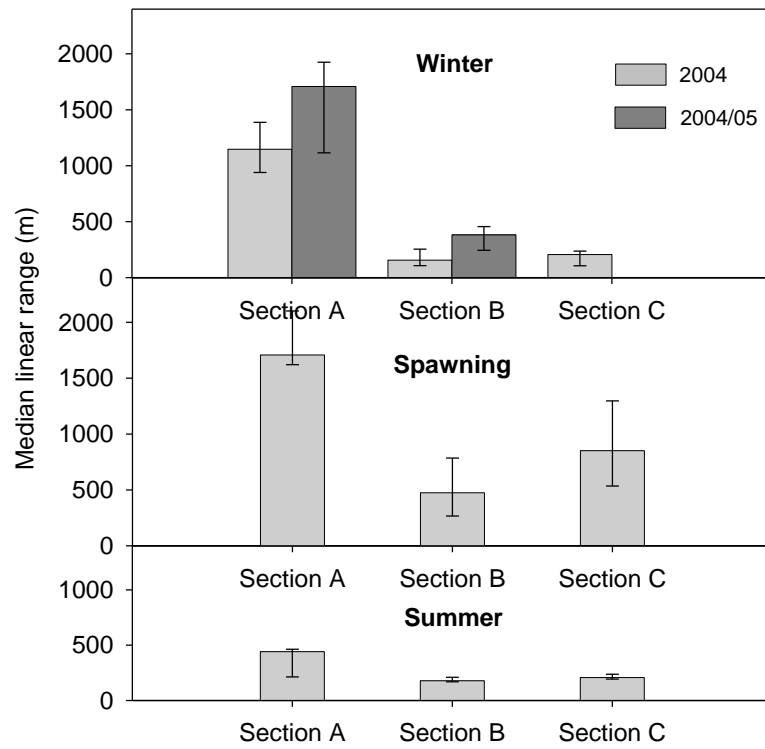
475 Figure 3. Principal component plots (mean \pm SD) of habitat use of radio-tagged grayling across
476 seasons and between contiguous river sections (A: downstream; B: middle; C: upstream). Axis
477 loadings of PC1 (depth, dominant substrate particle size and current velocity) and PC2 (riparian
478 cover) are presented in the top-left panel. Grayling in all sections, used relatively deep, slow
479 water with smaller sediment particle size in winter, moved to shallower, faster water with larger
480 sediment particle size (gravel) in the spawning period and remained in shallower, faster water in
481 summer but were more closely associated with bankside riparian cover than in winter or the
482 spawning period.

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488 Fig. 1

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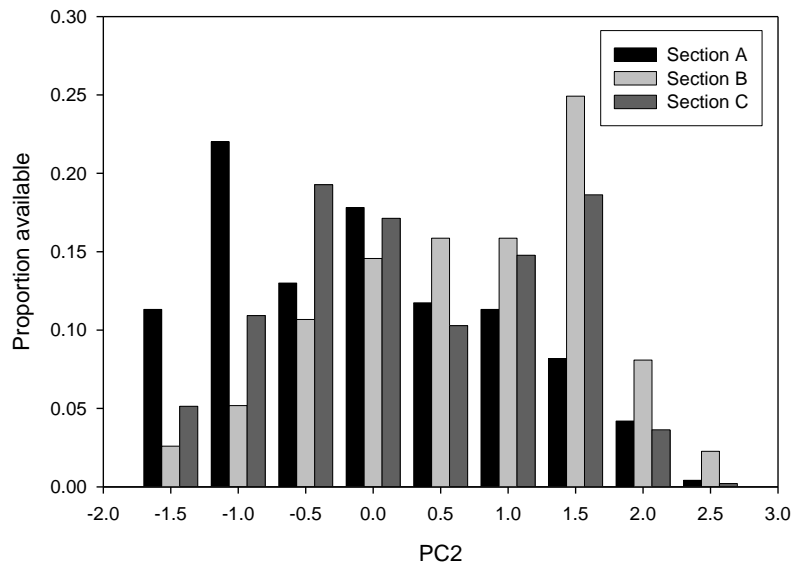
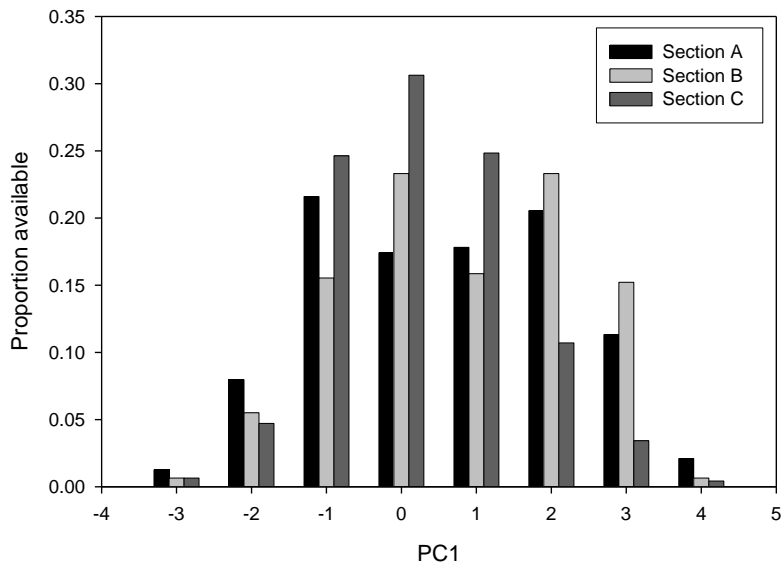
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502 Fig. 2

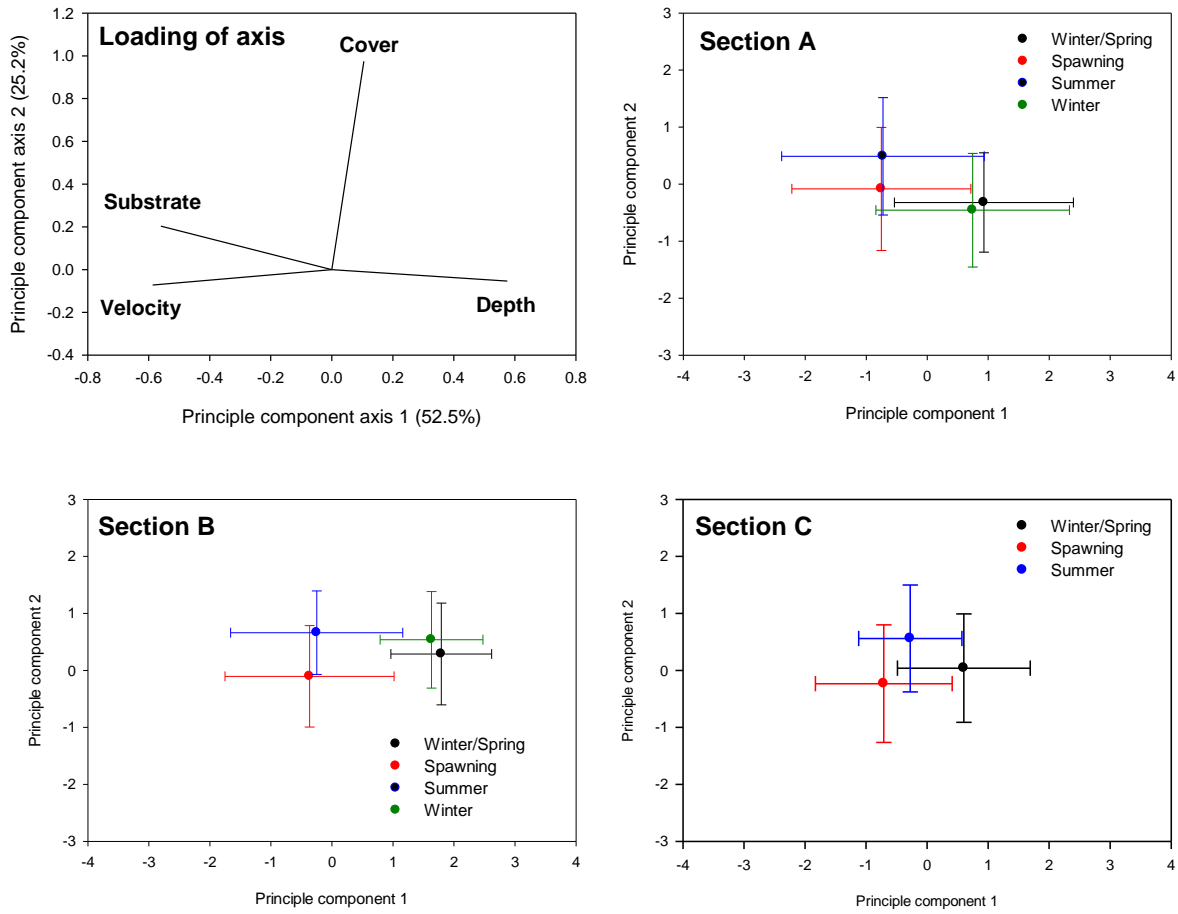
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510 Fig. 3

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