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

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Abstract

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

Introduction

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

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

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

Materials and Methods

Study area

The study was carried out on the River Rye, the major tributary of the River Derwent (Humber River System), in Northeast England (Whitton & Lucas, 1997). The Rye is typically 10-15m wide, with an average mid-channel depth of 0.7m and mean discharge of 3.5m^3 s^{-1}. The study area (centred on 54º12'N, 0º57'W) was separated into three contiguous reaches, bordered by pastureland, and is private, with low human disturbance. The middle section (B), 2.5-km long, was bounded at the downstream limit by a sloping 1.2-m high flow-gauging weir and at the upstream limit by a 1.4-m high sloping mill weir. The lower (A) and upper (C) sections each stretched unobstructed for over 10km downstream and upstream respectively but are defined here as the distance from the boundary with section B to the furthest radio-fix of tracked fish in each section, approximately 4.0km for section A and 5.2km for section C. Although the weirs can be passed, with difficulty, by salmonids (M. Lucas, pers.obs.), in this study no tagged fish passed upstream or downstream from one section to another. The river is characterised by riffle-glide sequences with mostly gravel bed in the former and sandy areas in the latter habitat. In-stream macrophyte growth (mostly *Fontinalis* spp. and *Ranunculus fluitans*) is sparse but substantial riparian tree-cover occurs, principally from *Alnus glutinosa* and *Salix* spp., with the latter more common in the downstream section. In the downstream section, bank regrading has resulted in steeper banks, with less extensive riparian cover.

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

Tagging and recording

Adult grayling for radio-tagging were obtained by electric fishing or rod-and-line. Radio-tracking was carried out in two periods, with a total of 40 fish radio-tracked. In the first period eight grayling were released in each section in late winter (median, 19 February 2004) and tracked until 1 July 2004. In the second period eight fish were released in late autumn (median, 6 November 2004) in sections A and B and tracked until 5 January 2005. Mean ± SE fork length of tagged fish, 318 ± 44mm, did not vary between experimental groups (ANOVA, F=1.09, P=0.378). Fish were radio-tagged (173 MHz, biocompatible silicone-potted PIP, Biotrack, UK) by implantation of the tag into the body cavity, with the tag's whip antenna exiting through the body wall and closure of the incision with absorbable sutures (Lucas and Baras, 2000). Tag weight to body weight ratio did not exceed 1%. Tagging was carried out under general anaesthetic (buffered tricaine methansulphonate, 0.1g L^{-1}) on the bankside under UK Home Office licence PPL60/3260. Fish were released within 10m of the capture site when swimming strongly (< 1h post-surgery). Fish captured in groups were released together, combining several untagged fish and tagged fish.

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

Home range, activity and habitat use analysis

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

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

Habitat along the entire reach was measured at the end of the study at ~Q75 flow by carrying out cross-channel surveys to record habitat availability. Sampling occurred every 10-30m of channel length, covering repeated glides, riffles and transition zone, and at every radio-fix location. Variables measured were riparian cover (scale of 0-5), instream macrophyte cover (0-5), bank slope (0-5), channel width and depth (m), velocity at 60% of depth (ms^{-1}), and substrate composition (percent silt, sand, gravel, pebble, cobble, boulder, bedrock) by visual estimation in quadrats. All in-channel variables were measured at 0.25, 0.5 and 0.75 of river width. Data from a total of 1253 sites (section A, 477; section B, 309; section C, 467) were obtained. Due to the co-linear and highly correlated nature of the habitat variables Principal Components Analysis (PCA) was carried out on the range of habitat variables. Combining all the survey sites, so section-wise PCA of fish habitat use was not compromised, the first two principal components extracted explained 77.8% of variation. Loadings of PC1 (52.6% of variation) were depth 0.575, velocity -0.587 and dominant substrate –0.560 and of PC2 (25.2% of variation) was riparian cover 0.975. Habitat use by grayling in the different sections and seasons were generated from average values for each fish, quantified in terms of the extracted principal components.

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

Grayling (*n*=183) and brown trout (*n*=399) sampled during electric fishing surveys and captured by rod-and-line along the study reaches (Dec 2003 - March 2004; Oct-Nov 2004) were inspected for evidence of healed scars and fresh wounds, indicative of damage from unsuccessful predation attempts, using Carss (1988) as an information source on scar types characteristic of different avian predators.

Results

Predator densities

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

Incidence of scarring in grayling and trout was used as an indicator of failed predation attempts. Recent scars included narrow, parallel marks across the fish's flanks, puncture marks and lesions, all associated with scale loss without regrowth. Of 30 such scars greater than 1 cm^2, 26 fitted the visual characteristics given by Carss (1988) for damage by cormorant (17), sawbill duck (7) and heron (2). Older scars were much more frequent, but it was more difficult to attribute the cause of these because of tissue repair and scale regrowth, but these included patterns typical of bird predation attempts. The frequency of occurrence of fish with scars varied significantly between sections (grayling, $\chi^2 = 11.15$, $P < 0.01$; brown trout, $\chi^2 = 20.56$, $P < 0.001$). The incidence of recent and healed scars larger than 1 cm^2 was greatest for grayling and trout in the downstream section compared to the middle and upstream sections (Table 2). No radio-tracked fish are known to have been removed by predators during the study, although two tags in the downstream section (A) were lost within 12h of a previous fix, with over half of battery life remaining, and could not be relocated despite extensive searches. The most likely explanation for these losses is from avian predators capturing tagged fish and moving out of detection range.

Home range and activity of grayling

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

Rates of movement by grayling differed between sections in the first winter (Kruskal-Wallis, $P=0.001$), second winter (Mann Whitney, $P<0.001$), and the spawning period (Kruskal-Wallis, *P*=0.022) but not in summer (Kruskal-Wallis, *P*=0.215). In the first winter, median rates of movement in section A, were six times greater than in the other sections (Table 3). In the second winter period, median rates of movement in section A, were five times higher than in adjacent section B. In spring, median rates of movement approached three times higher in section A, than the other sections. Because successive fixes were usually 1-4 days apart, these are conservative measures of movement. Winter movement in the lower section was characterised by repeated upstream and downstream movements, rather than movements around one or more core areas as occurred in middle and upstream river sections.

Habitat availability and use

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

Discussion

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

The home ranges of adult grayling in all three sections in summer and in the middle and upper sections in winter were of similar magnitude to other studies (Nykänen *et al.*,2001; Nykänen, Huusko & Lahti, 2004; Ovidio *et al*., 2004), the former two being in a sub-Arctic river, but the latter occurring in a Belgian stream of similar size to the Rye. By contrast, winter home range of grayling in the downstream-most section was 5 (Ovidio *et al*.,2004) to 20 times (Nykänen *et al*., 2001,2004) greater than published studies, and 3-5 times higher than in adjacent study sections at the same time. Winter-time movement rates in the downstream, predator-rich section were significantly greater in both winter periods. We interpret the clear difference in space use by grayling in the downstream-most section as being a response to avian predators. It was not possible to carry out a predator exclusion experiment in this study; neither have most other studies of predation risk in the natural environment (e.g. Frair *et al*. 2005; Willems & Hill 2009; Skov *et al*., 2013), so the results are correlative. However, the elevated levels of scarring, including a high proportion characteristic of avian attack, observed in the section with highest predator density provide strong supporting evidence of the role of predation threat there.

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

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

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

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Tables

Table 1. Seasonal changes in fish-eating bird densities in contiguous study reaches (downstream: 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)

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

	Frequency of scarring (%)					
	grayling			trout		
Section (*n*)	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

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

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

	Mean (SD)			
Section	A	B	C	*Significance*
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

Figure legends

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

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

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

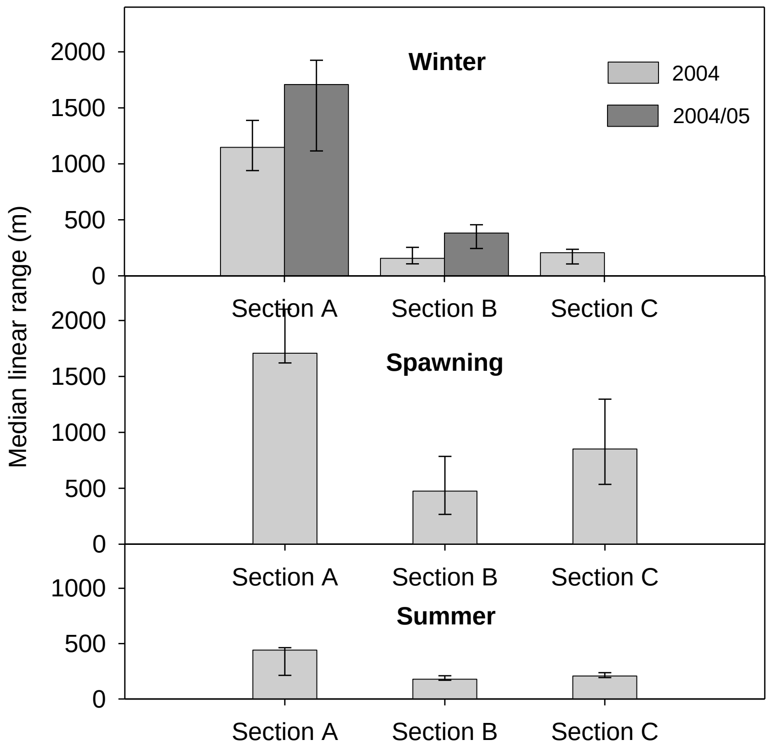
Median linear range (m)
Winter
2004
2004/05
2000
1500
1000
500
0
Section A
Section B
Section C
Spawning
2000
1500
1000
500
0
Section A
Section B
Section C
Summer
1000
500
0
Section A
Section B
Section C

Fig. 1

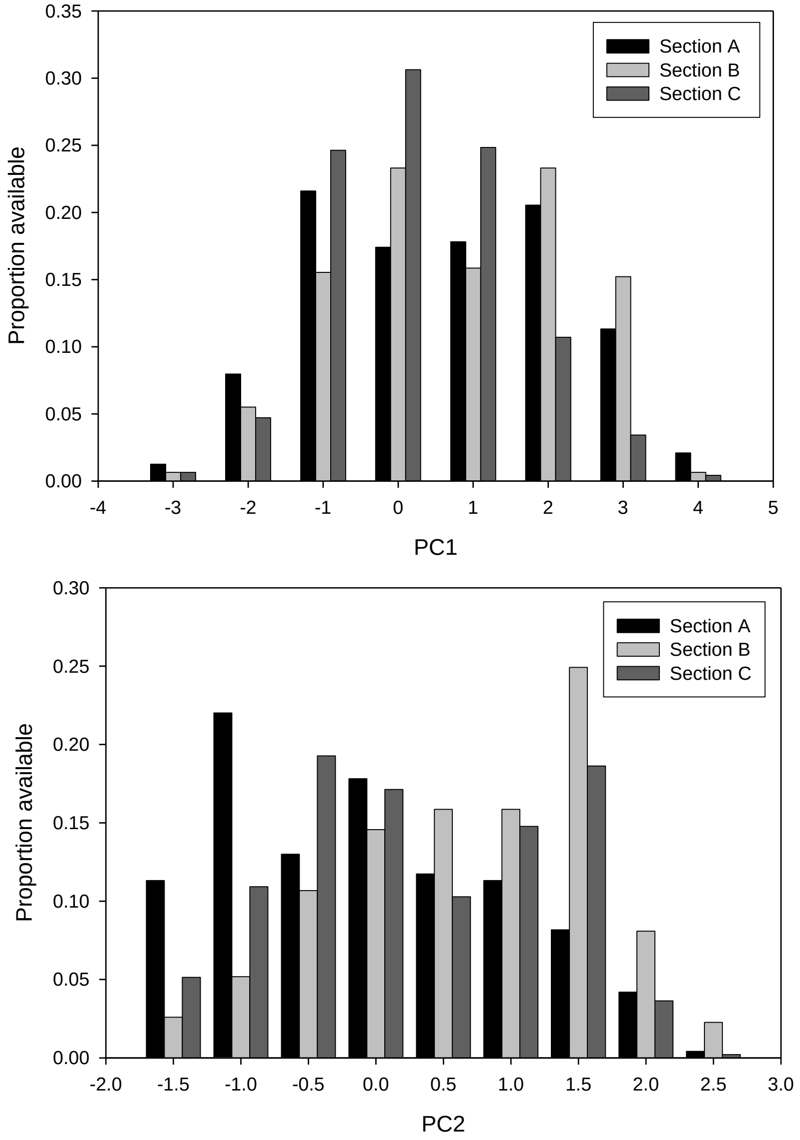
Proportion available
0.35
0.30
0.25
0.20
0.15
0.10
0.05
0.00
-4
-3
-2
-1
0
1
2
3
4
5
PC1
Section A
Section B
Section C
Proportion available
0.30
0.25
0.20
0.15
0.10
0.05
0.00
-2.0
-1.5
-1.0
-0.5
0.0
0.5
1.0
1.5
2.0
2.5
3.0
PC2
Section A
Section B
Section C

Fig. 2

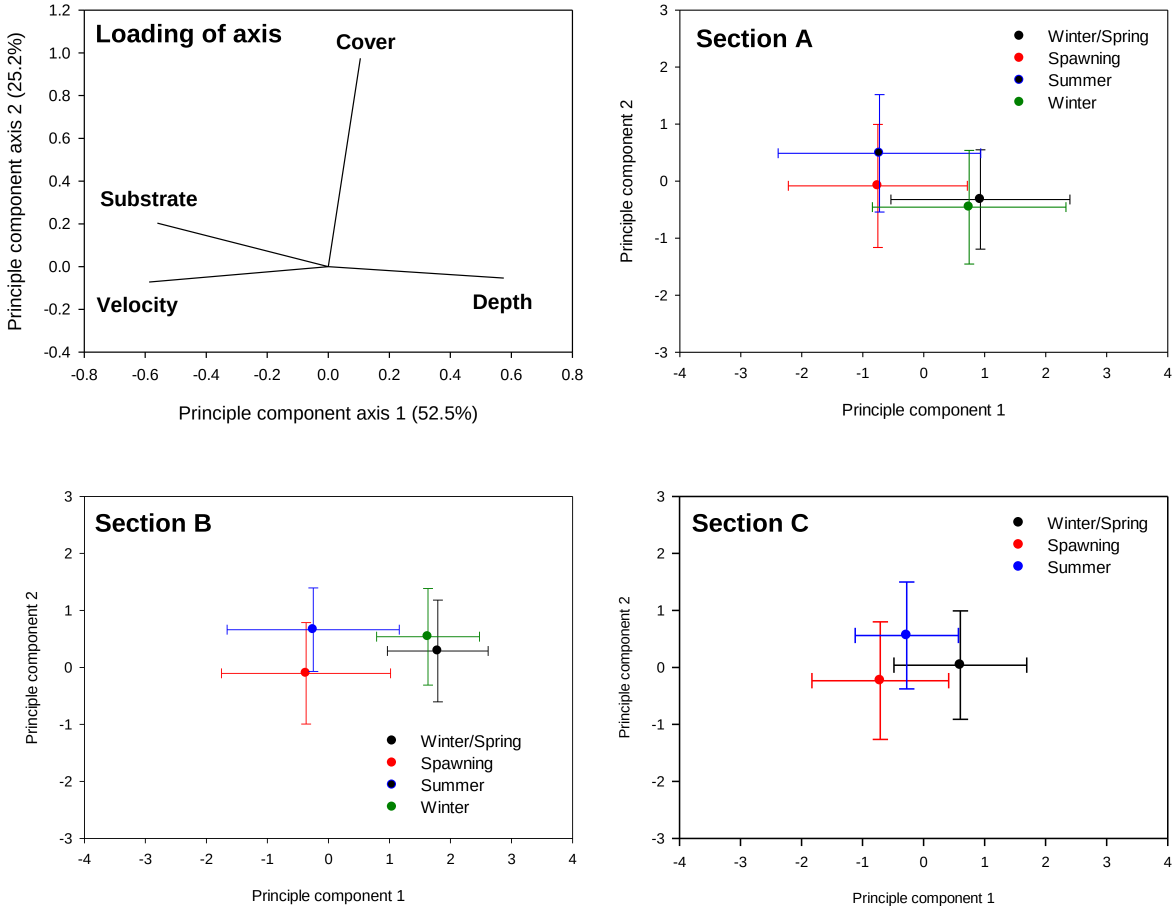
Loading of axis
Cover
Substrate
Velocity
Depth
Principle component axis 2 (25.2%)
Principle component axis 1 (52.5%)
1.2
1.0
0.8
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.8
-0.6
-0.4
-0.2
0.0
0.2
0.4
0.6
0.8
Section A
Winter/Spring
Spawning
Summer
Winter
Principle component 2
Principle component 1
Section B
Winter/Spring
Spawning
Summer
Winter
Principle component 2
Principle component 1
Section C
Winter/Spring
Spawning
Summer
Principle component 2
Principle component 1
3
2
1
0
-1
-2
-3
-4
-3
-2
-1
0
1
2
3
4

Fig. 3