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Seasonal movements and habitat use of grayling in the UK

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Grayling Research Trust

University of Durham

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Steve Killeen

Head of Science

Executive Summary

Following a review of grayling ecology, status and management practice (Environment Agency Technical Report W245), to aid the sustainable management of grayling and its fisheries, The University of Durham was commissioned by the Environment Agency and the Grayling Research Trust to examine the seasonal movements and habitat use of European grayling *Thymallus thymallus* in unregulated rivers dominated by surface flow. The aims were to:

- measure the frequency, extent and patterns of migration by adult grayling, especially during the main feeding and spawning periods of a year, in relation to changing environmental variables;
- measure habitat use and preference of grayling;
- assess the ability and willingness of grayling to pass upstream and downstream over artificial or natural obstructions;
- identify and recommend for phase II the principal periods of migratory activity for replicate studies on other river types.

The study was carried out mainly on the River Rye catchment in North Yorkshire. Radio-tracking was undertaken on the Rye over two periods, January to July 2004 and October 2004 to January 2005, as well as habitat surveying, environmental monitoring and limited electric fishing surveys and mark–recapture. A subsidiary radio-tracking study was carried out on the River Ure, North Yorkshire, between February and April 2004.

A total of 24 adult grayling (276-428 mm fork length) were radio-tagged in the Rye between January and March 2004. The study length was divided into three sections; a lower section (A, >10 km) with no weirs, a middle section (B, 2.8 km) including two weirs (one a 1.2-m high Flat-V gauging weir and the other a 1.4-m high disused mill weir) and an upper section (C, about 10 km) without any obstructions. A large proportion of the lowest section has steep banks and flood levees, with less habitat typical of the grayling zone. Eight grayling were radio-tagged and released at the capture sites in each section and tracked by hand and remotely by logging stations.

Fish moved between 0.2 and 3.5 km during the tracking period, with greatest distances moved occurring mostly in late March and April, associated with pre-spawning, spawning and post-spawning movements. Marked differences in inter-individual patterns of space use occurred, with some fish wintering in a single glide and apparently spawning on an adjacent gravel riffle, while others moved much longer distances between winter, spawning and summer sites. There were significant differences in the total linear home range between fish from section A and those in other sections, for the whole period from January to July 2004 and for the winter period (January 11 to March 2004). Section A fish ranged much more widely than fish in other sections in the winter period, but in a similar manner during the summer period. Six out of the 16 grayling tagged more than 400 m below either weir (sections A and B) were detected moving upstream to respective weirs, but none passed. No radio-tagged grayling were detected passing downstream over either weir.

16 (eight in section A, eight in section B) adult grayling (264-356 mm fork length) were radio-tagged in the Rye in October and November 2004 and tracked until January 2005. Movement patterns were similar to those in the period January to mid March 2004, with section A fish moving significantly more widely than section B fish.

During 2004, several grayling tracked in section A of the Rye entered the Dove, a major tributary, one of which migrated 2.4 km upstream to spawn. In several cases during tracking, high-flow events were associated with downstream movement of tagged fishes.

Habitat use by adult grayling in the Rye changed between seasons, with radio-tagged fish from all sections selecting deeper, slower water with sand substratum during the two winter study periods. During the spawning season fish selected faster, shallower water with gravel, pebble and cobble substrate and tended to remain in similar habitat in the summer, but with greater use of overhead cover. There was some evidence that grayling in section A, which appeared to provide the least suitable habitat, used a wider range of habitats than those in sections B and C.

Changing habitat availability under different river conditions is unlikely to be the main reason for the high mobility of grayling in section A because fish often moved extensively during periods when environmental factors, especially discharge, were relatively stable. The difference in mobility patterns was most marked in late winter 2004 and autumn–winter 2004-2005 samples, when significantly more fish-eating birds, especially cormorant, occupied section A than section B or C. This appears to have been a contributory factor influencing grayling behaviour.

Eight adult grayling (280-353 mm fork length) radio-tagged in the Ure in February 2004 were tracked until mid April 2004. Fish were found in shallow, smooth glide and deep, slow glide habitats until April, when several tagged spawning fish were located in or immediately upstream of riffles.

Passive integrated transponder (PIT) telemetry, to examine the passage of grayling at obstacles, was carried out at flow-gauging weirs on the River Dove and Costa Beck, tributaries of the Rye. A method that utilised the homing tendency of translocated grayling was developed to measure their ability to pass obstructions. In summer 2004, PIT telemetry at a 0.2 m high Crump flow-gauging weir (water velocity 0.87-1.85 m s^{-1} on the downstream face) on Costa Beck showed that a high proportion (96 per cent) of tagged grayling that attempted to ascend the weir succeeded in doing so. At a 0.4 m high Flat-V flow-gauging weir (water velocity 1.07-2.98 m s^{-1} on the downstream face) on the Dove, 36 per cent of grayling that attempted to ascend the weir were successful, whereas the equivalent efficiency for brown trout of similar size was 84 per cent. This suggests strongly that grayling are less willing or able than brown trout to ascend relatively small Flat-V weirs characterised by complex flow circulation patterns.

The study demonstrated that within the Rye, a small river, upriver migrations for spawning are common but not universal. The extent of migration associated with spawning was generally less than that observed in continental European studies. Outside the spawning season grayling tended to adopt restricted home ranges, although in some cases the day-to-day movements of grayling may be quite extensive

(Ure, with long distances between adjacent glides) or extensive and erratic (Rye, section A). Other studies in continental Europe have found relatively localised home-ranging behaviour, though not as extreme as the very limited movement observed in some English chalkstreams.

A series of recommendations are made based upon this research. The adaptive pattern of seasonal movements by grayling in many rivers, which probably helps to enhance survival probability and sustain populations, especially in those rivers with variable flow and/or greater spatial dispersion of key habitats, needs greater consideration in river management. This study, as well as other published material, suggests that many barriers across which brown trout can gain easy access may not be easily passed by grayling. Careful assessment of the need for new obstructions, operation of existing structures and possible removal of potential barriers to movement should therefore be considered.

Further research should be directed in several areas, using the effective methodology developed here to determine the passage efficiency and behaviour of grayling at barriers. Further studies to examine these aspects for grayling, and perhaps other species also, at a variety of barriers and fishways would be highly illuminating, with direct management benefits in terms of understanding how the efficiency of passage can be improved. Such an approach would be strengthened by integrating this field experimental approach with controlled laboratory flume studies of macro- and micro-scale behaviour to environmental stimuli. Complementary evidence from this and other studies suggests that the behaviour of grayling, in addition to swimming performance, may be very important in determining whether they traverse many types of barriers.

This study concentrated on adult grayling movements and habitat use. Although much is known of the summer habitat use by juvenile grayling, almost nothing is known in other seasons, despite this being a potential recruitment bottleneck in environments where refuges from predators or high flows may be limited, including in modified rivers. Therefore, substantial effort should be placed upon understanding the seasonal habitat requirements of juvenile grayling, especially during autumn and winter, and how these influence survival, growth and space use, especially during autumn and winter. Field experiments and studies in semi-controlled flume environments would be highly informative here.

Following experiences in small river systems, additional research concerning the space and habitat use of adult grayling in larger river systems, perhaps including those subject to water discharge regulation, over the full annual cycle could be informative to management, but are of lower priority. Similarly, the apparent sedentary nature of grayling in chalkstreams, based upon tracking and mark–recapture during summer, may be worthy of further study over a broader seasonal scale, including the spawning period, if justified by sufficient regional management issues.

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1. Introduction

1.1. Background

From ecological and recreational fishing perspectives, the European grayling *Thymallus thymallus* (hereafter referred to as grayling) is an important salmonid species (Northcote, 1995). Although formerly regarded as a pest in some English chalk rivers, the grayling is increasingly regarded as a valued sport fish throughout its range in Great Britain (Ibbotson *et al.,* 2001; Cove, 2004). The grayling occurs in cool, well-oxygenated waters, both in swiftly flowing streams and in lakes, usually characterised by gravel, pebble and cobble substrate. Originally occurring in rivers of several catchments in England (including the Thames, Trent and Yorkshire Ouse) and possibly Wales (including the Welsh Dee), the grayling's distribution has been widened through introduction in England, Wales and Scotland (Ibbotson *et al.,* 2001; Cove, 2004). Although characteristic of many coolwater rivers, including chalkstreams, grayling have become scarce in some habitats in which they were formerly abundant, with habitat degradation, pollution and river regulation believed to be among the main reasons. Partly as a result of this the grayling is now considered a species that requires a degree of conservation assistance, at a European scale, through its listing in Annex V of the European Council (EC) Habitats Directive 92.43.EEC (European Council, 1992).

Following a review of the ecology, status and management of grayling in England and Wales (Ibbotson *et al.,* 2001), the Environment Agency and its partners, including the Grayling Research Trust, embarked upon further research to provide better information on which to base sound management of grayling stocks in England and Wales. Included in this plan was the objective to determine seasonal patterns of movement and habitat use, principally of adult grayling, as well as their tendency and ability to traverse potential river obstructions that could interrupt normal movements. This led to the current project funded by the Environment Agency and the Grayling Research Trust, together with additional contributions from the University of Durham.

1.2. Terms of reference

The primary research aims of this study were to:

(i) Examine and report the frequency, extent and patterns of in-river migration by adult grayling throughout a year on one river type, but principally during the main feeding and spawning periods. This should include information on fish response to changing environmental variables.

(ii) Identify specific areas utilised by grayling under various flow conditions and measure the physical habitat parameters in order to distinguish principal habitat preferences for adult and juvenile grayling (this should relate to river type).

(iii) Assess the ability and/or willingness of grayling to pass upstream and downstream over artificial and natural obstructions, such as weirs, sluices, etc.

(iv) Identify and recommend for phase II the principal periods of migratory activity for replicate study. Should funding become available, phase II would undertake replicate research, but for a shorter duration, on a chalkstream and possibly other river type (rain-fed or regulated).

The project originators decided that the research should be carried out on a river typical of many grayling-supporting rivers in England and Wales. Such rivers typically originate in upland environments and are often characterised by elevated flow in response to precipitation.

1.3. Patterns of movement and habitat use of grayling

Ibbotson *et al.* (2001) provided a review of the ecology of grayling, including information concerning spatial behaviour and habitat use and the reader is directed to that information. Several new research papers have subsequently been published and a brief review of their spatial ecology is provided here.

European grayling are commonly regarded as strictly freshwater fish, although this species does occur in mildly brackish water of the northern parts of the Baltic Sea (Peterson, 1968) and is reported to occur in the brackish estuary of the Kara and the Kara Bay (Russia), where salinity is reported to approach that of the open sea (Probatov, 1936). While there is some evidence to suggest that northern Swedish grayling populations may spawn (as well as grow and overwinter) in the mildly brackish waters of the Gulf of Bothnia, they usually enter rivers to spawn (Peterson, 1968). However, in the Kara region of Russia, downstream movement into the estuary and bay principally appears to be associated with overwintering (Probatov, 1968). Migration through estuarine regions to winter habitat has been demonstrated from radio-telemetry of Arctic grayling *T. arcticus* in the harshest part of its range (West *et al.,* 1992), and the use of brackish water by graylings, therefore, appears to be a response associated with harsh Arctic and sub-Arctic climates. In more temperate climates, there appear to be no records of grayling populations that occur outside freshwater rivers and lakes.

The grayling's typical habitat of cool, well-oxygenated waters in swiftly flowing streams and rivers, usually characterised by stony substrate, is often associated with an intermediate river gradient (usually 2-5 m km^{-1}) that generates these physical conditions, thus coining the term 'grayling zone' in Huet's classical work, used to describe longitudinal biological zonation in European rivers (Huet, 1949). Grayling are lithophilous spawners that create shallow spawning-redds in the gravel in which the fertilised eggs are deposited, develop and hatch. The young emerge from the gravel several days after hatching and occupy dead current zones initially, but as the larvae and then fry grow, they move further out into the river channel into faster water (Sempeski and Gaudin, 1995a, 1995b, 1995c; Nykänen and Huusko, 2003). Within rivers, the fry, juveniles and adults utilise a variety of faster water habitats, mostly characterised by glide, pool or riffle morphotypes and gravel–cobble bottoms (see Ibbotson *et al*., 2001, for review). Although this is a major generalisation, it is worth recognising that in many rivers where grayling are found, all of these habitats may be found within a few hundred metres or less. This point was made by Ibbotson *et al*. (2001) in the context of lowland chalkstreams, but it could apply to many more upland rivers with repeating pool/glide–riffle sequences. Thus, there lies a capacity for all of the life-cycle processes of grayling to be completed on a scale of a 100 metres or so, where such habitat complementarity exists.

Lake-dwelling grayling usually migrate into tributaries to spawn (Gustafson, 1949; Woolland, 1972; Witkowski and Kowalewski, 1988; Haugen and Rygg, 1996; Kristiansen and Døving, 1996), but may spawn in the gravel margins of lakes (Gustafson, 1949). Usually, the adults return to the lake soon after spawning (Gustafson, 1949; Kristiansen and Døving, 1996), while fry may also leave the tributaries soon after spawning (Haugen and Rygg, 1996) or remain there until autumn (Kristiansen and Døving, 1996). Evidence of within-river spawning migrations of grayling is provided in a wide range of papers (Woolland, 1972; Andersen, 1973; Pavlov *et al*., 1998, 2000b), including an increasing number that used radio-tracking (Parkinson *et al.,* 1999; Meyer, 2001; Ovidio and Philippart, 2002; Nykänen *et al.,* 2004a; Ovidio *et al*., 2004). These studies have show that the migration tends to be upstream directed, but that this may depend on the local availability of suitable spawning areas and, in some cases, pre-spawning migrations are not evident or may occur in a downstream direction (Nykänen *et al.,* 2004a; Ovidio *et al*., 2004). Distances travelled by radio-tracked adult grayling during pre-spawning 'migrations' are from as little as 70 m (and therefore barely perceptible from the home range) to 11 300 m (Parkinson *et al.,* 1999; Meyer, 2001; Ovidio and Philippart, 2002; Nykänen e*t al.,* 2004a; Ovidio *et al*., 2004), but in large river systems longer distances, up to 120 km, have been recorded in mark–recapture studies, believed to reflect movements between feeding–wintering areas to spawning sites and *vice versa* (Andersen, 1973; Witkowski and Kowalewski, 1988; Linløkken, 1993). The timing of pre-spawning migrations by grayling is typically associated with increasing water temperature and decreasing discharge and turbidity (Parkinson *et al*., 1999; Ovidio *et al*., 2004), but in sub-Arctic climates it is associated with ice break-up and snow melt and so associated with increasing temperature, but elevated discharge (Nykänen *et al.,* 2004a). Spawning habitat has been characterised (Fabricius and Gustafson, 1955; Gönczi, 1989; Sempeski and Gaudin, 1995a; Nykänen and Huusko, 2002) and typically comprises gravel and pebble substrate (with diameters 8-64 mm), depths of 10-80 cm and water velocities of 30-80 cm s^{-1}. Movements often occur from the main river stems into small tributaries for spawning (Woolland, 1972; Pavlov *et al*., 2000b), and in small tributaries of the Upper Volga Pavlov *et al*. (2000b) found that most spawned grayling overwintered in the tributary and emigrated the following spring as yearlings.

Following spawning, river-resident grayling may return (home) to the areas they inhabited previously, with the proportion of fish confirmed as homing varying between 57 per cent and 100 per cent in several studies (Parkinson *et al*., 1999; Meyer, 2001; Ovidio *et al*., 2004). Post-spawning habitat use (pools and riffles) in these studies was reported to be similar to that of pre-spawning, which is to be expected if there is a high proportion of homing. However, in these studies, tagging was carried out in late February to late March and only Parkinson *et al*'s study tracked fish until June, so it is possible that wider habitat use by those grayling may have occurred, especially in autumn and winter. Several studies characterised habitat use by grayling in summer using techniques such as electric fishing (Greenberg *et al*., 1996), snorkelling (Mallet *et al*., 2000) and radio-tracking (Nykänen *et al.,* 2004a, 2004b). The studies by Greenberg *et al.* and Mallet *et al*. considered fish of varying sizes and ages. Mallet *et al*. found that by day 0+, 1+ and adult grayling in the River Ain (France) all preferred high water velocities of 70-110 cm s^{-1} and substrate particle sizes of 0.5-16 mm, but that larger, older fish preferred deeper water (50-60 cm, 80-120 cm and 100-140 cm for 0+, 1+ and adults, respectively). Greenberg *et al.*'s study in the River Vojman (Southern Sweden) found that by day, small (typically 0+ and 1+) grayling preferred fine substrate and slower moving water than large grayling, but that there was no size-related segregation with respect to depth. Large, adult grayling tracked by Nykänen *et al.* (2004a, 2004b) in the sub-Arctic River Kuusinkijoki (Finland) selected areas with depths of 140-300 cm, velocities 40-100 cm s^{-1} and particle sizes 16-256 mm in early summer and depths of 80-120 cm, velocities that exceeded 40 cm s^{-1} and mainly boulder habitat in late summer. This indicates a substantial degree of plasticity in summer habitat use between rivers.

In sub-Arctic climates grayling have been shown to move to deeper, slower habitats in autumn in which they overwinter, often under ice (Zakharchenko, 1973; Nykänen *et al.,* 2001; 2004b). However, definition of the scale of space use and habitat use of adult grayling has not been very well defined in Britain and for summer, autumn and winter in temperate climates.

Homing behaviour occurs in European and Arctic grayling and may help to structure stocks, for which differences in morphology and genetic structure are apparent (Pavlov *et al*., 2000a; Koskinen *et al*., 2002; Meldgaard *et al*., 2003). Reproductive homing was reported in lake-dwelling grayling in Lake Mjosa (Norway), where 84.5 per cent of 284 grayling recaptured came from the tributaries in which they were tagged and the remainder of recaptures came from adjacent tributaries. Since all grayling leave the tributaries and mix in the lake during winter and there are 13 lake tributaries in which grayling spawn, this indicates strong reproductive homing, although because fish were marked as adults, it does not indicate natal homing. A similar pattern of reproductive homing appears to have been demonstrated for tributary-spawning grayling of the Upper Volga (Pavlov *et al*., 1998), but the paper lacks clarity and although 0+ and older grayling were tagged in tributaries, only 2.5 per cent of fish tagged as 0+ were ever recaptured. Between-year site fidelity to summer feeding areas has been demonstrated for Arctic grayling (Buzby and Deegan, 2000), while Woolland (1972) found that tagged grayling translocated 250 m from their capture site in summer, tended to return to that site.

Several studies have shown that barriers may interfere with migratory behaviour of grayling, typically allowing downstream drift of young, or downstream-directed movements by adults, but precluding or limiting upriver movements (Jungwirth, 1996; Meyer, 2001; Ovidio and Philippart, 2002). In a study by Meldgaard *et al*. (2003) of grayling from the River Skjern (Denmark), a waterway fragmented by weirs, DNA microsatellite data from samples collected recently were compared with samples from scales collected 60 years ago. They demonstrated that although there were no signs of any loss of genetic variation from the river system, pair-wise multilocus F-ST estimates were correlated with the number of intervening weirs, but not waterway distance. This is consistent with the hypothesis of restricted movement patterns associated with weirs.

2. Seasonal movements and habitat use of grayling

2.1. Rationale of radio-tracking studies and site choice

To study the seasonal movements and habitat use of grayling, the principal method employed was radio-tracking. Study sites were chosen that had no major water regulation in the form of substantial upstream impoundments, and that exhibited substantial discharge variation, moderate gradient and a variety of in-river habitats. Unimpeded access to the main study reach was important to enable active tracking and sampling to be stratified throughout the day, year and reach as necessary, while close liaison with anglers was vital to avoid or confirm the loss of tagged grayling to angling. Access to neighbouring reaches was also required in case fish moved long distances. The main study reach needed to be secure, so as to minimise the likelihood of removal of fish or damage to passive monitoring equipment. The grayling stock needed to be self-sustaining and of natural origin as far as records could show. Study reaches needed to contain one or more potential barriers (artificial and/or natural) to migration. Measurements of discharge close to the study site were necessary, with the reach being amenable to habitat sampling and fish capture. Although these criteria may appear superfluous, it is appropriate to describe them, since such sites may be limited in availability.

The main study site chosen was the River Rye, the major tributary of the River Derwent (which runs into the Ouse) in North Yorkshire (*Fig. 2.1*). This relatively small river met all of the criteria given above. The River Ure (North Yorkshire; *Fig. 2.1*) was chosen as a subsidiary site for a less extensive radio-tracking study, since this river represents a relatively large, upland river with a good grayling stock. While work concentrated on the Rye, the Ure study was intended to provide a comparative context to the data from the Rye.

2.2. Study sites

2.2.1. River Rye

The main tracking study was carried out on the River Rye, centred at West Ness (SE 690 794), west of Malton, North Yorkshire. The Rye (about 10-18 m wide) in this area is subject to substantial flow variation, since it has its headwaters on the North York Moors. Long-term mean flow is about 3.5 $m^3 s^{-1}$ at the Ness gauging weir, with summer base flows (Q_{75}) of approximately 1.4 $m^3 s^{-1}$ and transient high flow events, which quite often exceed 20 $m^3 s^{-1}$. The main study reach comprised a river length of over 10 km (*Fig. 2.2*), mostly run as a low-maintenance, fly-only trout and grayling fishery, in which grayling are normally released. For the duration of the study, anglers agreed to release all grayling captured and to report any marked fishes. The upper part of the valley is a mixture of moorland, woodland and rough pasture, the middle valley is mostly improved pasture, while the lower valley, which includes the Ness area, mostly comprises a mixture of improved pasture and arable land, often to within

20 m of the river banks. At moderate flows, and especially outside the summer months, substantial turbidity occurs because of high levels of suspended fine sediment, an increasingly common problem in many English rivers (Walling *et al.*, 2002). During stable low flows, turbidity is very low and so water clarity is very high. Elevated levels of fine sediment are likely to be associated with changes in land use practices and increased erosion within the catchment.

The upper and middle sections (C and B, respectively, *Figs 2.2, 2.3*) are quite typical of the 'grayling zone', with glide–riffle sequences and a few pools, large areas of gravel, substantial riparian alder *Alnus glutinosa* growth and some, but limited, in-stream macrophyte growth, mainly long-leaved water crowfoot *Ranunculus fluitans* and water moss *Fontinalis antipyretica*.

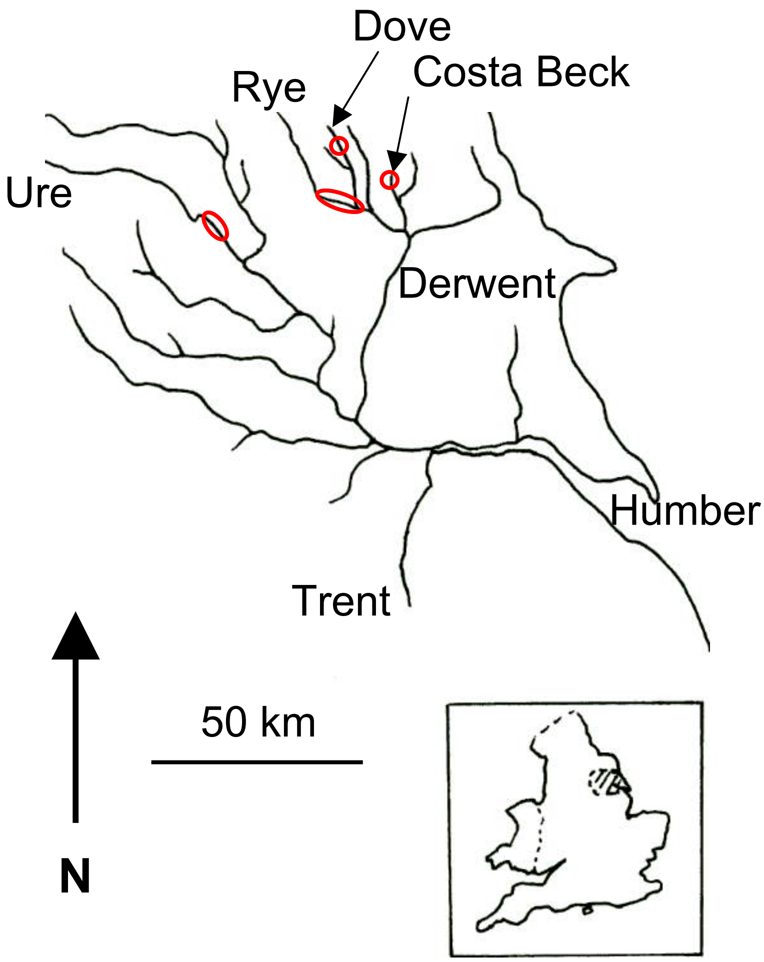

Figure 2.1 Map of the Humber catchment, showing the two catchments, the Rivers Rye and Ure, used for fieldwork. Red ellipses show locations of study sites.

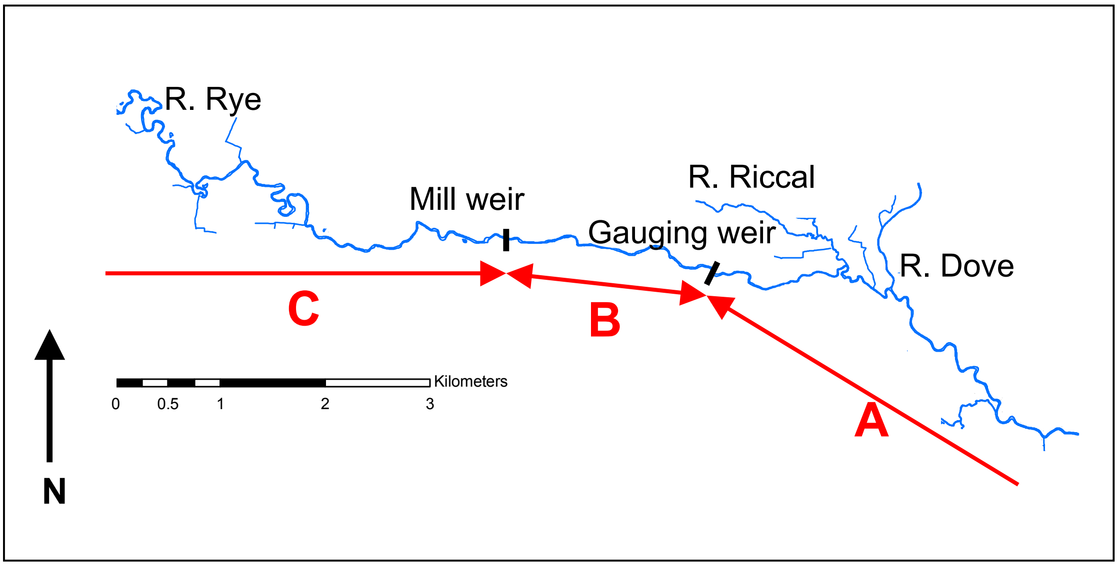

Figure 2.2 Sections of the River Rye used for the radio-tracking study of grayling movements and habitat use.

Typical depths at base flows are 0.2-1.5 m (up to about 2.2 m, section C has a greater proportion of shallow habitat than B) and typical channel widths of 10-16 m. The banks are relatively natural in form, often with one bank exhibiting a gentle slope and with flood defence levees absent or adjacent to one bank only. There is a relatively high degree of habitat heterogeneity within the channel. All of the lower section (A), except the upper 500 m, is characterised by much steeper banks in many areas, and with flood levees on both sides of the river (*Figs. 2.2, 2.3*). Channel width is mainly 12-18 m. The steep banks are eroding in many areas and old wooden piling reinforcement, installed in the 1970s, was evident. The overall depth distribution is similar to that in section B, but further downstream there is an increasing proportion of deeper water. In much of section A's shallow areas, water current is fast and turbulent during elevated discharge, as the increased water volume tends to be channelled between the steep banks. The channel bed often consists of gravel, especially in the upper 1 km of section A, but sand or bare clay is more common than further upstream. The banks of section A, except for the upstream 500 m, are characterised by fewer trees than in the upper sections, and mostly comprise scrubby willow *Salix* spp. further downstream. Sparse in-stream macrophyte growth (mainly *R. fluitans* and *F. antipyretica*) occurs in section A, mostly in the upper 1 km. Much of section A would not be regarded as typical grayling habitat – in appearance much of it would be considered more typical of rheophilic cyprinid habitat.

Figure 2.3 Examples of river morphology on sections A (left panel) and C (right panel) showing the tendency for the downstream section (A) to be characterised by steep, eroding banks, deep water and sparse willow riparian vegetation and the middle and upper sections (B and C) to be characterised by riffles and glides, more gently sloping banks, variable depths and greater riparian vegetation, mostly alder.

The middle Rye and adjoining tributaries, such as the Dove, Holbeck, Seven and Costa Beck, contain moderate natural grayling stocks, with a good range of age classes (Hopkins, 2003; M. Lucas, personal observation), together with a mixture of wild and stocked brown trout *Salmo trutta*. Bullhead *Cottus gobio* and minnow *Phoxinus phoxinus* are abundant and small numbers of chub *Leuciscus cephalus*, dace *L. leuciscus*, pike *Esox lucius*, eel *Anguilla anguilla*, stone loach *Barbatula barbatula* and brook lamprey *Lampetra planeri* occur. Grayling are present throughout sections A, B and C, although probably less abundant in section A, based upon a combination of Environment Agency electric fishing surveys and angler catch records.

The study reach has a Flat-V flow-gauging station at West Ness, which provides excellent information on discharge variations in the middle of the reach (*Fig. 2.2*). Although possibly not an absolute barrier to upstream movement, the weir has a head loss of approximately 1.2 m at base flows, a water depth of less than 0.2 m over much of the downstream face, water velocities of 2 m s^{-1} or more on the downstream face and recirculating side eddies (*Fig. 2.4*).

Figure 2.4 Ness Flat-V flow-gauging weir showing an oblique view from downstream at moderate winter flows (left panel) and a close-up view of the downstream weir face at low summer flows, which highlights the shallow water on the weir face, hydraulic jump at the base and the flow eddies on each side (right panel). The weir is approximately 12 m wide.

Figure 2.5 View of disused mill weir that marks the intersection between section B and section C. The photograph was taken during summer base flows and shows the shallow depth over the crest and downstream face across the full width (about 34 m) of the weir.

A second major weir occurs 2.4 km upstream of Ness gauging weir (*Figs 2.2, 2.5*). This disused mill weir runs obliquely across the river at a site where the river is approximately 34 m wide. The weir has a headloss of about 1.4 m at low flows, with very shallow water depth over it (<8 cm), except during high flows, which makes fish passage for all species very difficult.

Several tributaries enter the Rye study reach within section A, including the Rivers Riccal (1.4 km downstream of Ness weir) and Holbeck (5.5 km downstream of Ness weir), both of which are about 3-5 m wide. The River Dove is a more substantial tributary, with a typical channel width of 7-10 m, mean flow of about 1 $m^3 s^{-1}$ and summer base flow around 0.5 $m^3 s^{-1}$. Grayling are quite abundant in the Dove and also occur in the smaller streams (Hopkins, 2003; M. Lucas, personal observation), all of which provide potential spawning, nursery or refuge areas.

2.2.2. River Ure

The Ure study site was centred on Bellflask (SE 294 775), 7 km north of Ripon, North Yorkshire (*Fig. 2.6*). The Ure is a major tributary of the Yorkshire Ouse and is subject to substantial flow variation, since it has its headwaters on the Pennine Hills. At Bellflask, the Ure is 20-40 m wide with a variety of habitats, mostly glide and riffle, with gravel and cobble substrate and, in some areas, scattered boulders. Some river banks are open, but most retain a narrow or wider wooded fringe. The gradient is typically 2 m km^{-1}. Base level summer discharge at Kilgram, approximately 25 km upstream, is about 6 $m^3 s^{-1}$, but during floods gauged discharge may exceed 200 $m^3 s^{-1}$. This area is a site of special scientific interest (SSSI) and is relatively natural in character, although a substantial level of gravel extraction takes place on site. The water is part of the Norton Conyers estate and the fishery (about 5 km) has been run by the same manager as an unstocked, non-maintenance, mixed fishery for over 20 years. The small syndicate of 60 anglers fish the water at a low intensity and grayling are normally released. For the duration of the study anglers agreed to release all grayling captured and to report the capture of any tagged fish.

The reach has a substantial natural grayling stock, representing all size classes, including adult fish over 250 mm (B. Morland, personal communication, M. Lucas, personal observation), together with some wild and stocked brown trout, which originate from upstream of the study reach, and an abundance of coarse fish, especially chub, dace and barbel *Barbus barbus*. It is at the lower end of the grayling zone, but grayling are known to spawn at a number of sites within the reach. The reach contains a wide variety of habitats, including a number of deep (>3 m) glides. Typical summer depth range is 0.3-0.5 m in riffles, 0.5-2.0 m in shallow glides and 3-4 m in some of the deepest glides, where gravel has been extracted in the past. Several potential barriers lie upstream of Bellflask, including Sleningford, West Tanfield and Mickley weirs (with fish passes) within (2-7 km upstream of the primary reach) and downstream of Bellflask, including Hewick Weir (with fish pass, 5 km downstream of the primary reach), but none within the primary reach itself. No significant tributaries enter the river within the primary study reach, but the Skell (7 m wide) enters in Ripon, where the Skell is somewhat degraded.

Since the aim of the tracking study on the Ure was to provide preliminary radio-tracking data on the movements of a necessarily small sample of grayling from the middle reaches of a large river, to complement more complete data from the Rye, it was not feasible to survey in-river habitat in detail. Consequently, habitat was characterised over the range of space used, in terms of fluvial geomorphic units after the Ure tracking study had been completed (*Figs 2.6*, *2.7*, *Table 2.1*). In reality, these units grade into one another, rather than halting abruptly, but they provide an appropriate characterisation of habitat type.

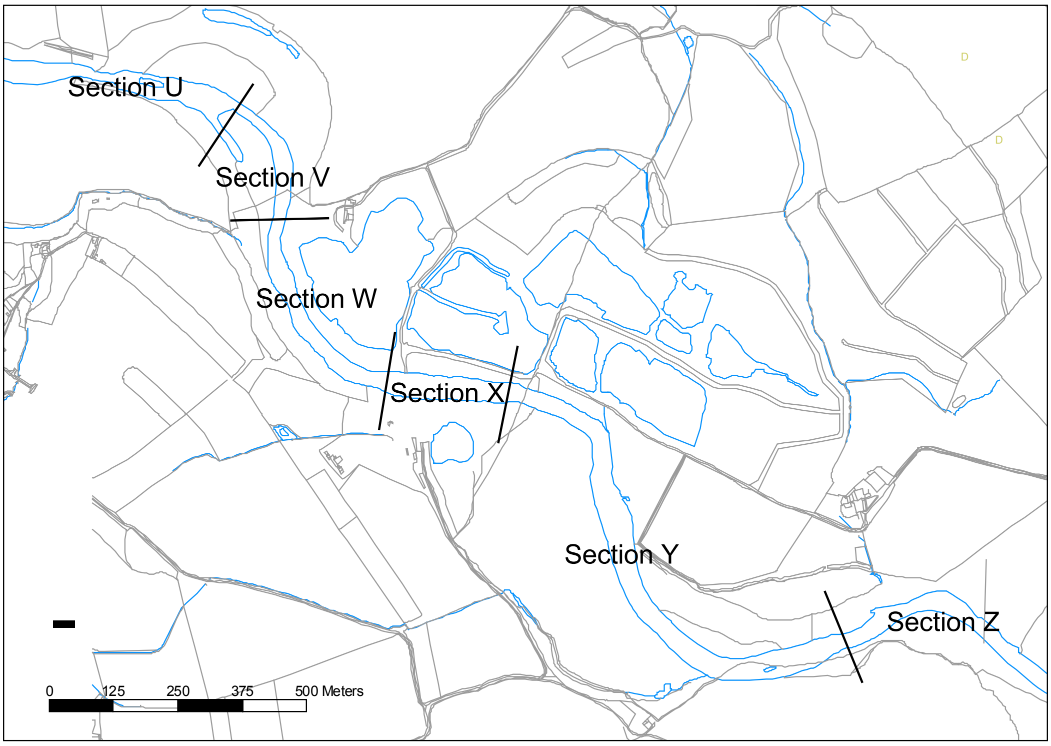

Figure 2.6 River Ure study site at Bellflask. Flow is in the direction of sections U to Z. The sections are used to characterise fluvial geomorphic habitat types along the study length used by radio-tagged grayling.

Figure. 2.7 Photographs of the River Ure study site at Bellflask. Right photograph shows part of section V and left photograph shows part of section W.

Table 2.1 Habitat types, based upon fluvial geomorphic units, along the Ure study length used by radio-tagged grayling.

Section	*Habitat description*
U	Moderate speed glide, accelerating towards riffle; gravel substrate; average depth about 0.7 m; wooded and/or scrub banks
V	Turbulent rapid, slowing to riffle at downstream end; cobble, boulder, gravel substrate; average depth about 0.7 m; wooded and/or scrub banks
W	Moderate speed, steady glide, accelerating towards riffle; gravel substrate, some cobble; average depth about 1.2 m; wooded and/or scrub banks
X	Riffle; gravel, cobble substrate; average depth about 0.5 m; wooded and/or scrub banks
Y	Very slow glide; mostly clay–sand substrate after gravel extraction; average depth about 4 m; wooded and/or scrub banks
Z	Moderate speed glide, accelerating towards riffle; average depth about 1.5 m; wooded and/or pasture banks

2.3. Methods

2.3.1. Radio-tracking – River Rye

A sample of grayling were radio-tagged in January 2004 and tracked until July 2004 in order to study spatial behaviour and habitat use through wintering, spawning and summer growth periods. It was intended that further fish would be tagged in summer 2004, but this was not achieved because of other research commitments within this project and wet weather. A further sample of grayling were radio-tagged in autumn 2004 and tracked until January 2005.

Grayling of a minimum fork length of 260 mm (about 200 g) were considered to be of sufficient size to be tagged with radio-tags large enough to give usable lives of at least 10 weeks. Where larger fish were available, larger tags with longer life and/or greater power output were used to increase detectability in deep water. The ratio of tag weight in air to fish body weight in air was always less than 1 per cent, meeting the ‘2 per cent rule’ suggested by Winter (1996) in order to minimise effects on fish behaviour. Pulse rates between tags varied between 30 and 50 pulses per minute, pulse width was 20 ms and frequency was in the range 173.2-173.4 or 173.7-174 MHz, with individual fish identified by the unique tag frequency. Tags used were PIP type single-stage circuits, potted in plastidip or medical grade silicone. Whip antennas (14-16 cm in length, 0.15-0.3 mm diameter) were used because of the need to maximise power output to aid tag detectability in deep water. Tags used 1 x 1.5 V Ag393 cell (tag weight in air 1.8 g), 2 x 1.5 V Ag393 cells (3 V, tag weight in air 2.9 g), 1 x 1.5 V Ag386 cell (tag weight in air 2.6 g) or 2 x 1.5 V Ag386 cells (3 V, tag weight in air 4.1 g).

Fish were collected mostly by rod and line, either bait or fly fishing, using small, barbless hooks, except for four grayling captured by electric fishing in section A in February 2004. All fish tagged in sections A and B were caught and released at least 400 m from the nearest weir, to ensure that their spatial behaviour was not influenced by the presence of a weir in the locality. Details of the locations of capture, fish characteristics and tag frequencies are given in *Table 2.2*. Radio-tags (previously sterilised in alcohol and rinsed in distilled water) were implanted surgically into the body cavity under general anaesthesia (buffered 3-aminobenzoic acid ethyl ester methanesulphonate salt, MS-222), using a modification of the sterile shielded needle technique to enable the whip antenna to be exited through the body wall and trail alongside the fish (*Fig. 2.8*). The incision was made immediately anterior to the pelvic fin muscle bed, in a ventrolateral position, and closed with absorbable sutures (Vicryl 4/0). During surgery the fish was retained in a surgical tray and the gills were irrigated with aerated anaesthetic solution. Each tagged fish was tattooed with a dye-mark on the underside adjacent to the pelvic fins (section A), midway between the pelvic and pectoral fins (section B) or by the pectoral fins (section C) to aid identification of any fish caught by anglers. Sex of large grayling was determined by external morphology, particularly the size and shape of the dorsal fin, but was confirmed in all fish by internal inspection of the gonad using a small endoscope-type device. This was relatively easy in late winter when gonads were well developed, but for small fish in autumn, sex determination was not always conclusive. Following surgery, the fish was transferred to aerated fresh river water and retained until able to hold station and swim upstream with vigour. Fish were released less than 50 m from the site of capture and normally within 10 m of the site of capture. Where several fish were captured in close proximity, they were released together – sometimes combining untagged with tagged fish. The duration of the surgical procedure was 3-5 minutes, with a similar period required for general anaesthesia and recovery of body posture after anaesthesia. No mortality from tagging occurred in any fish prior to fish release.

A total of 40 grayling were radio-tagged during the Rye study. Between 2 January and 6 March 2004 eight fish from each of sections A, B and C were tagged (24 in total). Between 10 October and 7 November 2004 eight fish from each of sections A and B were tagged (16 in total).

Figure 2.8 Radio-tagged grayling recovering after surgery. The whip antenna (0.3 mm diameter) is visible exiting above the left pelvic fin and extending obliquely from the fish’s body.

Table 2.2 Details of grayling radio-tagged in the River Rye.

Fish	*Frequency (MHz)*	*Section*	*Sex*	*Fork length (mm)*	*Weight (g)*	*Date of capture*	*Capture method*	*Capture location*
1	173.924	A	F	276	230	02-Jan-04	Rod and line	71204 78971
2	173.973	A	M	283	246	02-Jan-04	Rod and line	71204 78971
3	173.932	A	M	314	348	14-Feb-04	Rod and line	71470 78656
4	173.258	A	M	325	399	19-Feb-04	Rod and line	70920 79105
5	173.249	A	F	300	293	24-Feb-04	Electrofished	70905 79103
6	173.324	A	F	320	342	24-Feb-04	Electrofished	70905 79103
7	173.235	A	F	279	242	24-Feb-04	Electrofished	70700 79120
8	173.231	A	M	421	885	24-Feb-04	Electrofished	70000 78980
9	173.785	B	F	283	241	08-Feb-04	Rod and line	68890 79380
10	173.745	B	F	310	314	14-Feb-04	Rod and line	68193 79480
11	173.757	B	M	401	741	14-Feb-04	Rod and line	68173 79490
12	173.767	B	M	348	541	19-Feb-04	Rod and line	68865 79374
13	173.725	B	F	360	585	19-Feb-04	Rod and line	68865 79374
14	173.775	B	F	325	410	19-Feb-04	Rod and line	68865 79374
15	173.707	B	F	348	626	19-Feb-04	Rod and line	68248 79418
16	173.302	B	M	284	284	24-Feb-04	Rod and line	68034 79480
17	173.897	C	F	278	246	19-Jan-04	Rod and line	65895 79460
18	173.733	C	M	370	599	07-Feb-04	Rod and line	65400 79973
19	173.828	C	F	310	355	15-Feb-04	Rod and line	65395 79932
20	173.220	C	F	291	265	19-Feb-04	Rod and line	65499 79751
21	173.266	C	F	286	247	19-Feb-04	Rod and line	65499 79751
22	173.204	C	M	318	347	24-Feb-04	Rod and line	65423 79818
23	173.275	C	M	411	710	06-Mar-04	Rod and line	65372 79970
24	173.295	C	F	428	885	06-Mar-04	Rod and line	65372 79970
25	173.230	A	F	343	512	10-Oct-04	Rod and line	70019 78984
26	173.209	A	M	336	435	10-Oct-04	Rod and line	70019 78984
27	173.935	A	M	302	305	6-Nov-04	Rod and line	70791 79203
28	173.817	A	M?	267	198	6-Nov-04	Rod and line	70791 79203
29	173.254	A	F?	306	370	6-Nov-04	Rod and line	70791 79203
30	173.962	A	F	265	232	7-Nov-04	Rod and line	71209 78970
31	173.332	A	F	355	436	7-Nov-04	Rod and line	71209 78970
32	173.938	A	M	267	202	7-Nov-04	Rod and line	71042 78978
33	173.752	B	F?	264	223	10-Oct-04	Rod and line	68763 79342
34	173.953	B	M	312	327	30-Oct-04	Rod and line	68876 79379
35	173.797	B	M?	268	205	30-Oct-04	Rod and line	68876 79379
36	173.881	B	M?	277	241	30-Oct-04	Rod and line	68876 79379
37	173.200	B	F	356	502	6-Nov-04	Rod and line	68053 79481
38	173.236	B	F	304	323	6-Nov-04	Rod and line	68053 79481
39	173.896	B	F?	297	273	6-Nov-04	Rod and line	68053 79481
40	173.248	B	M	324	348	7-Nov-04	Rod and line	68961 79413

Grayling were radio-tracked on foot, typically every 2-3 days, between January and July 2004 and in more intensive, but more widely spaced sessions, between October 2004 and January 2005. Tracking was partially stratified across the 24 hour cycle, with sessions at night, dawn, dusk and by day, although the number of daytime sessions was much greater. Fish were usually inactive during darkness, so tracking at this time was found to be unimportant. In preliminary analyses, no diel trends in space use were evident, so they were not considered further. Sections on which tracking started were also randomised, so as to avoid any consistent bias. Radio-tracking was mostly carried out with Biotrack Sika and Lotek SRX400 programmable, frequency-scanning receivers and three- or five-element Yagi antennas. Fish locations were estimated by triangulation or from localising the signal by reducing the gain. Fish distance across the river was estimated as right side, mid-channel or left side. Bankside locations were identified by a combination of bankside features on a 1:5000 field map and use of a GPS receiver (Garmin etrex). This resulted in location precision of approximately ±3 m along the river bank and ±2 m across the river channel. These data were translated to a digital map of the river in ArcGIS (ESRI), from which fish locations, distances moved and ranges were calculated along the river midline.

Four frequency-scanning, data-logging receivers (Lotek SRX400) were set up along the study reach, one at either end, one pointing downstream at the mill weir and one with a multiplexer having antennae pointing upstream and downstream at the flow-gauging weir. Automatic receiver gains at the weirs were set to pick up signals within a localised zone of less than 50 m river length.

During the tracking period, flow and water temperature were logged continuously at Ness. Individual measurements, usually during each tracking session, were made of oxygen concentration, turbidity and pH using calibrated hand-probes (Hanna Instruments). Initial tests showed no significant differences in any of these variables measured at different points of the Rye study reach, so all measurements were made at Ness.

2.3.2. Habitat surveys and analysis of habitat use on the River Rye

As part of the study, habitat utilisation of tracked grayling was to be quantified. The most common approach is to ‘sample’ fish, either by electric fishing or observation, and to characterise the habitat for each fish location (Greenberg *et al*., 1996; Mallet *et al*., 2000), usually by comparing use to availability of habitat types through broader survey. While some fish telemetry studies have radio-located fish and measured the habitat at the fixes, this was inappropriate for grayling because of the disturbance it would cause, as well as the practical problems that many locations were in deep or fast water. Therefore, a habitat survey was carried out along most of the Rye study reach (all sections, >10 km) in which fish were tracked and on to which fixes could be overlaid. The Environment Agency’s River Habitat Survey approach, which maps in detail alternate 500 m sections, was inappropriate for analysis, because of its inability to reflect the nature of habitat along the complete study length. Instead, cross-channel habitat surveys were carried out, stratified across geomorphic units to provide adequate representation (typically repeated every 10-30 m, therefore covering repeated glides, riffles and transition zones). Additionally, surveys were carried out at radio-locations of fishes. Variables measured were channel width (m), bank slope (scale of 0-5), riparian and/or overhead cover (scale 0-5), channel depth (m), substrate composition (per cent silt, sand, gravel, pebble, cobble, boulder, bedrock, bare clay), in-stream macrophyte cover (scale of 0-5), root and/or woody debris cover (scale of 0-5). All but the first two factors were measured at 0.25, 0.5 and 0.75 of river width, equating to track fixes associated with the left bank, mid-channel and right bank. The complete survey took several weeks to perform, during which discharges were low (2-4 $m^3 s^{-1}$). While variable conditions, especially velocity, may change with discharge and so not be identical when surveyed to when the fish was located, this method had the advantage of not having to enter the water to record data at the focal point, which would risk serious disturbance of fish behaviour.

Data from a total of 1253 sites (section A, 477; section B, 309; section C, 467) were obtained in the survey. These data were used to produce histograms of available habitat for selected resource factors and were compared with use of those factors by tagged fish. Where a cross-channel habitat survey was not sited at a fix, the nearest survey location was used to provide habitat data. Habitat preferences were determined using the electivity index of Jacobs (1974):

$$D = (r - p)(r + p - 2rp)^{-1} \tag{2.1}$$

In Equation (2.1), r is the proportion of a resource interval used by grayling (for example, depth) and p is the proportion of resource interval available to them. The index can obtain values between –1 and +1, where –1 indicates complete avoidance and +1 indicates total preference. Analyses were separated by section (A, B and C) and season (late winter 2004, spawning 2004, early summer 2004 and early winter 2004), because of distinct differences in spatial behaviour and habitat use between sections and seasons (see Section 2.4). We evaluated the general microhabitat use and availability by Principal Component Analysis (PCA). All of the sections were combined and the measurements of depth, velocity, cover and dominant substrate were subjected to PCA. The first two principal components extracted by PCA explained 77.7 per cent of variation and were used in the analysis of microhabitat use by fish from different sections. The combination of environmental data from the three sections is appropriate as the PCA reduces the environmental variables by identifying those that are colinear and correlated, so section-wise PCA of fish habitat use is not compromised.

2.3.3. Surveys of large piscivorous birds on the River Rye

It was known that substantial numbers of piscivorous birds occurred on the Rye, particularly in winter and early spring (M. Turnbull, personal communication; M. Lucas, personal observation), and so at the outset of fieldwork it was decided to record the identity and numbers of large, piscivorous birds observed in each section while carrying out active tracking sessions. The birds in question, goosander *Mergus merganser*, cormorant *Phalacrocorax carbo* and grey heron *Ardea cinerea*, were easily identified and counted as they were encountered while walking the sections of bank during tracking between dawn and dusk. Usually, the birds flew off and did not appear to land again in the section being walked, or adjacent sections, although this cannot be discounted. The length of bank walked on each tracking session and river section was recorded and the number of birds of each species recorded as the relative abundance per unit distance of bank walked.

2.3.4. Radio-tracking – River Ure

Eight grayling were captured by angling on two occasions, all from the same location (*Figs 2.6*, *2.7*, section W), and were tagged with 3 V Ag 393 dual-cell, high-power radio transmitters. The method of tag attachment and fish release followed the description given in Section 2.3.1. Details of the fish tagged are given in *Table 2.3*.

Fish were tracked on foot using Mariner M57 radio receivers and three- or five-element Yagi antennae. Five-element Yagi antennae were preferred as they have greater receiving gain, which enhances the likelihood of detecting signals in deep water. B. and S. Morland, who live on the site, volunteered to track the grayling when possible and were trained to do so. Locations were made every 2-3 days, with the whole reach of over 5 km walked on several occasions.

Table 2.3 Details of grayling radio-tagged in the River Ure.

Fish	*Frequency (MHz)*	*Sex*	*Fork length (mm)*	*Weight (g)*	*Date of capture*
A	147.216	M	310	294	21 Feb 04
B	147.221	M	305	269	21 Feb 04
C	147.239	M	353	415	21 Feb 04
D	147.276	M	295	226	21 Feb 04
E	147.280	M	325	319	21 Feb 04
F	147.294	F	280	255	16 Feb 04
G	147.302	M	296	252	16 Feb 04
H	147.313	F	315	326	21 Feb 04

2.4. Results

2.4.1. Grayling movements in the River Rye

The radio-tracking studies on the Rye were characterised by periods of relatively stable flow, as well as several very high-flow events, only one of which occurred while a large number of fish were being tracked (April 2004), this being a substantial flood event with flows of almost 40 $m^3\ s^{-1}$ recorded at Ness (*Fig. 2.9*). Turbidity tended to vary with discharge, as would be expected, with peaks during high-flow events and lowest values during the summer base flows (*Fig. 2.9*). Water temperatures varied between approximately 3 and 14°C during tracking periods, while pH was relatively stable and approximately neutral (*Fig. 2.9*). Dissolved oxygen, expressed as absolute concentration, tended to vary inversely with temperature as expected, but relative concentrations were always greater than 80 per cent saturation. This indicates good aeration and relatively small oxygen demand, which provided plentiful oxygen for grayling at all times of the study (assuming no substantial variations in concentration along the study reach – see Section 2.3).

Individual track records of grayling for the first study period, January to July 2004, are presented in Appendix 1 as fixes along the longitudinal river distance, measured along the midline, relative to their release points. The same scale is applied for ease of comparison between individuals. Fish moved between 0.2 and 3.5 km during the tracking period, with the greatest distances moved occurring mostly in late March and April, associated with pre-spawning, spawning and post-spawning movements. Marked differences in inter-individual patterns of space use occurred, with some fish wintering in a single glide and apparently spawning on an adjacent gravel riffle, while others moved much longer distances between winter, spawning and summer sites. The individual tracks for fish from sections B and C tended to display a narrow range of locations for much of the tracking period outside of the spawning period, which reflects the adoption of relatively small and stable home ranges. By contrast, location data for section A fish tended to reflect much more excursive behaviour outside of the spawning period.

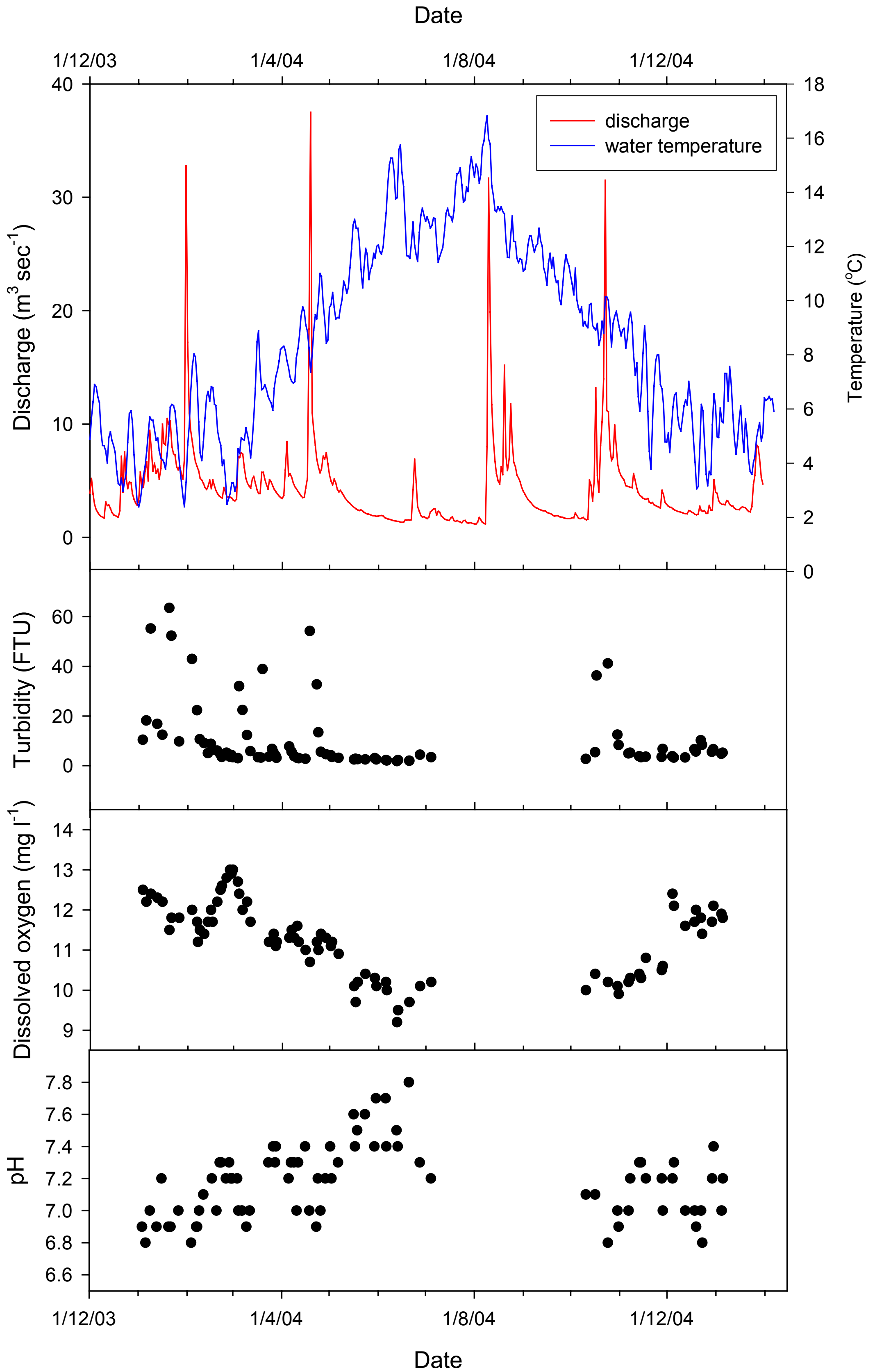

Figure 2.9 Environmental conditions in the Rye at Ness. Daily mean temperature and discharge were measured throughout the study. Dissolved oxygen, turbidity and pH were measured during daytime when visiting the site to radio-track.

Inspection of the individual tracks identified clear longitudinal movements soon before and after the period over which spawning and courtship were observed across the whole population. It was therefore felt appropriate to split the track periods into time segments that characterise the winter and summer periods associated mostly with home range adoption, and the pre-spawning, spawning and post-spawning period associated with high mobility in many, but not all, grayling. Logically, this should be centred around the spawning period. Courtship and/or spawning activity were observed between 5 and 18 April 2004. In order to define the start of the upstream migration observed in most fish (symptomatic of the breakdown of home range behaviour prior to spawning), an analysis of the mean distance of all fish upstream from a fixed reference point against date of location was carried out.

Segmented regression analysis was conducted (SEGREG; Saila *et al*. 1988) to identify the function that best fitted the data and the optimum break points. The selection of the best function type and break point is based on maximising the statistical coefficient of explanation. Break points were calculated between winter and spawning movements and between spawning and summer movements. The optimum break point between the late winter period and the period in which spawning and associated movements occurred was 7 March 2004 (*Fig. 2.10*). Prior to the break point a line was fitted by the model, with fish locations relatively stable and no relationship between date and fish location (r^2 = 0.053, P = 0.113). After the break point there was a highly significant positive relationship between position and date (r^2 = 0.905, P < 0.001). The optimum break point between the spawning and associated movements period and the summer period was 5 May 2004 (*Fig. 2.10*). Prior to the break point there was a strong, highly significant negative relationship between position and date (r^2 = 0.575, P = 0.001). After the break point a line was fitted, with fish positions relatively stable and no relationship between date and fish location (r^2 = 0.002, P = 0.329). Although overall positions of fish were stable before and after spawning and the associated movements, fish tended to remain further upstream after spawning than before (*Fig. 2.11*). Some fish returned to their pre-spawning home range, but many did not, especially in section A where they tended to remain in the shallower, gravel-covered riffles and glides further upstream in that section.

There was a significant difference in the total linear ranges of fish tracked in sections A, B and C over the whole period January to July 2004 (Kruskal–Wallis test, K = 15.16, d.f. = 2, P = 0.001; *Fig. 2.12*). The linear ranges of fish in section A (median 2576 m; lower quartile 2162 m, upper quartile 2861 m) were significantly greater than the linear range of fish in sections B (432 m; 259 m, 1262 m) and C (1023 m; 625 m, 1551 m) – Mann–Whitney test A *vs* B, U = 1.0, P = 0.001; A *vs* C, U = 2.0, P = 0.002. There was no significant difference between the linear ranges of fish in sections B and C (Mann–Whitney test U = 17.0, P = 0.130). There was no difference between the sexes in linear ranges of males and females (ANOVA with section and sex as factors, section P < 0.01, sex P > 0.05). The data in *Figs 2.12-2.15* are presented as total linear ranges and also as the 90 percentile range values, since although total linear range is commonly used as a measure of ranging behaviour in riverine fishes, the value may be strongly influenced by infrequent, highly excursive behaviour. The 90 percentile value is therefore a linear estimator, which removes the greatest excursions and is more indicative of space use closer to a core, that is commonly considered in area-based home range analysis by methods such as bivariate kernel analysis (White and Garrott, 1990).

When the winter, spawning and summer periods are considered separately (*Figs 2.13-2.15*), there was a significant difference between the linear ranges of fish tracked in sections A, B and C in the winter period and those in the spawning period (Kruskal–Wallis, both $P < 0.01$), but not those in the summer period (Kruskal–Wallis, $P > 0.05$), although the sample sizes for the summer period were small. In both the winter and spawning period the linear range of fish in section A was significantly greater than that of fish in sections B and C (Mann–Whitney, all $P < 0.05$), but there were no significant differences between the linear ranges of fish in sections B and C (Mann–Whitney, both $P > 0.05$).

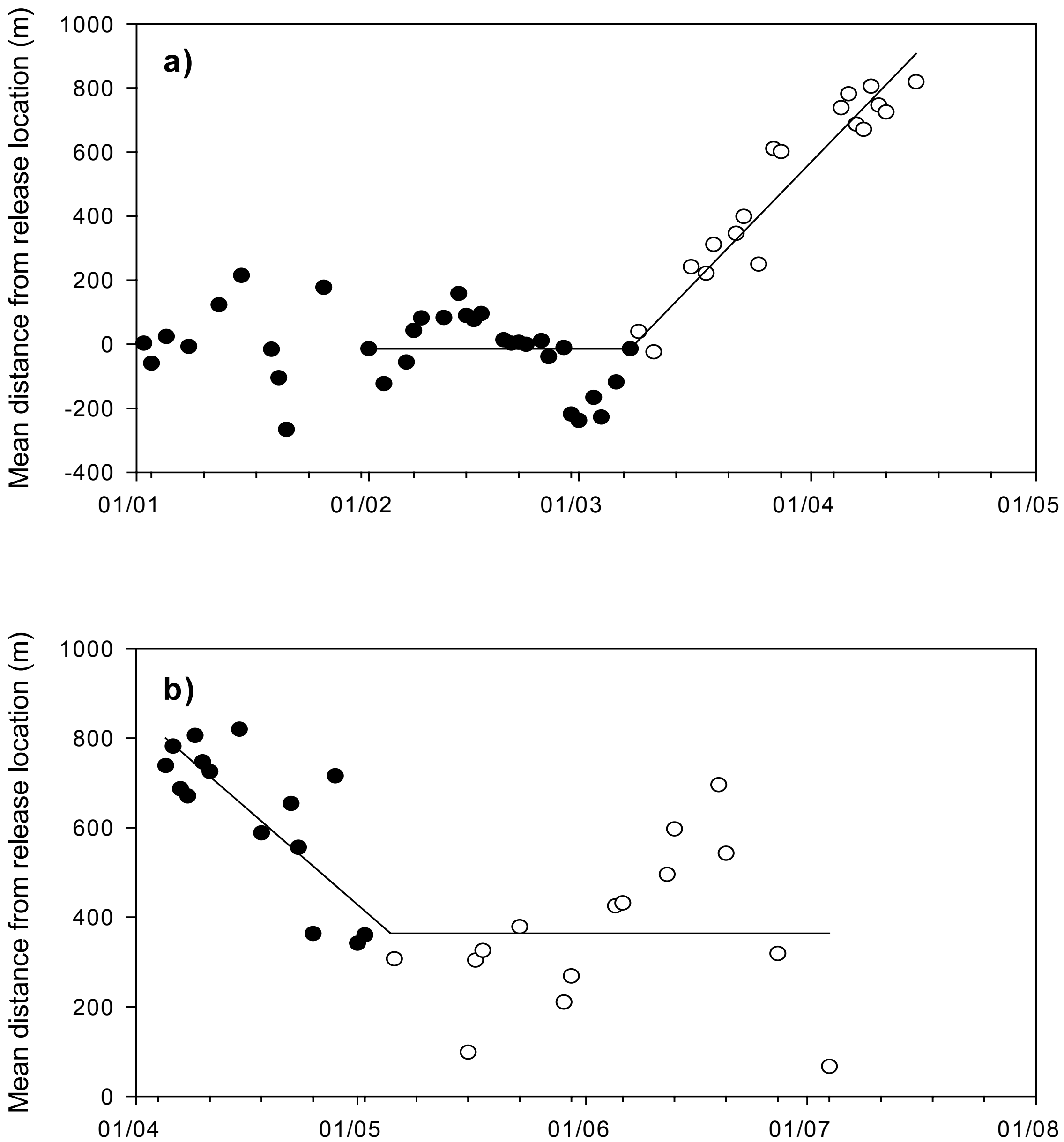

Figure 2.10 Mean distance from release location of radio-tagged grayling: (a) January to April 2004, (b) April to July 2004. Days on which less than four fish were located are discarded. Lines show fitted regression lines and break points.

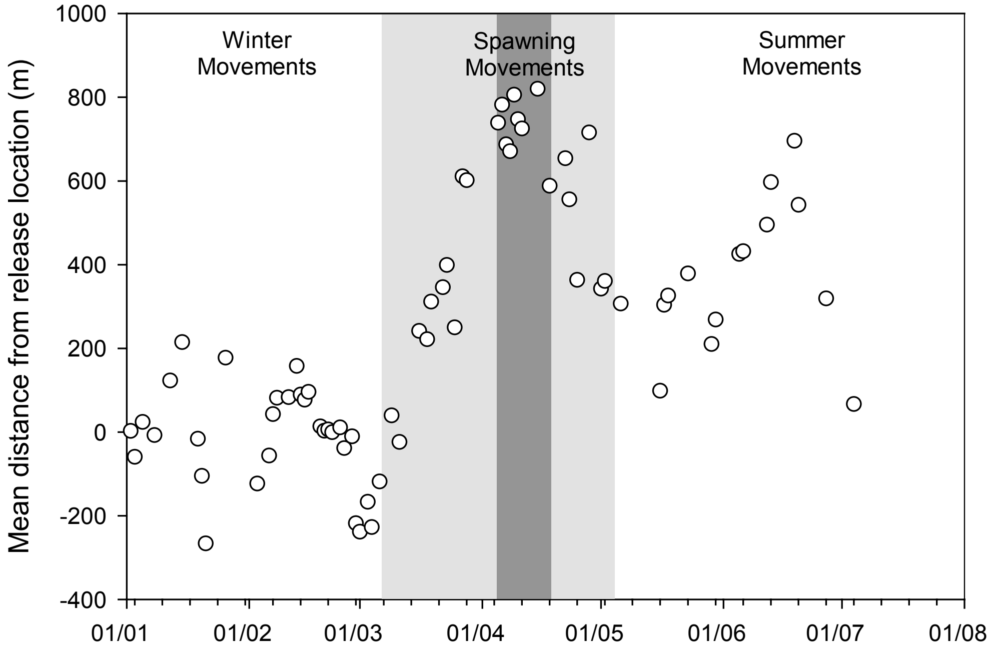

Figure 2.11 Mean distance from release location of radio-tagged grayling, January to July 2004. Days on which less than four fish were located are discarded. The dark grey bar represents the period in which spawning and courtship were observed and the light grey bar represents the period estimated to be associated with pre- and post-spawning movements, modelled by segmented regression analysis.

The total linear ranges of all fish tracked in each section between January and July 2004 are illustrated by relative distance from Dovemouth in *Fig. 2.16*. This shows the relative magnitude, variability and pattern of range between sections and in relation to the weirs in section B. It reaffirms the large movements of section A fish relative to those in sections B and C. Six out of 16 grayling tagged in sections A and B (more than 400 m below a weir) were detected moving upstream to the weir, but none passed. On inspection of *Fig. 2.16* and the ranges of movement within sections, there is little evidence that data on seasonal ranges were skewed because weirs limited the range of movement of fishes. All six grayling detected at weirs were picked up by loggers, but not all of these also by active tracking. With a minimum interval of 4 hours for classification as discrete events, a total of 36 detections for all fish at both weirs was recorded, with 1-6 detections per fish at Ness Weir and 1-13 detections per fish at Mill Weir, all but one of which occurred during the spawning season. No radio-tagged grayling were detected passing downstream over either weir.

Radio-tracking of grayling in sections A and B over the period 10 October 2004 to 5 January 2005 (*Fig. 2.17*) demonstrated space use patterns similar to those recorded in the period January to March 2004, with section A fish moving significantly more widely than section B fish (Mann–Whitney, P = 0.002). Median quartile values (lower and upper quartile values in brackets) of total ranges were 1708 m (955 m, 1926 m) for section A fish and 382 m (189 m, 519 m) for section B fish. Individual track records, relative to release point, presented on the same scale are given in Appendix 2. The stability of home ranges for section B fish by comparison to section A fish is very clear.

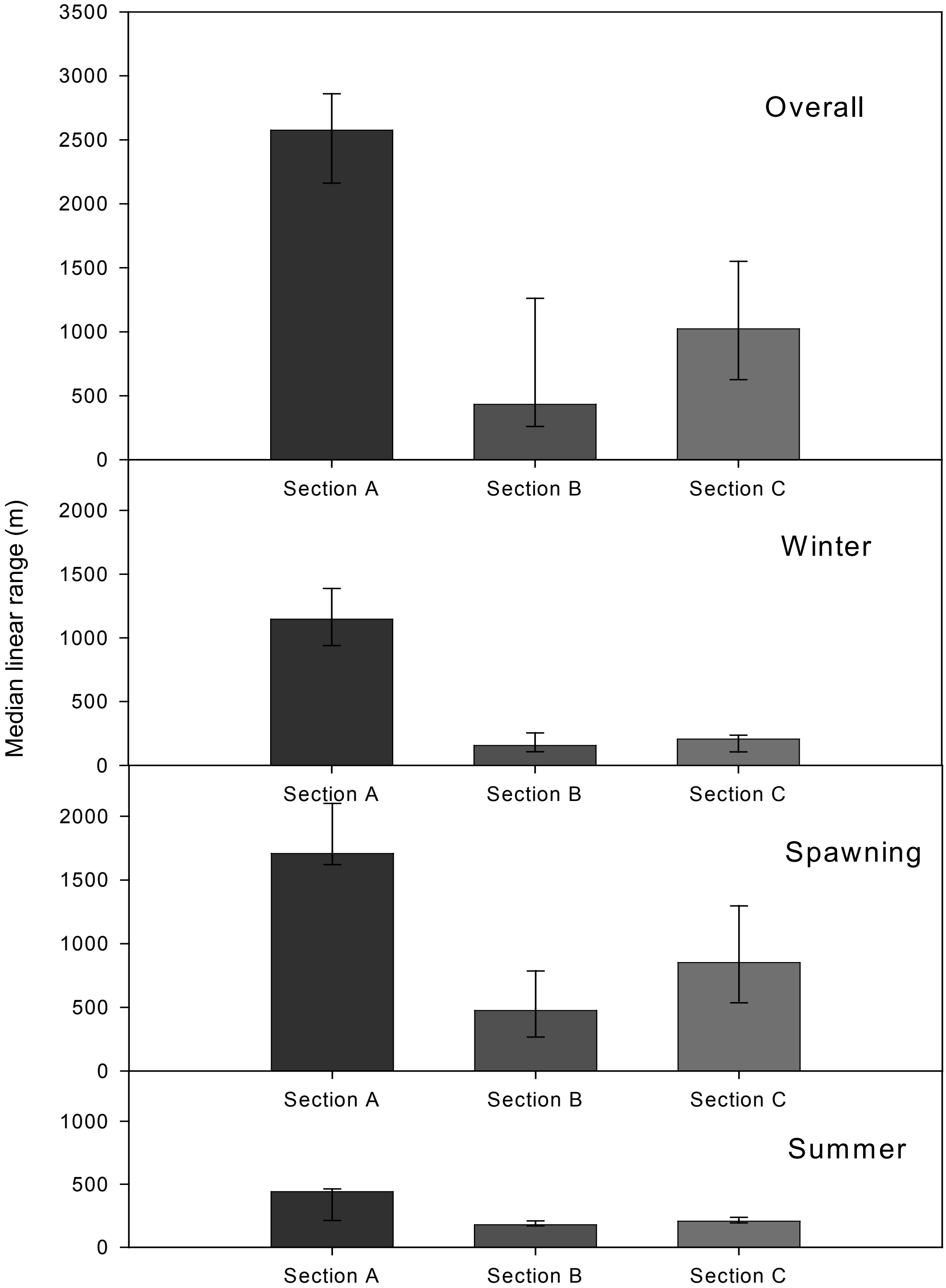

Figure 2.12 Median linear range of radio-tagged grayling during complete study period and during late winter 2004, spawning 2004 and summer 2004 periods. Error bars show 25 and 75 percentiles. Linear ranges were only calculated for fish for which >10 locations were recorded.

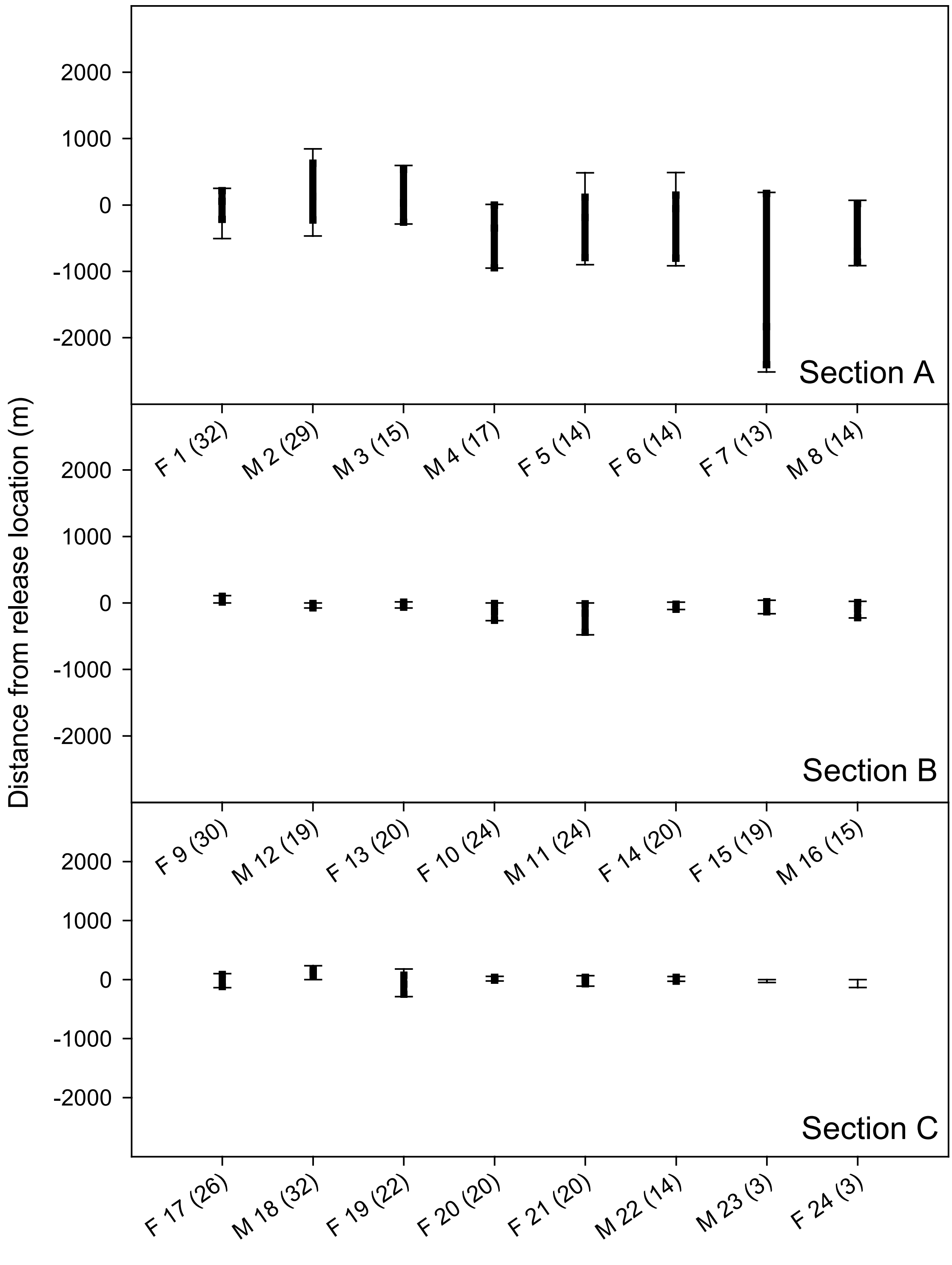

Figure 2.13 Linear ranges of all radio-tracked grayling during the late winter period and associated movements (2 January to 7 March 2004). Bold lines indicate 10 and 90 percentiles and error bars indicate total linear range. Figure in brackets denotes the number of positional records for each fish.

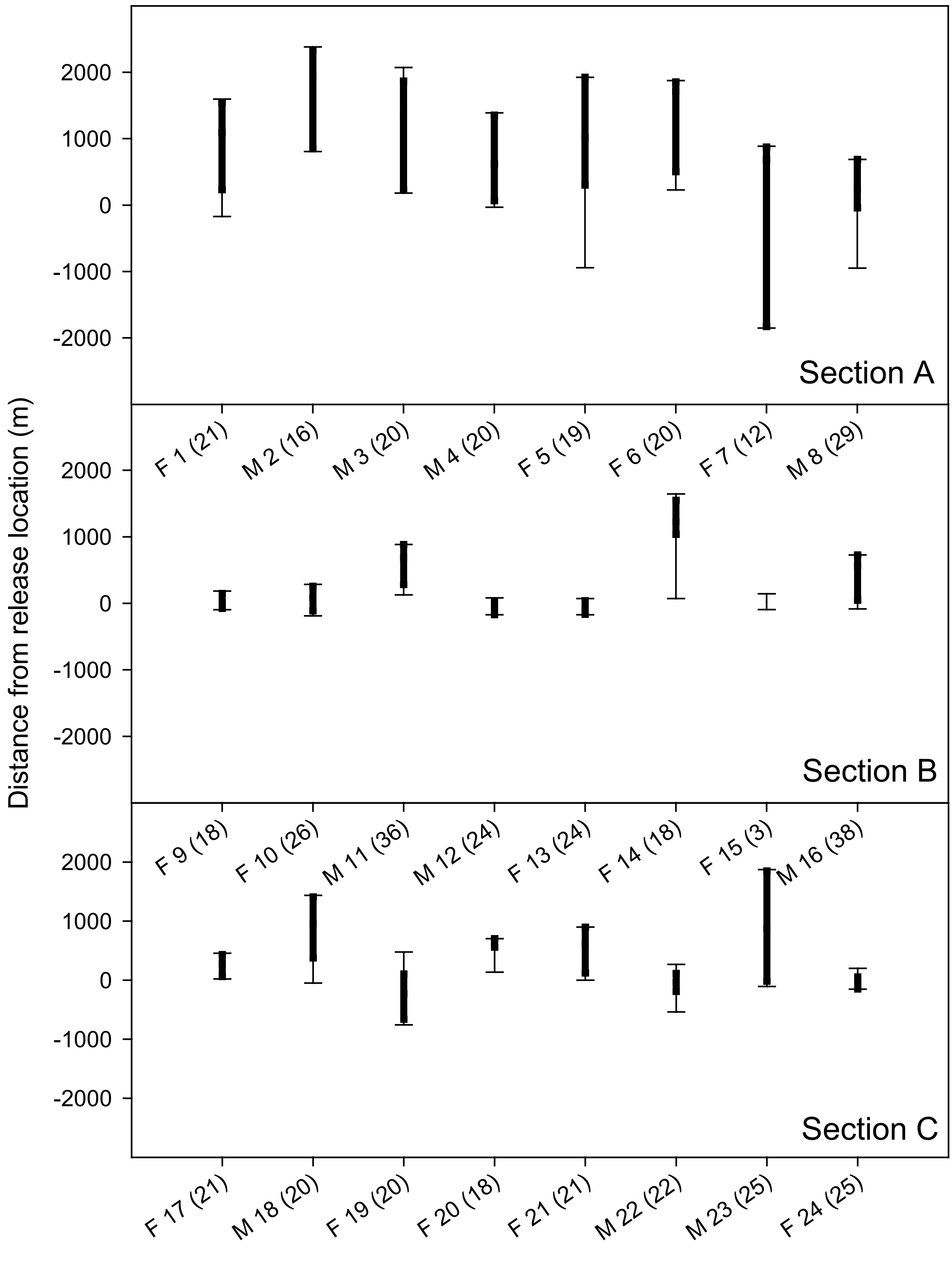

Figure 2.14 Linear ranges of all radio-tracked grayling during the spawning period and associated movements (8 March to 5 May 2004). Bold lines indicate 10 and 90 percentiles and error bars total linear range. Figure in brackets denotes the number of positional records for each fish.

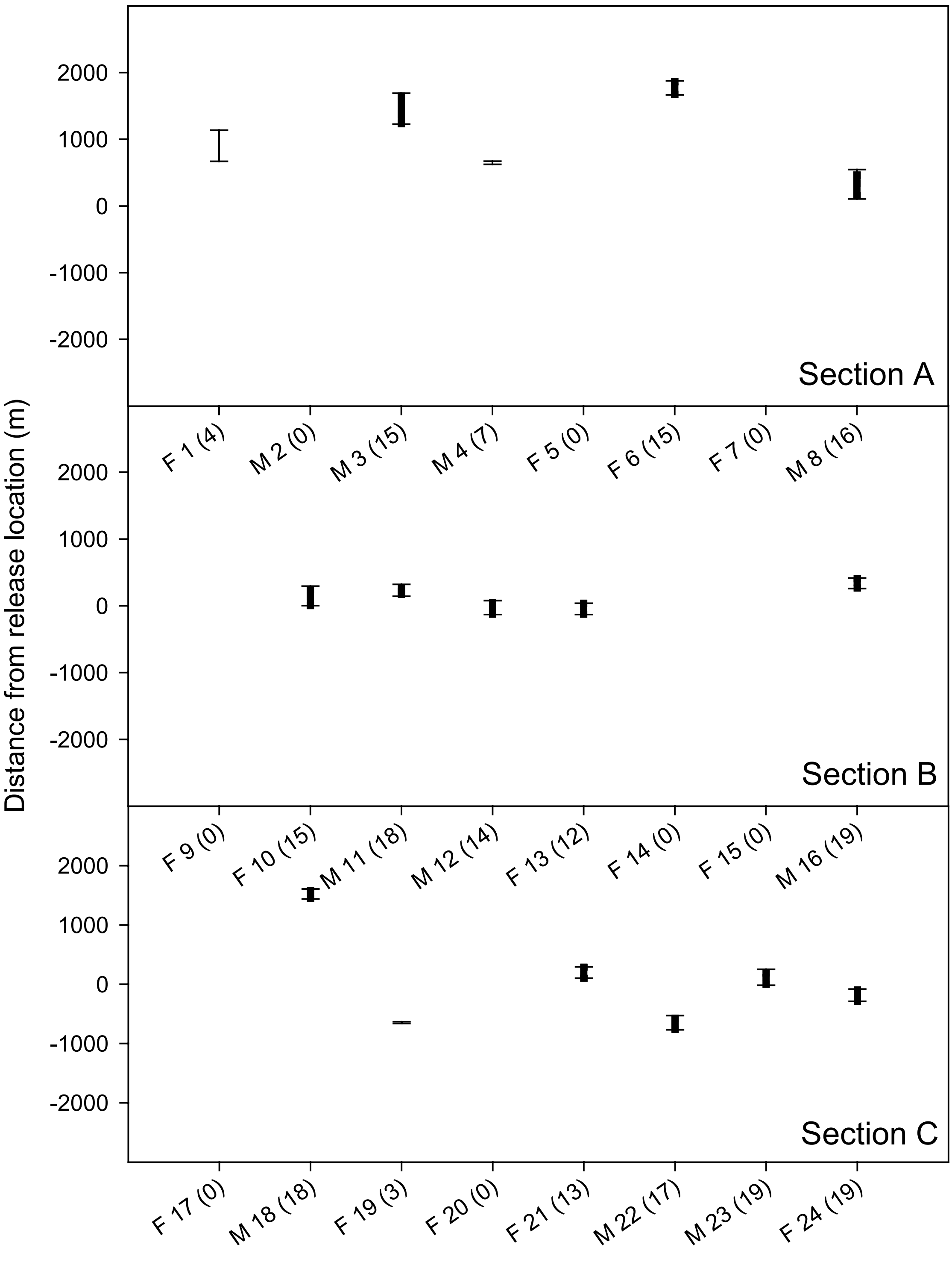

Figure 2.15 Linear range of all radio-tracked grayling during summer period (6 May to 4 July). Bold lines indicate 10 and 90 percentiles and error bars indicate total linear range. Figure in brackets denotes the number of positional records for each fish.

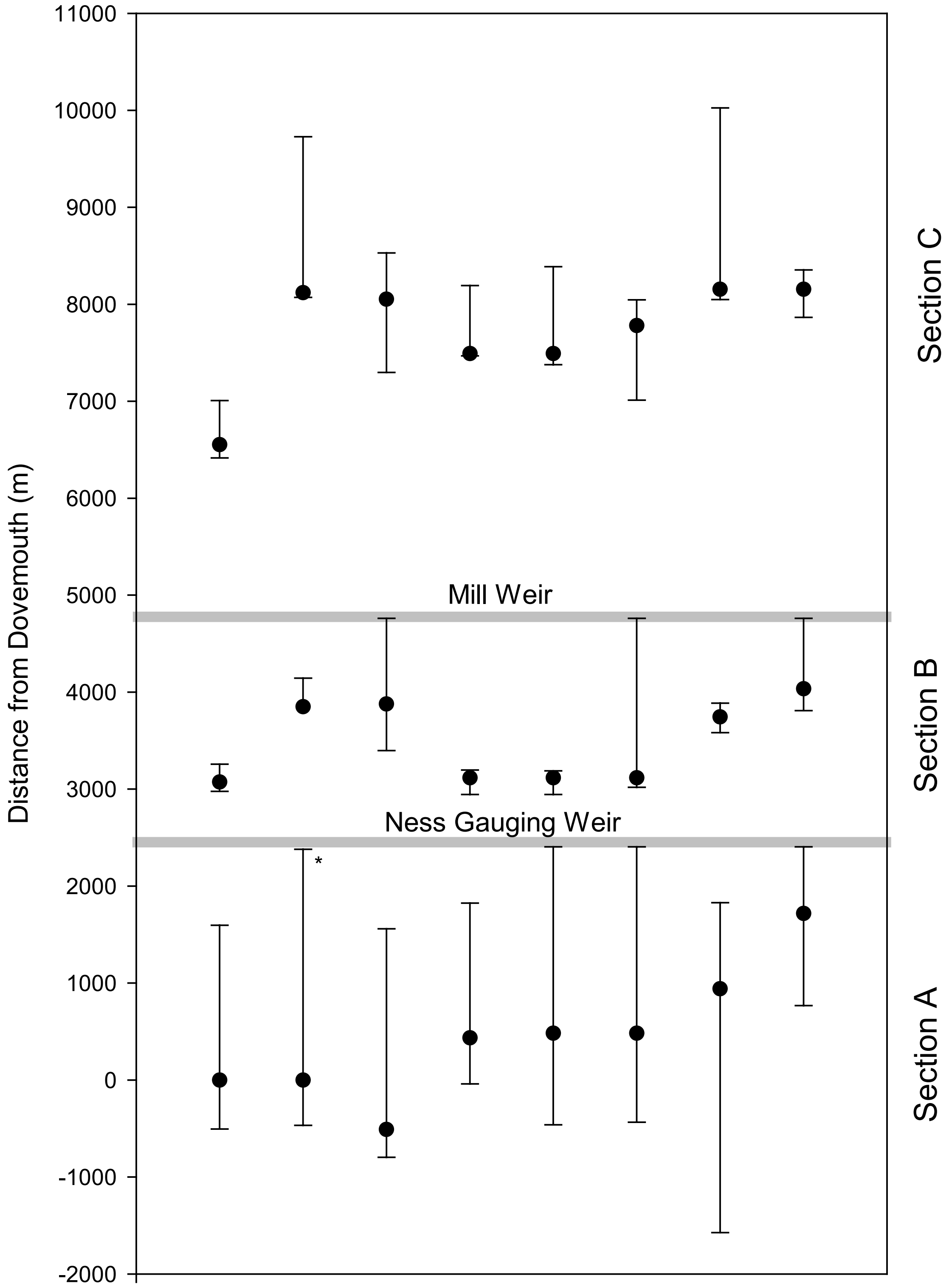

Figure 2.16 Linear range of radio-tagged fish. Error bars show maximum recorded upstream and downstream positions, and circles the capture and release location. The fish marked * moved upstream in the Dove not the Rye, so its upstream range limit was not below Ness gauging weir.

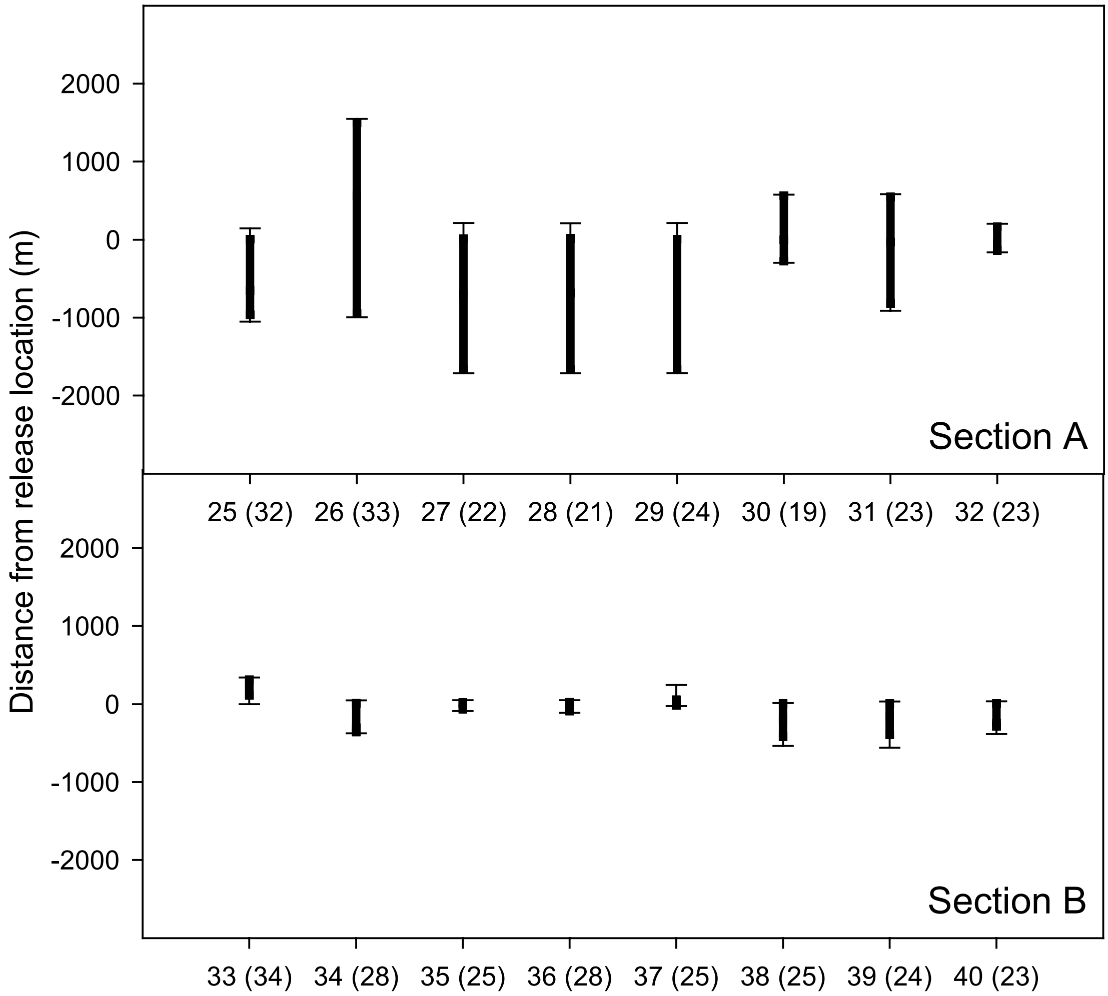

Figure 2.17 Linear range of all radio-tracked grayling during the autumn to early winter radio-tracking period (10 October 2004 to 5 January 2005). Bold lines indicate 10 and 90 percentiles and error bars the total linear range. Figure in brackets denotes the number of positional records for each fish.

2.4.2. Habitat use in the River Rye

The relative availability of in-stream habitats was broadly similar between sections A, B and C, with slightly higher availability of slow habitat in section B, slightly less deep water in section C and more sandy habitat in section A (*Figs 2.18-2.20*). Grayling tended to use deeper, slower habitats with smaller substrate in the period January to early March 2004 (winter to early spring), with positive selection for these habitats apparent across all sections. However, there was some evidence for use of a broader range of depths and velocities for fish from section A than for those from B and C (*Figs 2.18-2.20*).

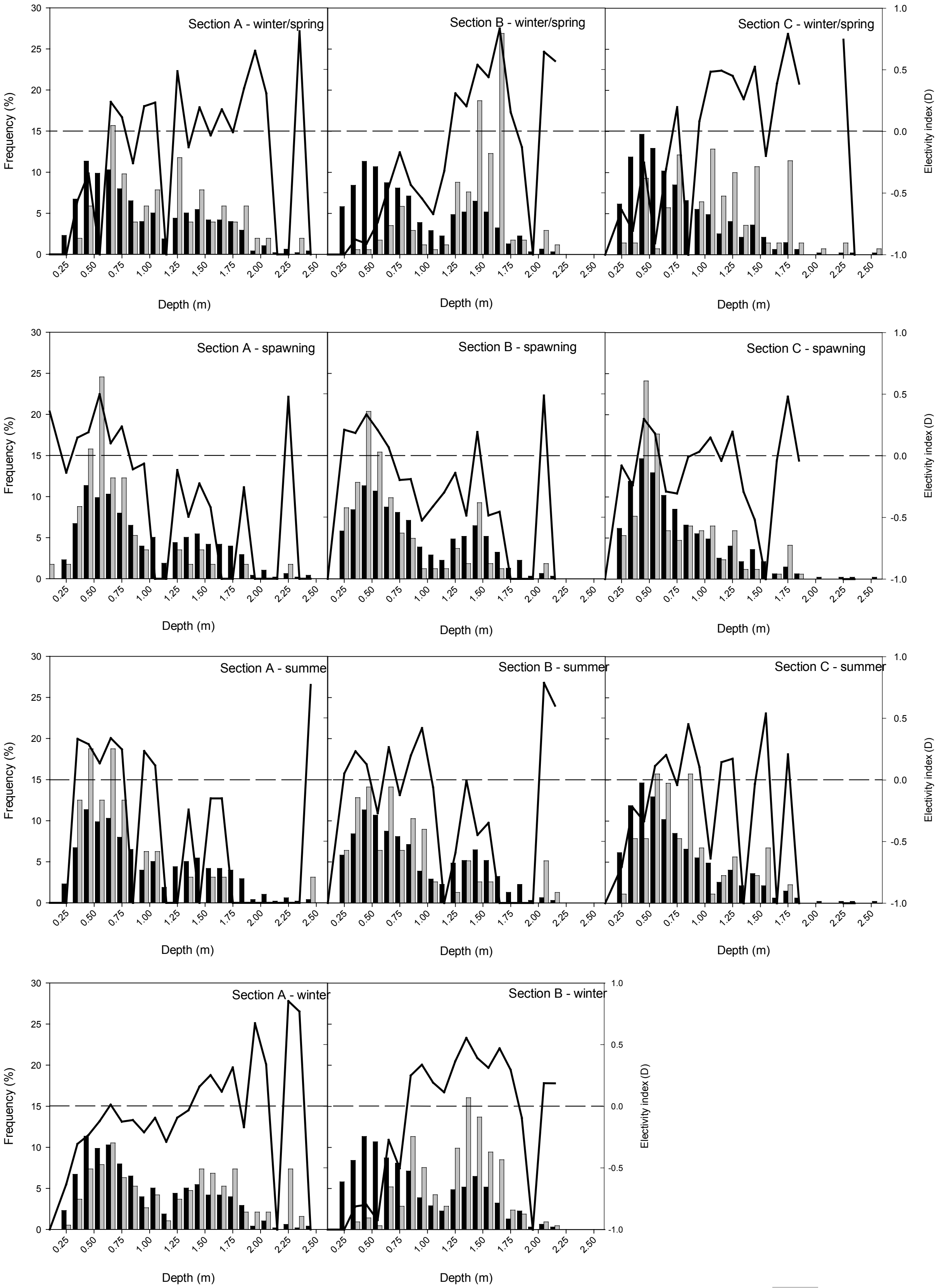

Figure 2.18 Frequency distribution of water depth used (grey bars) by radio-tracked grayling and those available to them (black bars). —, Jacobs (1974) electivity index for each variable class. Positive values of D indicate preference and negative values avoidance.

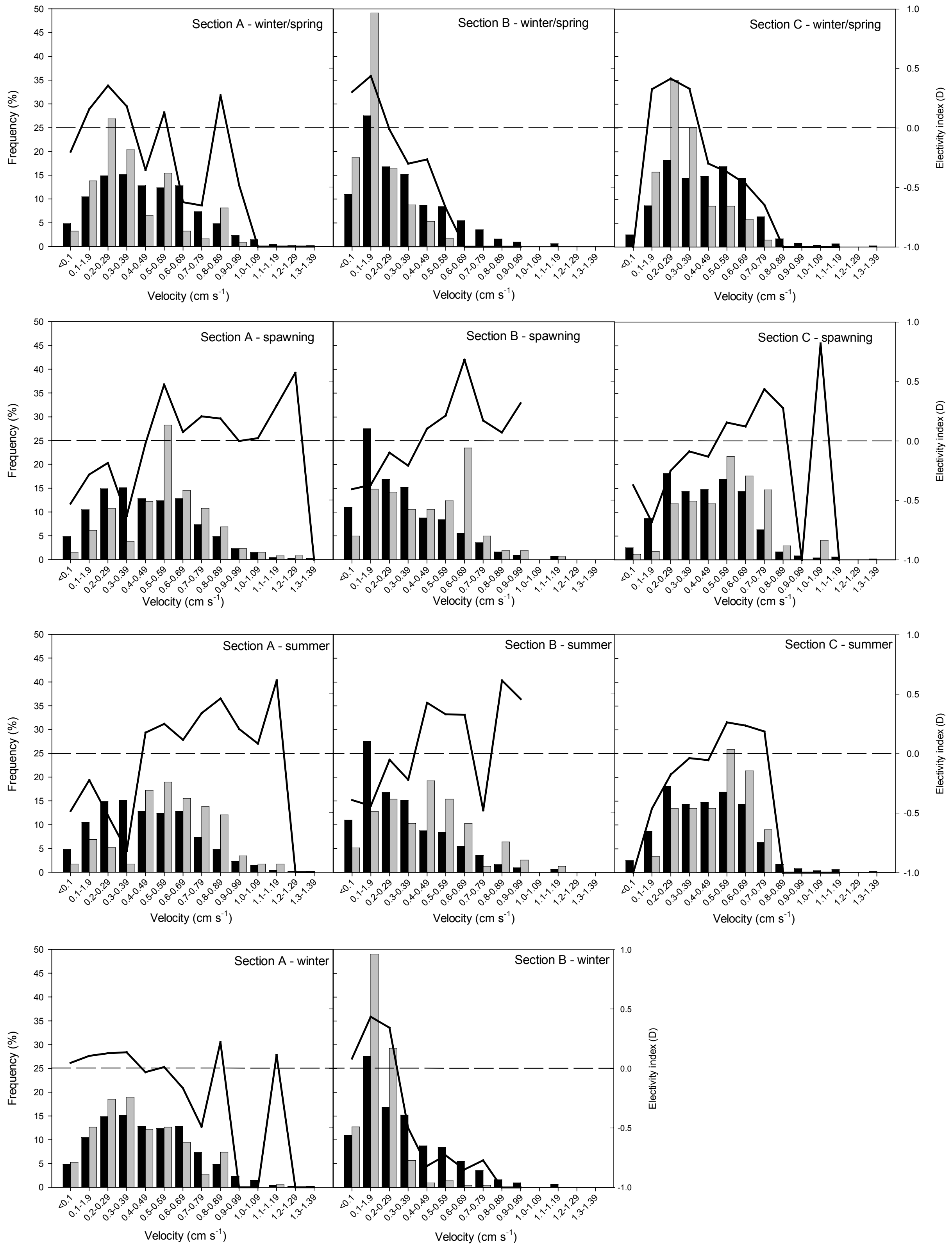

Figure 2.19 Frequency distribution of water velocity used (grey bars) by radio-tracked grayling and those available to them (black bars). —, Jacobs (1974) electivity index for each variable class. Positive values of D indicate preference and negative values avoidance.

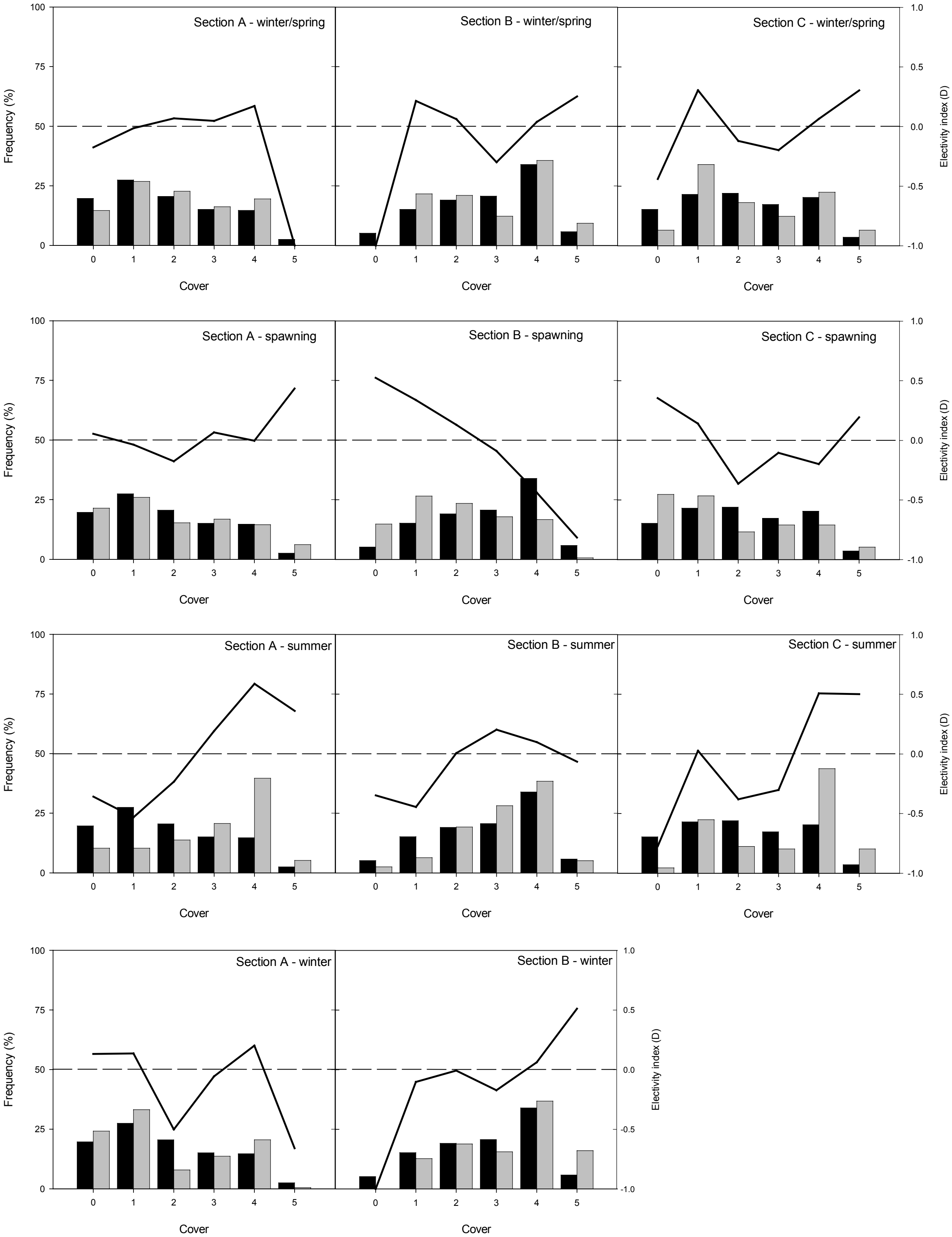

Figure 2.20 Frequency distribution of overhead cover used (grey bars) by radio-tracked grayling and those available to them (black bars). —, Jacobs (1974) electivity index for each variable class. Positive values of D indicate preference and negative values avoidance.

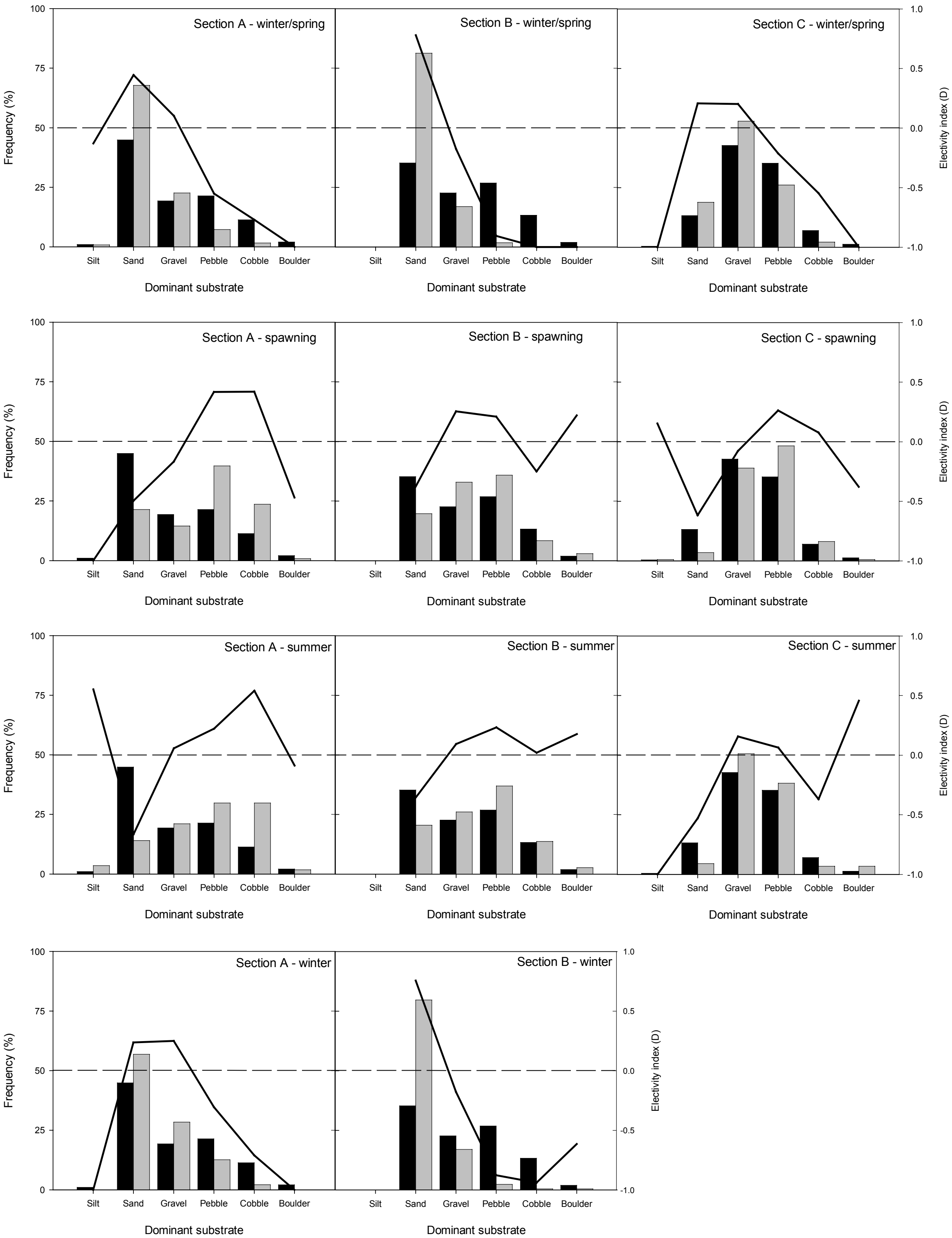

Figure 2.21 Frequency distribution of dominant substrate used (grey bars) by radio-tracked grayling and those available to them (black bars). —, Jacobs (1974) electivity index for each variable class. Positive values of D indicate preference and negative values avoidance.

During the 2004 spawning season, fish from all sections shifted habitat use towards swifter, shallower water, dominated by gravel, pebble and cobble (*Figs 2.18-2.20*). Such conditions are characteristic of the riffles and glides before riffles where grayling were observed to frequent during the spawning season. Grayling remained in similar habitats by summer across the three sections (*Figs 2.18-2.20*). Fish tended to use areas with greater overhead cover more in summer than in winter or the spawning season (*Fig. 2.21*). In autumn to winter 2004 to 2005 for the two sections, A and B, that were studied the patterns of use were similar to those of the earlier winter period, with fish selecting deeper, slower, sandy habitats (*Figs 2.18-2.20*). Again, grayling in section A used a broader selection of velocities and depths than those in section B, despite a similar range of availability, as in early 2004.

PCA showed that the greatest proportion of variance in habitat use was explained by incorporating four variables onto the first two axis loadings, explained 77.7 per cent of variation (*Table 2.4*). The axis loadings are graphically represented in *Fig. 2.22*, as are the means and standard deviations for habitat use for the three river sections and four seasons. These reflect, in a multivariate perspective, the same patterns observed in *Figs 2.18-2.21*, that grayling move from the deeper, slower water used in winter to faster, shallow habitats with stony substrate during the spawning season and summer, but that greater overhead cover is used in summer.

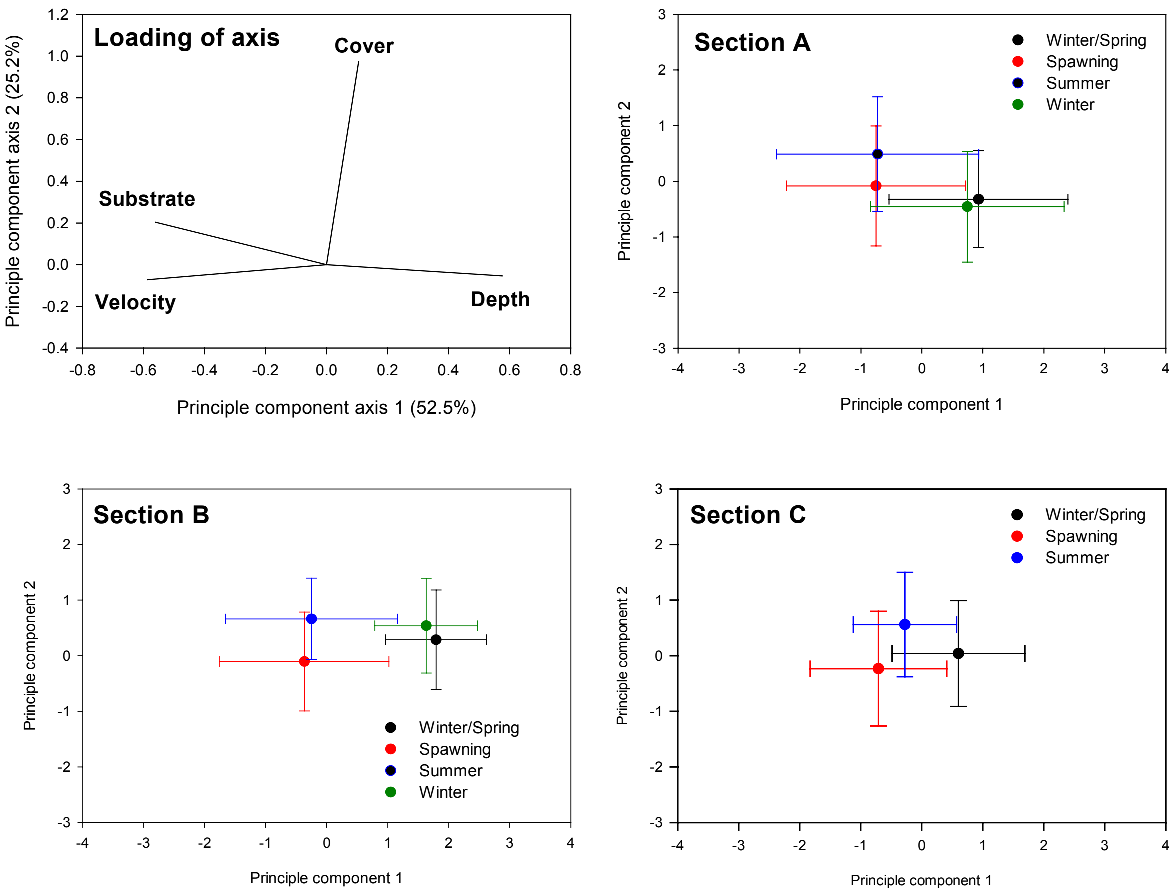

Figure 2.22 Principal component plots (PC1 against PC2) of fish habitat use in the three sections. Mean PC scores with one standard deviation shown for each season. The loadings for all the variables used in the analysis are also shown.

Table 2.4 Principal component loadings for four microhabitat variables produced by principal component analysis.

Variable	*Principal component 1*	*Principal component 2*
Percentage of variance explained	52.6	25.2
Eigenvalue	2.103	1.010
Depth	0.575	-0.054
Velocity	-0.587	-0.072
Cover	0.105	0.975
Dominant substrate	-0.560	0.203

2.4.3. Densities of large, piscivorous birds on the Rye

During radio-tracking surveys, numbers of large piscivorous birds were recorded in relation to the distance walked along the section on the first occasion during daylight. Substantial densities of fish-eating birds were present along the reach (*Table 2.5*), but cormorants were much more abundant on section A, characterised by a wider, more open river habitat (*Fig. 2.23*). Goosander were similarly abundant across all sections and heron were least abundant on section A, with its steep banks. Cormorant and goosander (*Figs 2.24, 2.25*, *Table 2.6*) densities declined sharply in spring and were at their highest in winter for cormorant and early spring for goosander. Heron densities showed more temporal stability (*Fig. 2.26*, *Table 2.6*).

There was a significant difference between the densities of cormorants over the three sections (Kruskall–Wallis, $P < 0.001$). The density of cormorants was significantly greater in section A compared with sections B and C (Mann–Whitney, both $P < 0.001$). There was no significant difference between the densities in sections B and C (Mann–Whitney, $P > 0.05$). There was no significant difference between densities of goosander recorded in the three sections (Kruskall–Wallis, $P > 0.05$). There was a significant difference between the densities of herons over the three sections (Kruskall–Wallis, $P = 0.008$). The density of herons was significantly greater in sections B and C compared with section A (Mann–Whitney, both $P < 0.001$). There was no significant difference between the densities in sections B and C (Mann–Whitney, $P > 0.05$).

Table 2.5 Variations in distances surveyed and fish-eating bird densities, given as mean (standard error), on the Rye between January 2004 and January 2005 (no data for part of summer and autumn 2004).

	n	*Mean distance surveyed (km)*	*Cormorant (no. km^{-1})*	*Goosander (no. km^{-1})*	*Heron (no. km^{-1})*
Section A	79	2.16 (0.57)	0.58 (0.71)	0.83 (0.80)	0.09 (0.20)
Section B	75	1.87 (0.57)	0.06 (0.22)	0.81 (0.76)	0.24 (0.43)
Section C	48	2.40 (0.59)	0.04 (0.14)	1.10 (0.76)	0.30 (0.30)

Table 2.6 Seasonal changes in fish-eating bird densities on the Rye, given as median (0.25 quartile, 0.75 quartile).

		Winter	*Spawning*	*Summer*
	Cormorant	0.92 (0.1, 1.18)	0.23 (0, 0.5)	0 (0, 0)
Section A	Goosander	1.56 (0.51, 1.57)	1.5 (0.63, 2)	0 (0, 0.5)
	Heron	0 (0, 0)	0 (0, 0)	0 (0, 0.5)
	Cormorant	0 (0, 0)	0 (0, 0)	0 (0, 0)
Section B	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)
	Cormorant	0 (0, 0)	0 (0, 0)	0 (0, 0)
Section C	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)

Records of scars larger than 1 cm^2 on grayling and brown trout captured from the three river sections during the course of the study (Durham electric fishing surveys, Environment Agency electric fishing, rod and line) showed a higher proportion of fish that carried recent (typically including open scars and/or recent scale loss without regrowth) and healed scars (with scale regeneration) in section A than in section B or C (*Table 2.7*). Field recording of scar shape and size was not sufficiently precise to determine the cause of such marks. However, they varied from surface scale loss in different areas of the flanks and caudal peduncle, to scale loss associated with a puncture mark or circular lesion on the flank(s), apparent bite marks in the dorsal region and narrow parallel marks, especially on trout.

Table 2.7 Incidence of scarring in grayling and brown trout larger than 150 mm fork length (FL) sampled in sections A, B and C of the Ness during the periods December 2003 to March 2004 and October to November 2004. Scars are classified as absent, healed or recent (these fish may also have had old, healed scars).

		Section A	*Section B*	*Section C*
	No. sampled	58	60	65
Grayling	Scars absent	24 (41.4%)	39 (65.0%)	45 (69.2%)
	Healed scars	27 (46.5%)	19 (31.7%)	17 (26.2%)
	Recent scars	7 (12.1%)	2 (3.3%)	3 (4.6%)
	No. sampled	85	147	167
Brown trout	Scars absent	43 (50.6%)	94 (63.9%)	133 (79.6%)
	Healed scars	36 (42.3%)	47 (32.0%)	31 (18.6%)
	Recent scars	6 (7.1%)	9 (6.1%)	3 (1.8%)

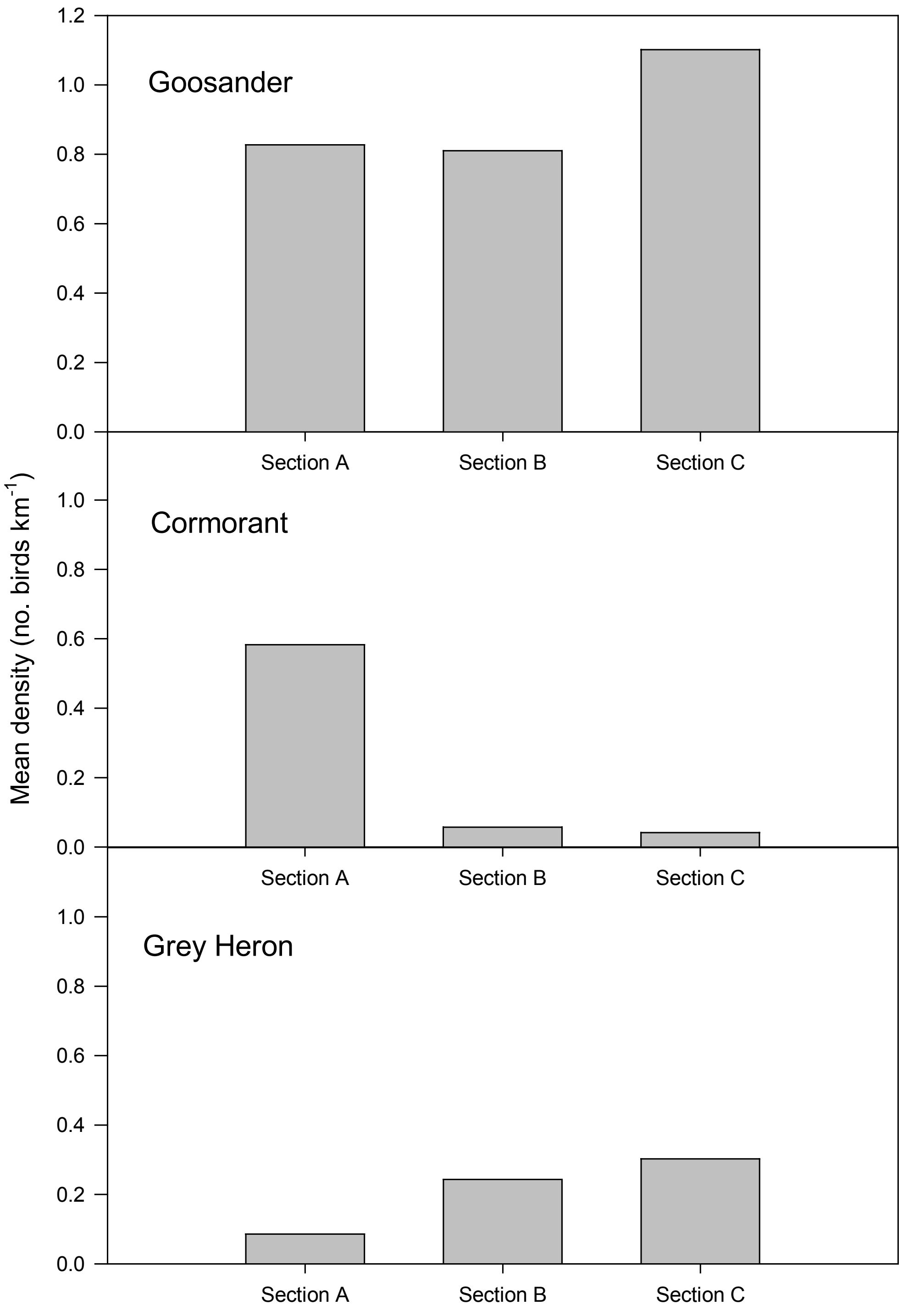

Figure 2.23 Mean densities of large, piscivorous birds along the three study sections of the Rye, based on all data, January 2004 to January 2005.

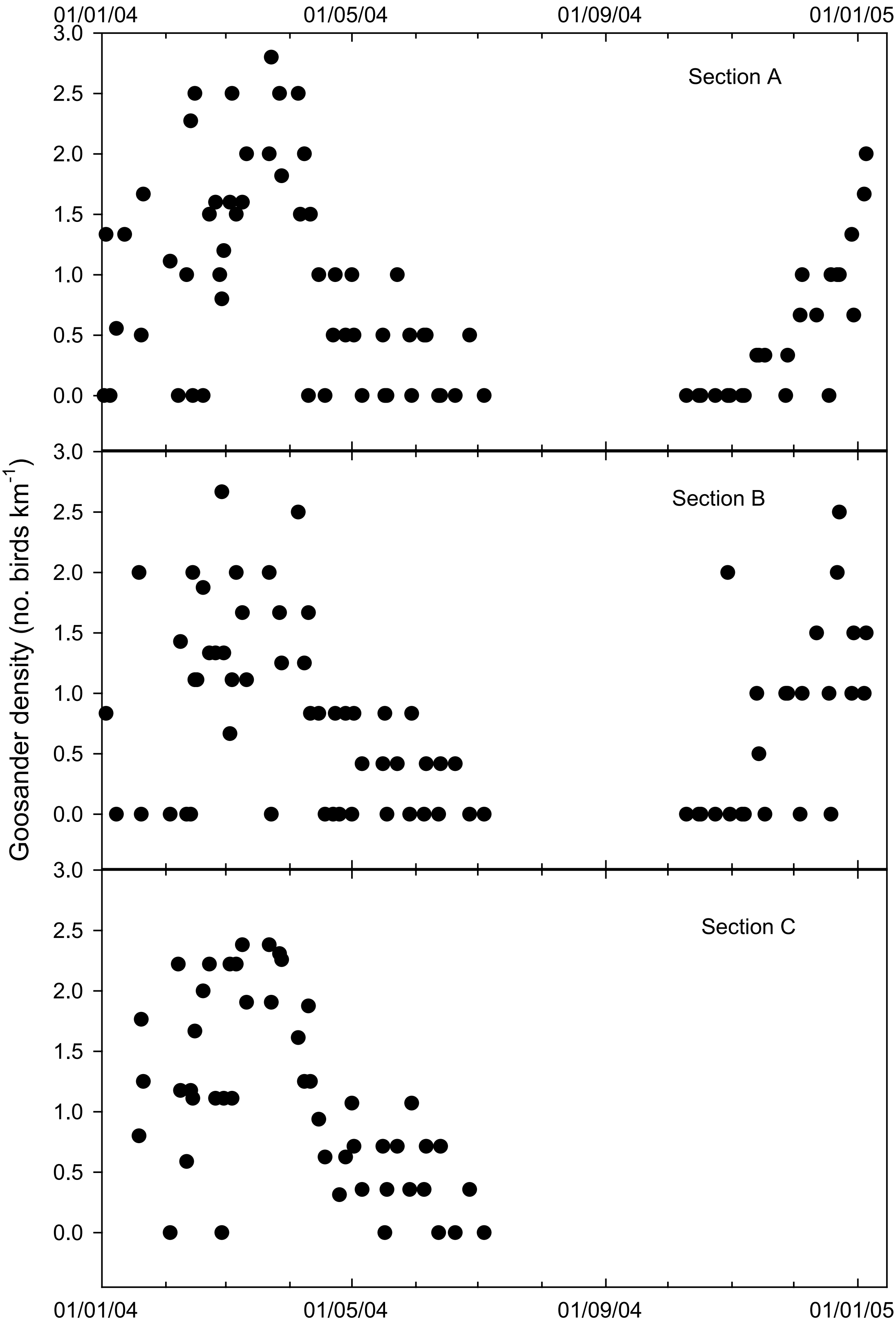

Figure 2.24 Seasonal changes in goosander density along the Rye study sections.

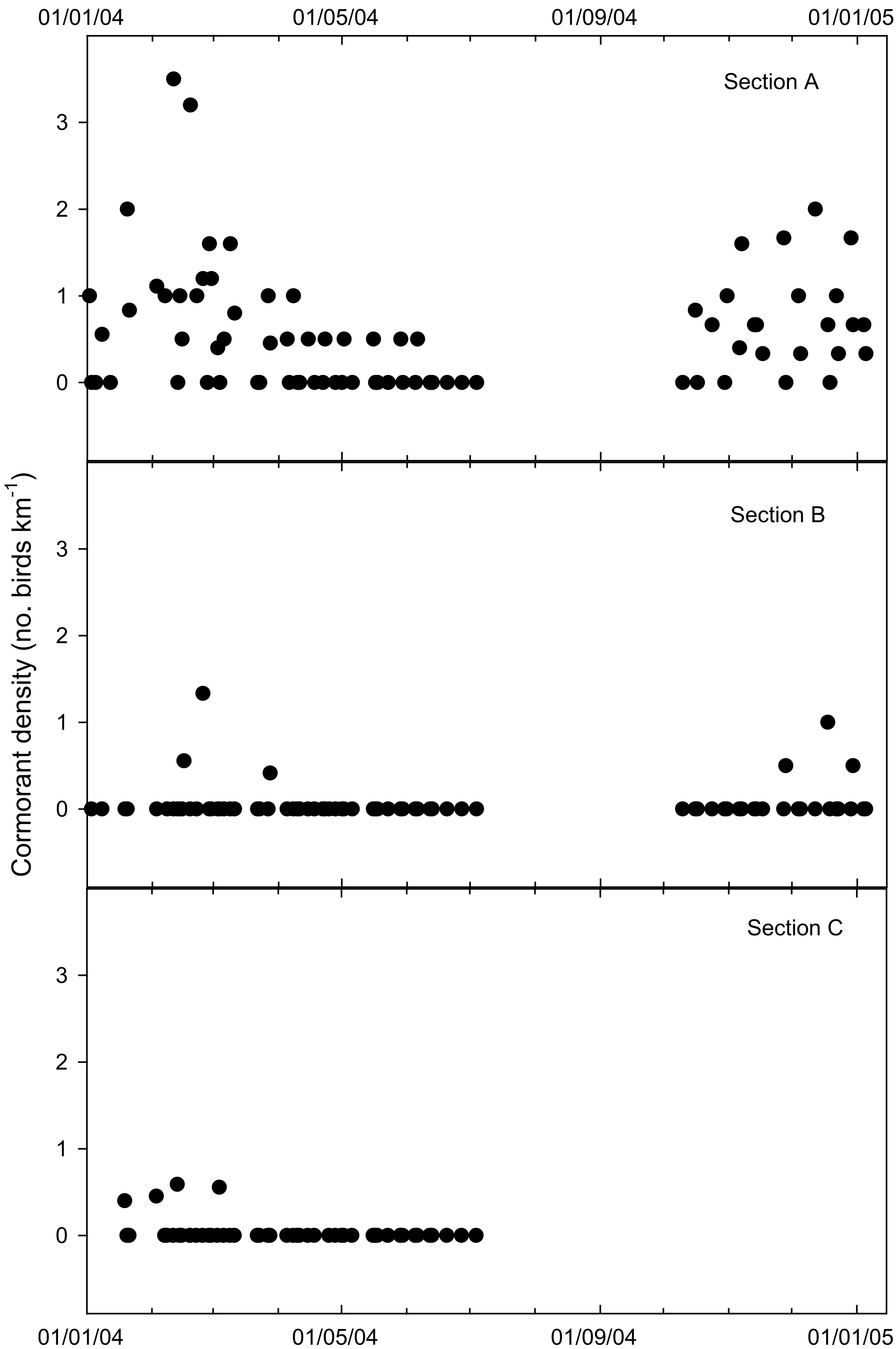

Figure 2.25 Seasonal changes in cormorant density along the Rye study sections.

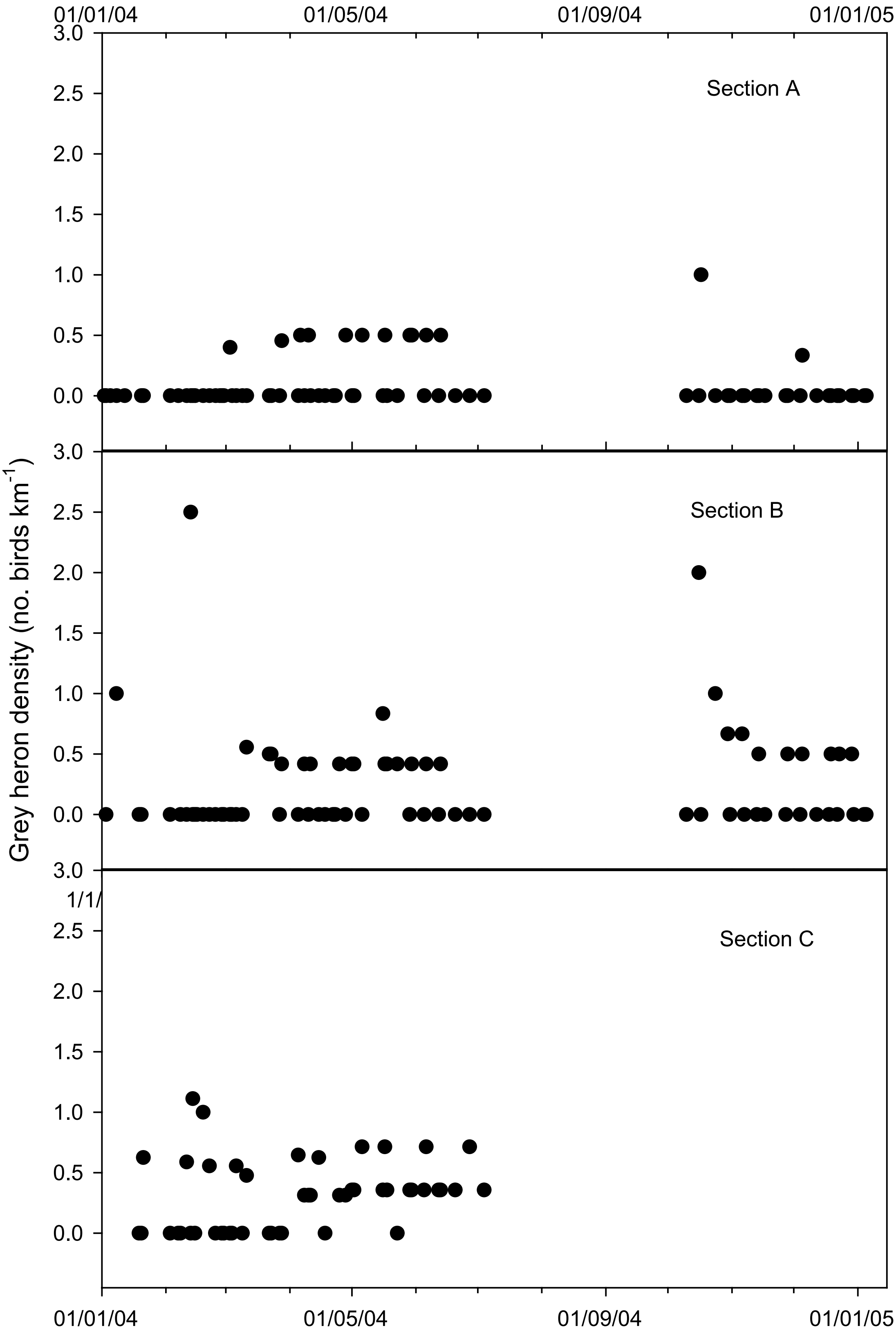

Figure 2.26 Seasonal changes in heron density along the Rye study sections.

2.4.4. Radio-tracking – River Ure

Environmental conditions during tracking were characterised by mild weather at tagging, followed by a very cold period when water temperatures fell to 2°C and flows were low (*Fig. 2.27*). During this period grayling moved slowly downstream and a substantial number were found in the deep slow-flowing section (Y), where signals were very weak. In the following weeks several fish were lost, some only a very short period after they had previously been located. Of those fish that continued to be tracked, as the water warmed and photoperiod increased, several moved back upstream and three tagged fish were observed on spawning grounds or spawning in April 2004 (B. Morland, personal communication; M. Lucas and R. Cove, personal observation). After this, tracking ceased because of the small number of fish still locatable and other research commitments of B. and S. Morland. Total linear ranges over the study period varied between about 0.4 km and nearly 1.6 km (*Fig. 2.28*).

Fig. 2.29 summarises the individual tracks for the River Ure fish, with approximate physical habitat types superimposed on the track maps. The first panel briefly describes the habitat in each section, but more detail is given in the methods. The locations of these habitat sections are given also on *Fig. 2.30*, together with a map that shows all locations of all fishes (*Fig. 2.31*). It is evident that these were grouped into shallow, steady glide and deep, slow glide sections, except for a few points close to riffle areas that were associated with fish immediately before and during the spawning period.

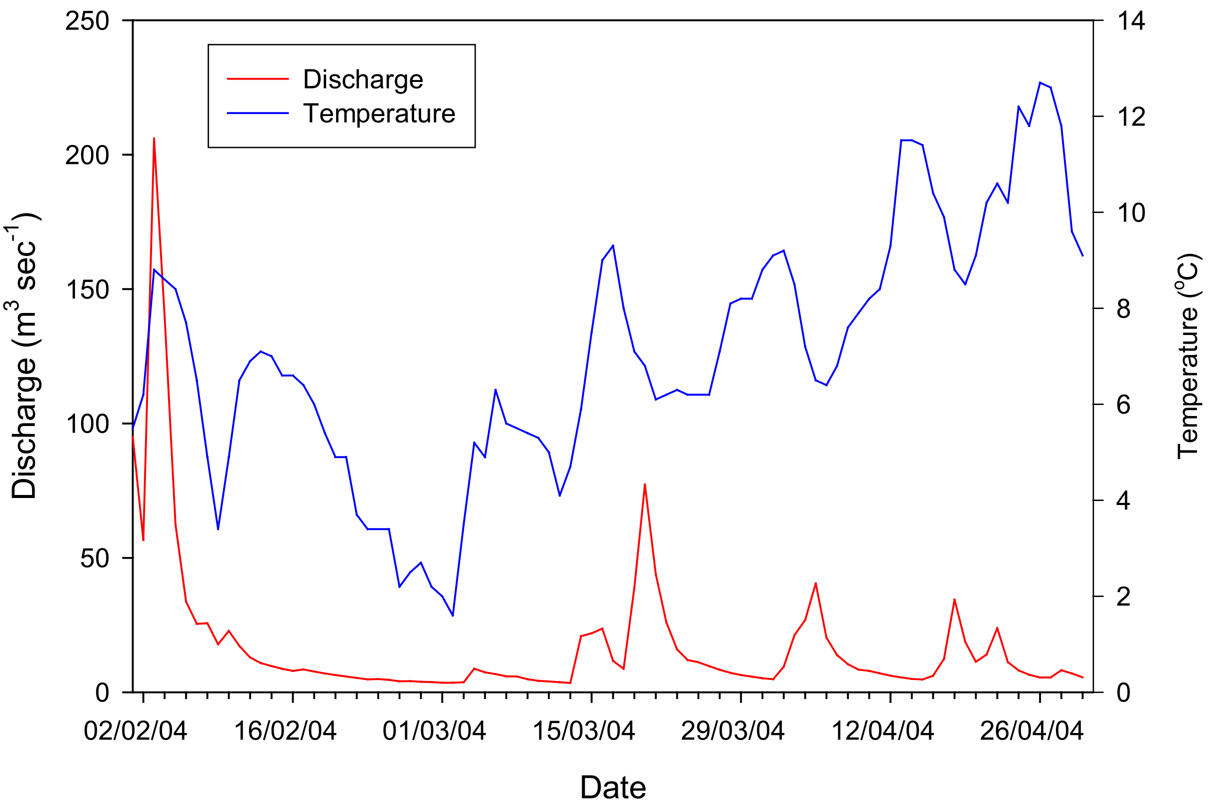

Figure 2.27 Discharge and water temperature on the Ure during the tracking period.

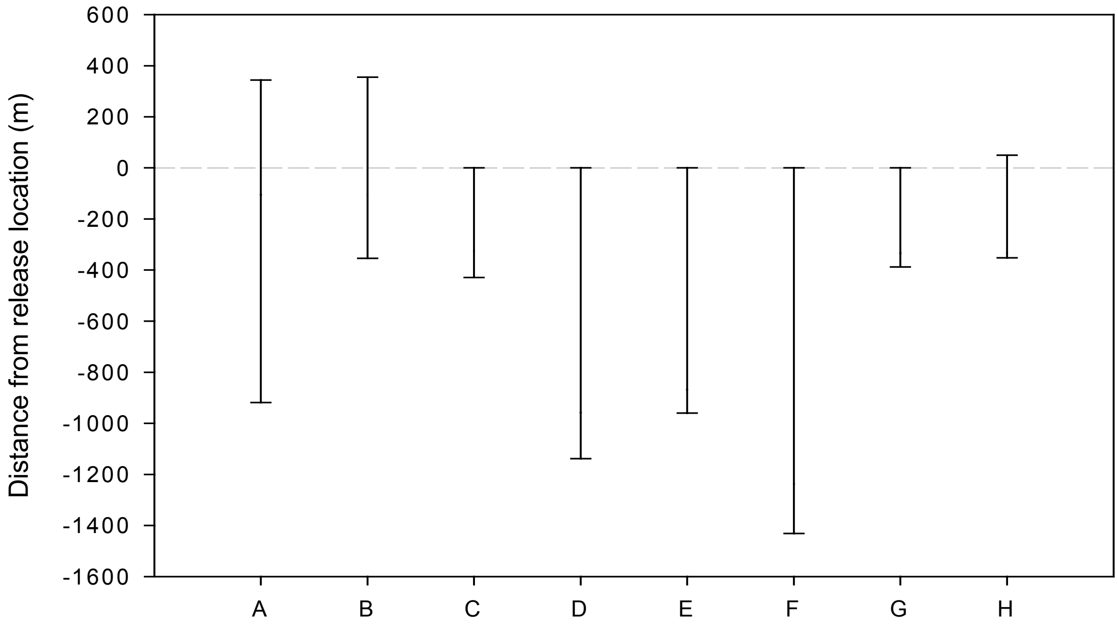

Figure 2.28 Total linear range of River Ure radio-tracked grayling. Zero represents the point of capture and release.

2.5. Discussion

2.5.1. Grayling behaviour and habitat use on the Rivers Rye and Ure

On the Rye in winter conditions radio-tracked grayling tended to show characteristic home-range use within a limited area of slow glide and pool habitat broadly similar to that found by Nykänen *et al.* (2004a, 2004b) for radio-tracked adult grayling. The fish in both studies were of similar size, but those of Nykänen were tracked in sub-Arctic conditions and spent winter under ice cover in distinct pool areas. Nykänen's fish displayed extremely clear step-change habitat use patterns that involved migration downstream from riffles in late summer to slow, deep glides and pools in autumn to other pools at the beginning of winter where numerous fish congregated. The mean linear range of locations in Nykänen's (2004b) study in winter was 63 m, about one-third of the median linear range for grayling from sections B and C in the current study, but approximately 25 times lower than the values from section A. The extremely low winter temperatures in northern Finland in Nykänen's study mean that very small home ranges and low daily movements are not unexpected, although summer and autumn ranges for radio-tracked adult grayling were small also. It therefore seems that the patterns of space use observed in sections B and C between January and March 2004 and in section B between October 2004 and January 2005 are quite typical of grayling behaviour. By contrast, the extremely wide-ranging behaviour of fish from section A, replicated in two winter seasons on two different samples of grayling, suggests strongly that their spatial behaviour was unusual.

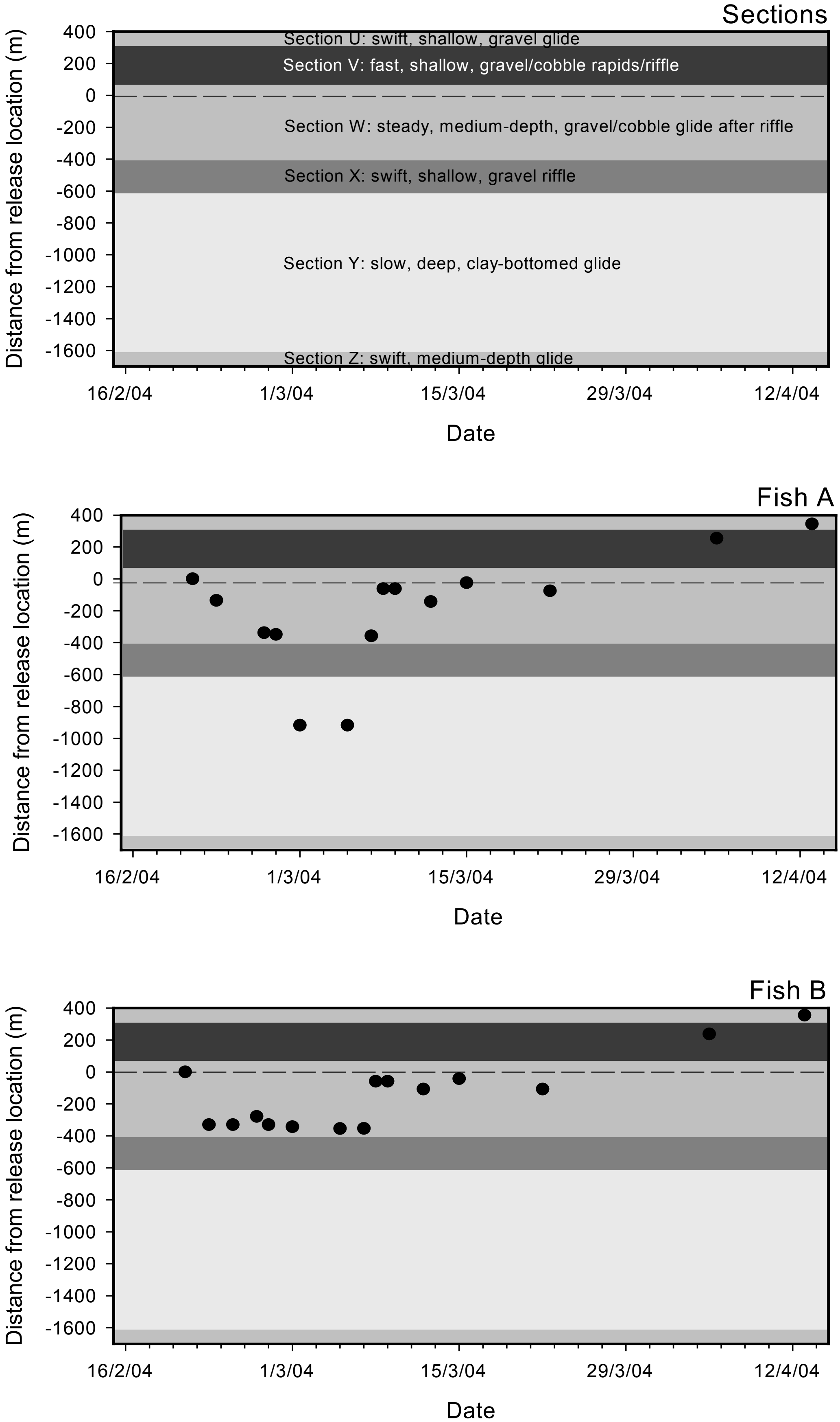

Figure 2.29 Individual track maps of grayling radio-tracked in the River Ure, 2004.

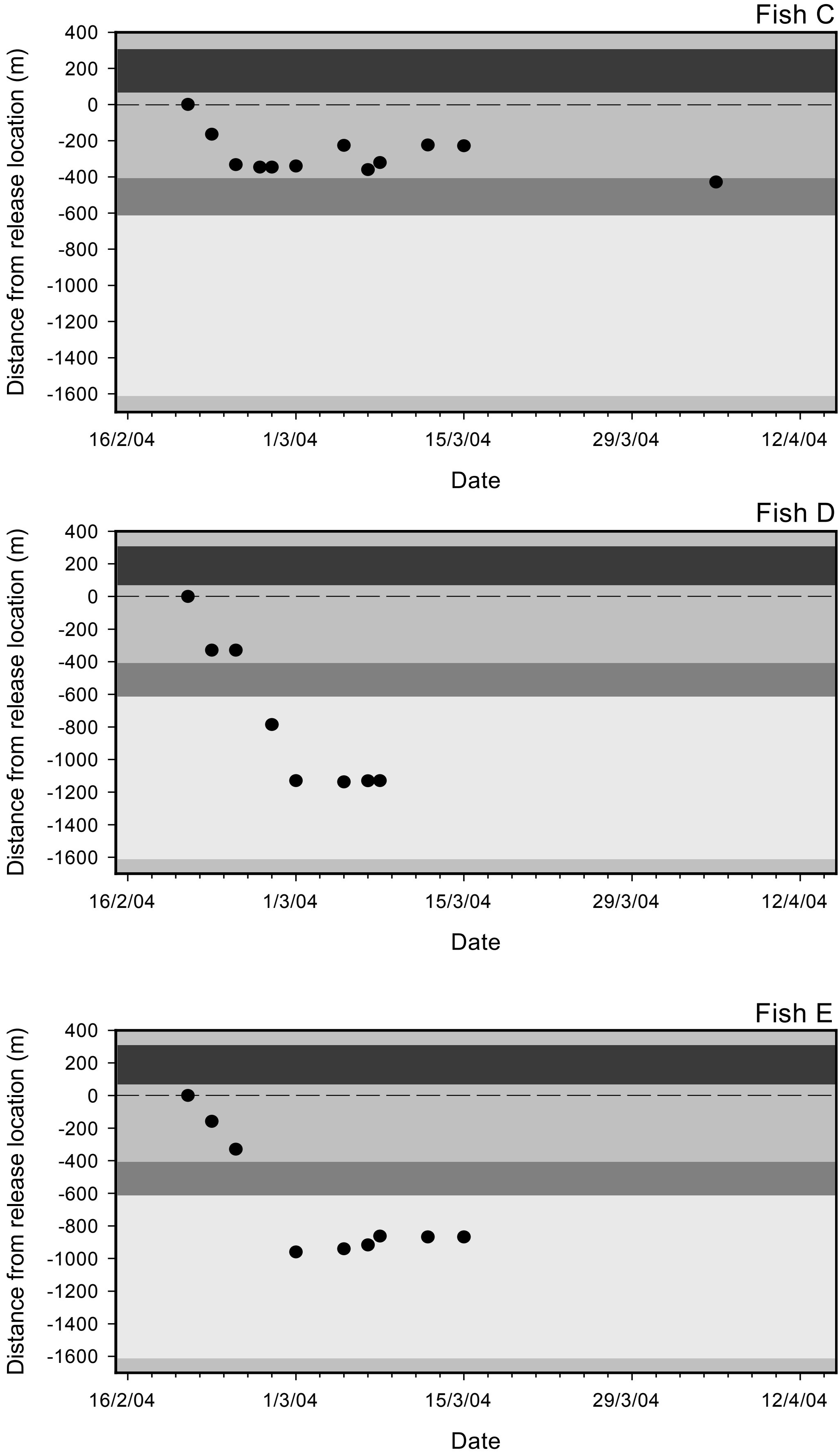

Figure 2.29 Continued

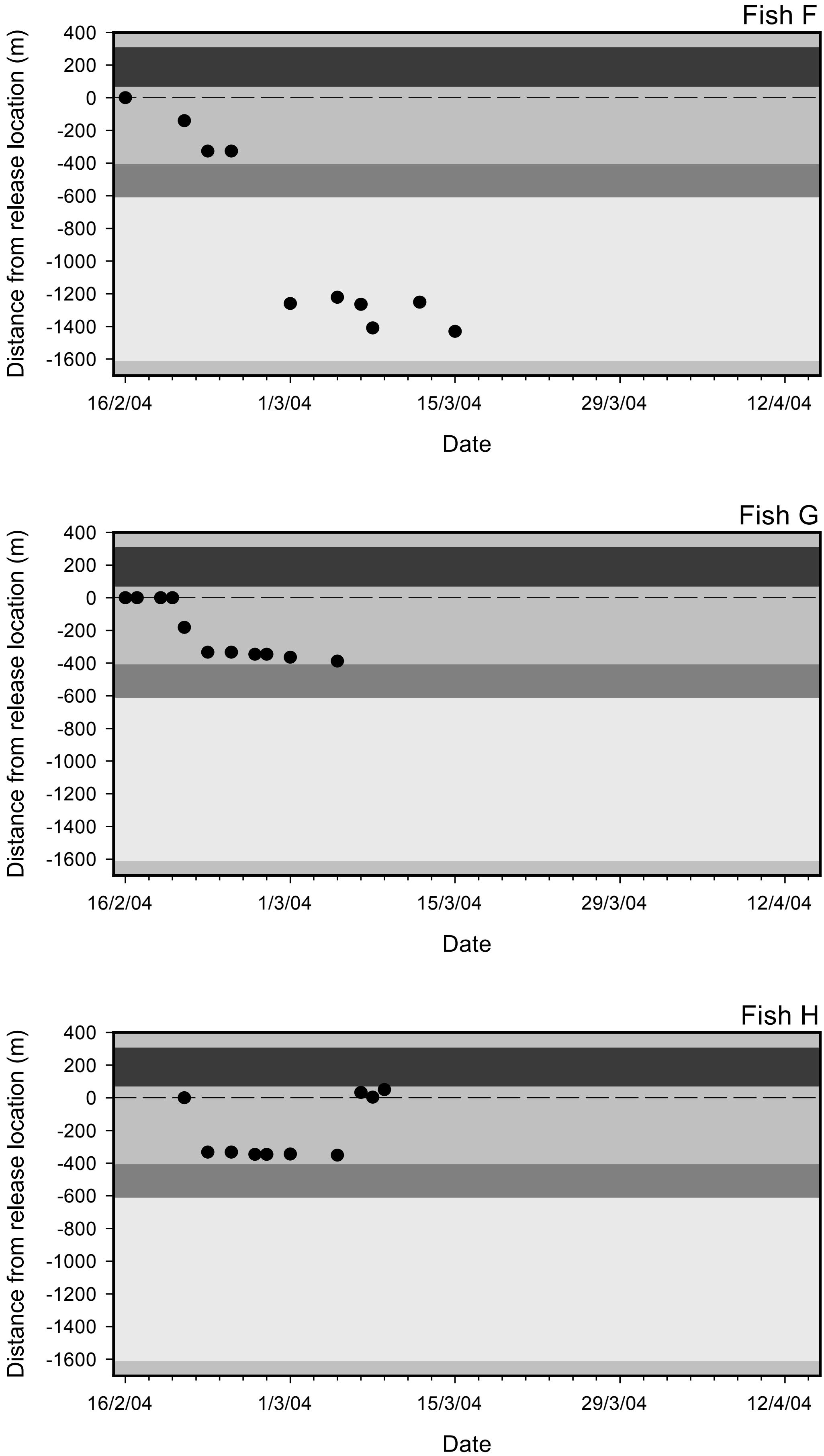

Figure 2.29 Continued.

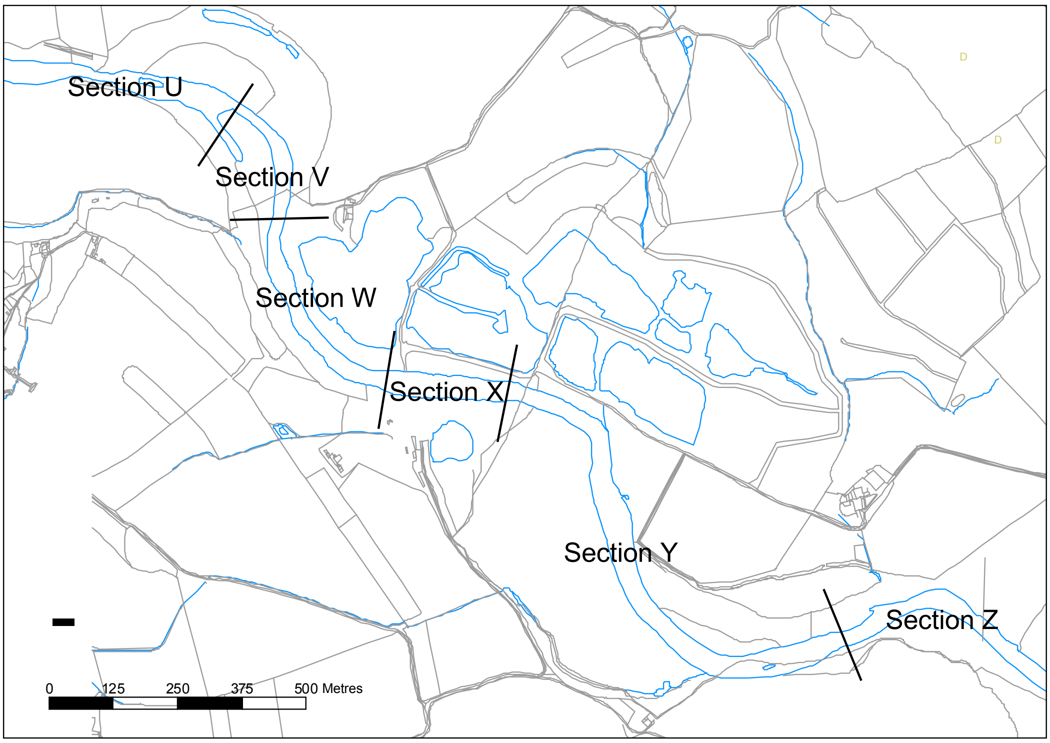

Figure 2.30 Division of Ure study section into physical habitats used by fish (see Section 2.3).

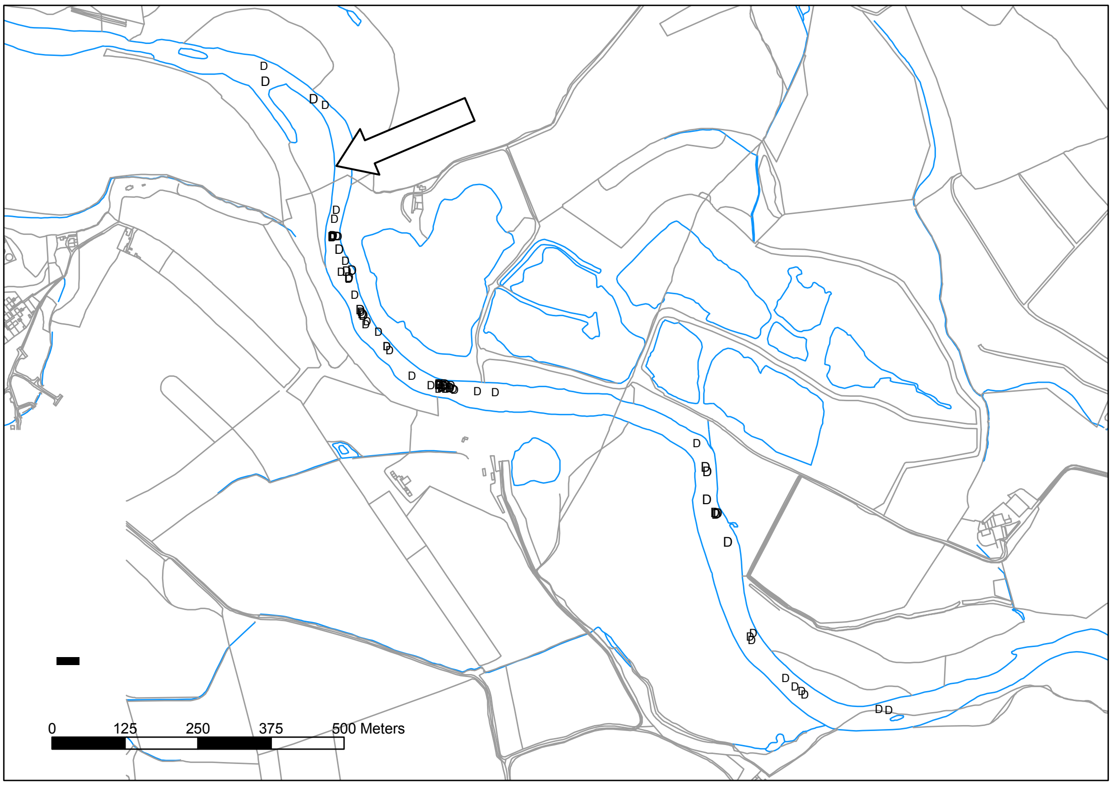

Figure 2.31 All recorded locations of radio-tagged grayling on the River Ure. Arrow denotes capture and release location.

In early to mid-March, a high proportion of grayling being radio-tracked started to move upstream into shallower, faster water with more gravel, pebble and cobble; this behaviour was apparent across all groups from the three sections. Not all fish moved upstream and some fish spawned close to where they overwintered, but the greatest distances moved during the tracking period mostly occurred immediately before and after the period during which courtship and spawning was observed. Fish moved between 0.2 and 3.5 km during the course of the study, but most upstream movements to spawning sites were less than 1.5 km and generally greatest in section A, where the largest amount of spawning habitat was situated in the upper kilometre of the river section. These distances of spawning migration are smaller than those recorded in much of the literature, but broadly similar to those of rivers in the Belgian Ardenne, Germany and Finland (Parkinson *et al.,* 1999; Meyer, 2001; Ovidio and Philippart, 2002; Ovidio *et al*., 2004; Nykänen *et al.,* 2004a). It is likely that the local availability of suitable spawning areas negated the need for distant migration in the current study. Patterns of habitat use during the spawning season, for all sections, were very similar to those reported elsewhere (Fabricius and Gustafson, 1955; Gönczi, 1989; Sempeski and Gaudin, 1995a; Nykänen and Huusko, 2002).

Following spawning, Rye grayling tended to remain in the spawning area or moved downstream, in some cases homing to areas they had been present in early in March, but generally they used swiftly flowing habitat of shallow-to-medium depth, often with substantial overhead cover. This pattern was shown by grayling from all sections. They adopted restricted home ranges and there were no apparent differences in the size of these between sections, although the sample size was smaller because by June approximately half of the tags had stopped functioning or been lost. The pattern of summer habitat use was quite similar to that reported in other studies, although there has been substantial variety in habitat used between different studies in different locations, which may be attributable to local differences in habitat, competition, predation and human interference, including angling. For example, Nykänen *et al*. (2001, 2004a, 2004b) and Greenberg *et al*. (1996) found that adult grayling select boulder areas in summer, but Nykänen *et al*. (2001, 2004a, 2004b) and Mallet *et al*. (2000) found them to prefer velocities greater than 40 cm s^{-1}, while Greenberg *et al*. (1996) found they selected velocities of less than 10 cm s^{-1}. Mallet *et al*. (2000) found adult grayling preferred sand and gravel habitat in summer.

The patterns of movement and habitat use shown by grayling in the River Ure were somewhat similar to those on the Rye but did involve greater movement than in Nykänen *et al*. (2004a, 2004b). However, a substantial amount of the movement by Ure grayling was from one glide, downstream through a riffle and into a long, very deep, slow glide and coincided with a very cold period. Several of these fish subsequently moved back upstream into the shallows, as the water warmed and day-length increased. Since the spatial scale of geomorphic units (pools, riffles, etc.) is greater in larger rivers, movement from one habitat unit to another would be expected to involve greater movements and it seems likely that the most conspicuous migrations by grayling will occur in large rivers with widely spaced habitat types.

Precision of depth and velocity measures at high discharges would have been improved by the use of a two-dimensional hydraulic model to predict these values, but to provide the measurements for meshing such a model and to run it over the very substantial lengths of river under study would have been vastly beyond the time and budget constraints of this project.

Six grayling out of 32 tracked in sections with a weir bounding the upper limit visited the upstream weir locality on at least one occasion during the track period, all but one visit occurring during the spawning season. None of these fish successfully negotiated the weirs and it is likely that they would have moved further upstream had they had the opportunity to do so. Where weirs or other obstructions cause delays in upstream migration to preferred spawning habitat for Arctic grayling, there is evidence they may use less suitable spawning habitat or fail to spawn if none is available (Fleming and Reynolds, 1991). Moreover, delays in accessing spawning grounds and spawning may reduce the viability of eggs, since delays in egg release after ovulation in other salmonids have been shown to be associated with reduced hatching rates and increased rates of abnormality (Sakai *et al*., 1975). However, ample spawning habitat appears to have been available for the grayling in this study. For grayling populations for which most spawning habitat is upstream of weirs or other river obstructions, prevention or delay of migration could have damaging consequences for the viability of existing populations or the colonisation–recolonisation of habitat upstream.

2.5.2. Reasons for differences in winter behaviour of grayling in section A of the River Rye

It has been established that the behaviour of grayling during spring and summer in section A of the Rye followed that of grayling in sections B and C and in a variety of published studies. Behaviour of grayling in sections B and C during winter was also similar to that in published studies. However, grayling in section A, associated with relatively little bank cover and steep banks in all but the upstream 500 m, showed very excursive behaviour in each of two winter seasons, for two different groups of fish. One possible explanation for this behaviour might be the drive to search out widely spaced alternative habitats as environmental conditions, especially discharge, changed. However, the preferred winter habitats across the three sections were sandy bottomed, deeper, slower water, which were relatively abundant in section A, so this seems unlikely. Furthermore, greater excursive behaviour, with total linear ranges an order of magnitude greater than those in sections B and C, was apparent in section A during periods of relatively stable discharge during November and December 2004, as well as during more variable discharge conditions between January and early March 2004. Additionally, during the two winter seasons, fish in section A exhibited a somewhat wider range of habitat use during their wider ranging than did fish in sections B or C. Thus, although varying environmental conditions might have a role to play in the wider space use of grayling in section B, it is unlikely to be the main reason.

The factor most likely to have caused the excursive behaviour of grayling from section A is predator avoidance, since avian predators, especially cormorants, were abundant on this section during the winter months, most leaving the river around March to April. The wider, more open and deeper nature of section A of the River

Rye would appear to suit cormorant, since the relative abundance in winter was much greater than that in section B or C, whereas there was no significant difference in the relative abundance of goosander between the sections. The relative occurrence of healed and recent scars on grayling and brown trout was greater on section A than on the upstream sections, although some caution must be given to the trout data as they will include some hatchery-reared fish.

The nature of at least some healed or recent scars possessed by grayling in section A were consistent with those of unsuccessful predation attempts by birds, including cormorant, on the basis of the images provided by Carss (1988). No injuries were observed that had the characteristic, broad ‘U’-shaped injury across the flanks associated with the grasping of prey by pike (M. Lucas, personal observation). Indeed, pike were very rare throughout the study stretch – none were caught or seen in any of the electric fishing surveys, radio-tracking sessions or habitat surveys (together representing many hundreds of hours in the river channel or on its banks). Although it is often possible to identify, with reasonable certainty, the identity of large avian predators that have caused damage to fishes (Carss, 1988), this was not possible in most cases in this study, partly because photographs were not taken of injured fish and only limited descriptions of damage were recorded in the field. It is possible that some injuries to grayling were sustained from attacks by otter *Lutra lutra* or mink *Mustela vison*, since these mustelids do occur along the river and may prey on grayling (Kozena *et al*., 1992). Spraints of both species were found on the river banks, as well as several partly eaten fish (M. Lucas, personal observation). Scars may also have originated from spawning activities or from angler damage, although anglers on this stretch of river take great care to release fish unharmed.

Goosander, heron and cormorant are all known to include grayling in their diet where this species is common. In the case of goosander, moderate levels of predation on grayling were recorded in the River Tweed (where grayling are quite abundant), mostly in the winter months (Marquiss *et al*., 1998). Goosander rarely take trout longer than 300 mm (Marquiss *et al*., 1998), a figure that is also probably applicable to grayling, which are similar in body shape. However, several fish tracked in this study were smaller than 300 mm long and the sudden disappearance of one fish on the River Ure was associated with intense foraging by a flock of goosander in the immediate vicinity of the tagged fish. Where cormorant forage in waters in which grayling are abundant, this species comprises a substantial portion of its diet (McIntosh, 1978; Suter, 1995, 1997; Keller, 1998; Marquiss *et al*., 1998; Staub *et al*., 1998). Marquiss *et al.* (1998) have also recorded grayling that exceeded 400 mm length in stomachs of cormorant shot on the River Tweed. Some evidence suggests that heavy predation by cormorant on Swiss grayling and trout stocks may have played a role in declines of yield, although interpretation of the data has been debated strongly (Suter, 1995, 1998; Staub *et al*., 1998). Heron are also recorded as predators of grayling in some circumstances (Uiblein *et al*., 2001), although grayling do not appear to be an important component of their diet under most conditions.

Although the Swiss studies have not conclusively demonstrated an impact on populations of grayling in rivers there, it is highly likely that cormorant foraging could cause changes in grayling behaviour such as increased movement that could be associated with increased net energy expenditure and perhaps increased stress.

However, the current study primarily underlines the plasticity in behaviour of sub-populations of fishes that may occur in relation to a variable environment.

3. Behaviour and passage of grayling at potential obstructions

One of the aims of this study was to examine the ability and willingness of grayling to pass potential natural and/or artificial barriers. This was partially examined using radio-telemetry on the River Rye, but using this technique sample sizes are inevitably low, data are only available for large fish and are collected only when fish choose to visit the vicinity of the weir. One solution to this is to tag more fish with remotely identifiable tags and use passive integrated transponder (PIT) telemetry to determine successful passage, relative to approaches to the obstruction. It was intended to carry this out at Ness gauging weir on the Rye, but the width and depth of the river meant this was not feasible, so alternatives were sought on tributaries of the Rye.

3.1. Study rationale

One of the difficulties in assessing behaviour of fish below potential river channel obstructions is to determine whether a lack of passage reflects a physiological inability to traverse the obstruction or a lack of motivation to pass, perhaps because habitat is suitable below the obstruction. A wide range of studies have demonstrated that many stream-dwelling salmonids, including European grayling and Arctic grayling, exhibit strong homing behaviour to formerly used areas (Stuart, 1957; Gerking, 1959; Kristiansen and Døving, 1996; Buzby and Deegan, 2000; Ovidio *et al.,* 2004). During the feeding and growth season, many stream-dwelling salmonids utilise clear home ranges, to which they exhibit strong affinity when they are displaced (Gerking, 1959; Saunders and Gee, 1964; Armstrong and Herbert, 1997). Deliberate translocation over short-to-moderate distances (tens to hundreds of metres or more) from the capture site typically results in a relatively rapid return (homing) to the home area, provided that the route is not obstructed, as has been demonstrated for grayling (Woolland, 1972). The mechanisms of such homing responses in rivers are not fully understood, but are known to include local chemical and flow directional cues, as well as spatial mapping by reference to landmarks (Lucas and Baras, 2001).

The basis of the experimental design used in this study was to employ translocation of grayling away from their home site, with the assumption that motivational drive to return to that home site would be strong, since home site fidelity has been reported for grayling species (Kristiansen and Døving, 1996; Buzby and Deegan, 2000; Ovidio *et al.,* 2004). Grayling translocated from downstream to upstream of a potential barrier would be expected to have lesser physical difficulties in returning to their original site than those translocated from upstream to downstream of the barrier, although cues available for homing would also be expected to differ. Reciprocal translocation would tend to ensure that original stock densities were not altered substantially. One would also predict that the proportion of fish that pass successfully upstream towards home sites should reduce with increasing barrier height (where alternative routes such as fishways are unavailable), but that for fish passing downstream, barrier height (for relatively small barriers, unlikely to cause physical damage to fish) would have a lesser effect. Ideally, the experimental design would incorporate control groups of fish released at their site of capture also.

3.2. Study sites

The movement and homing behaviour of grayling was studied at two flow gauging weirs, one on Costa Beck and one on the River Dove. Both are small tributaries of the River Rye in North Yorkshire.

3.2.1. Costa Beck

Costa Beck is a small, predominantly spring-fed river and therefore maintains a relatively stable flow. The beck originates at Keld Head spring, approximately 1 km upstream of the gauging weir. Although two main channels, Costa Beck and Oxfolds Beck, diverge from Keld Head, almost all flow is carried along Oxfolds Beck, which rejoins Costa Beck at Low Costa Mill, approximately 100 m upstream of the gauging weir (*Fig. 3.1*). Within the study reach upstream and downstream of Costa gauging weir, the channel width is typically between 5 and 8 m. The study reach receives shade from deciduous trees and bushes scattered along one or both sides. Downstream of the weir the river is highly channellised and ranges between 0.8 and 2 m deep, occurring in an alternation of glides and deep mechanically engineered silt traps. Upstream of the weir, Costa Beck and then Oxfolds Beck are shallower, with riffles interspersed with glides and the substrate comprises mainly gravel with smaller areas of cobble, sand and silt. Downstream of the weir gravel and sand occur in the shallower areas, with bankside rocks at the upstream limits of the silt traps, characterised by embedded gravel, overlaid by silt. Abundant in-stream plant growth was present upstream and especially downstream of the weir, dominated by *R. fluitans*, with lesser amounts of water starwort *Callitriche sp*.

The Costa Beck gauging weir is a 1:2 (upstream slope) 1:5 (downstream slope) Crump weir with a width of approximately 5 m and a downstream facing slope of approximately 2 m in length. Water velocities and depths are relatively even across the face of the weir. Although the drop in height between the upstream and downstream water levels may be approximately 0.3-0.4 m in winter, during summer extensive weed growth, particularly downstream, can result in negligible water height difference. Some weed cutting occurred downstream of the weir just before the study. During the study period flows were relatively stable, and the vertical drop was 0.25 m at the start of the period and declined variably to about 0.10 m by the end, because of weed growth. Water velocities on the weir, at the weir crest and downstream face, were measured at 60 per cent of depth using an impeller-driven digital velocity meter (Ohio model, Great Atlantic Flow Meters). At a summer discharge of 0.45 $m^3 s^{-1}$ (probability of exceedance, 79 per cent) mean ± standard error (SE) velocity and depth at the weir crest were 0.87 ± 0.04 $m s^{-1}$ and 0.11 ± 0.006 m, respectively, 0.5 m downstream of the crest on the face of the weir they were 1.69 ± 0.097 $m s^{-1}$ and 0.083 ± 0.010 m, respectively, and 1.0 m downstream of the crest on the face of the weir they were 1.85 ± 0.090 $m s^{-1}$ and 0.071 ± 0.004 m, respectively.

3.2.2. River Dove

The River Dove is much more strongly influenced by run-off than Costa Beck, although it still receives significant flow from springs. At the study site it is generally wider than Costa Beck, with typical widths of 7-10 m. It is partially shaded by deciduous trees for much of its length. Approximately 500 m upstream of the gauging weir a 1:1 slope, 1.5 m high mill weir across the width of the river precludes upstream access by non-leaping fishes, except during very high flows. Upstream and downstream of the gauging weir riffles (typically 0-0.3 m deep), interspersed with deeper glides and pools (typically 0.5-1.2 m deep), occurred, although downstream of the weir water tended to be deeper and pools over 2 m were present. At the lower limit of the study area, banks tended to be very steep. Substrate varied from sand and silt to cobble with substantial areas of gravel. Small amounts of *R. fluitans*, *Callitriche* sp. and *F. antipyretica* were present throughout the reach.

The River Dove gauging weir at Kirkby Mills is a Flat-V type weir (upstream slope 1:2, downstream slope 1:5) with a width of approximately 6 m and a downstream sloping face of about 4 m dropping into a concrete-based stilling basin. During base flows the vertical drop is approximately 0.45-0.50 m. The fastest flows and greatest water depth occur at the centre of the face of the weir, with distinct side eddies evident below the weir. At a 2004 summer base-level discharge of 0.4 $m^3 s^{-1}$ (probability of exceedance, 75 per cent), mean ± SE velocity and depth at the centre of the weir were, at the weir crest 1.07 ± 0.01 m s^{-1} and 0.17 m, respectively, 0.5 m downstream of the crest in the centre of the face they were 1.93 ± 0.03 m s^{-1} and 0.13 m, respectively, 1.0 m downstream of the crest in the centre of the face they were 2.30 ± 0.01 m s^{-1} and 0.12 m, respectively, and 2.0 m downstream of the crest on the face of the weir they were 2.98 ± 0.02 m s^{-1} and 0.45 m, respectively. Away from the centre of the weir the depth and water velocities measured declined. Water velocities in the tail race declined from a maximum of 2.45 ± 0.08 m s^{-1} at the drop off at the edge of the weir face to 0.477 ± 0.12 m s^{-1} three metres downstream of the edge of the weir. Although velocities were high in the tail race, flows adjacent (<1 m) to the tail race were low (<0.05 m s^{-1}) and fish would be able to approach the downstream edge of the weir in low-velocity water.

3.3. Methods

3.3.1. Fish capture

At both sites pulsed DC electric fishing equipment (Electracatch WFC4) powered by a 0.9 kW generator was used to obtain fish for tagging. A single anode was used and fishing was carried out at 50 pulses per second, with the minimum pulse width that enabled fish to be stunned. While being less efficient, this reduced the risk of damage to fish. Upstream and downstream sections of each study site were fished in separate single passes, without stopnets, by a team of three fieldworkers starting from downstream. Fishing was carried out by wading and equipment was towed in a small boat. Sites deeper than 1 m could not be fished effectively. On capture, those fish to be retained were temporarily placed in buckets of oxygenated water and then transferred to keepnets in the river until tagging was carried out.

Costa Beck
On the Costa Beck a 400 m section up to the weir and a similar distance upstream was electrofished on 23 July 2004 (*Fig. 3.1*). All captured grayling greater than 150 mm fork length were retained for tagging. All other fish were immediately released.

River Dove
Sections approximately 600 m upstream and downstream of Kirkby Mills weir on the Dove were electrofished on 6 August 2004 (*Fig. 3.2*). All grayling greater than 150 mm fork length and a proportion of brown trout longer than 140 mm were retained for tagging.

3.3.2. Tagging

Fish were tagged with 23 mm half duplex (HDX) PIT tags (TIRIS 2000) operating at 134.2 kHz and weighing 0.6 g in air after sedation using 3-aminobenzoic acid ethyl ester methanesulphonate salt (MS 222). The tags were provided sterile in blister packs. A small incision (5 mm) was made with a scalpel on the ventral surface of the fish, lateral to the midline, anterior to the pelvic girdle. Tags were inserted through the incision into the peritoneal cavity, and the incision was then sealed using cyanoacrylate tissue adhesive (Vetbond). Fish were returned to fresh oxygenated water to recover. After recovery, fish were translocated. On the Costa Beck no grayling were captured downstream of the gauging weir and so only those fish captured upstream were translocated downstream (*Fig. 3.1*). On the River Dove, grayling and brown trout were translocated upstream as well as downstream (*Fig. 3.2*). The limited samples of grayling obtained meant that control releases of fish back to the sections of capture were not performed.

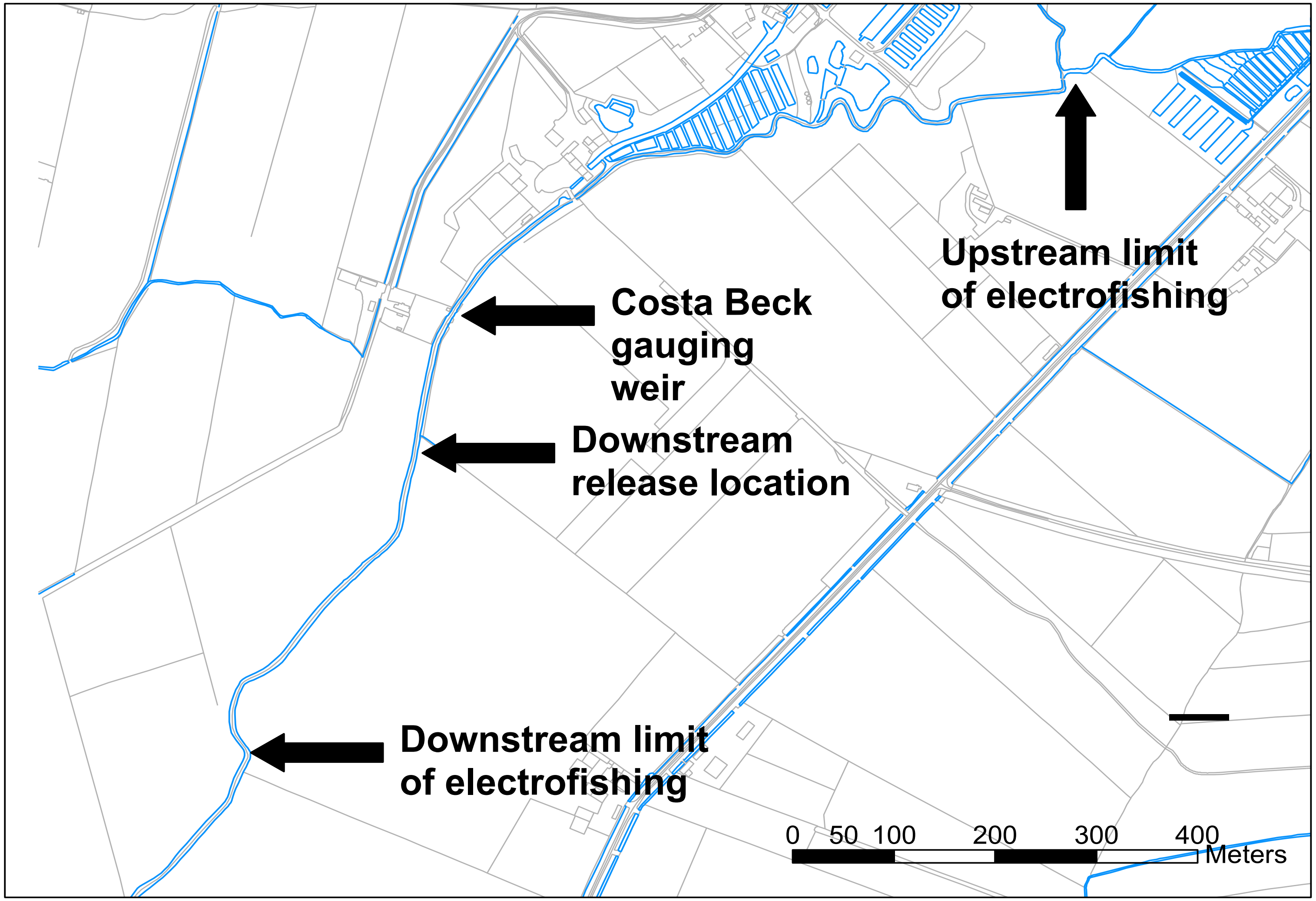

Figure 3.1 Map of Costa Beck study site showing location of weir and sampling reaches.

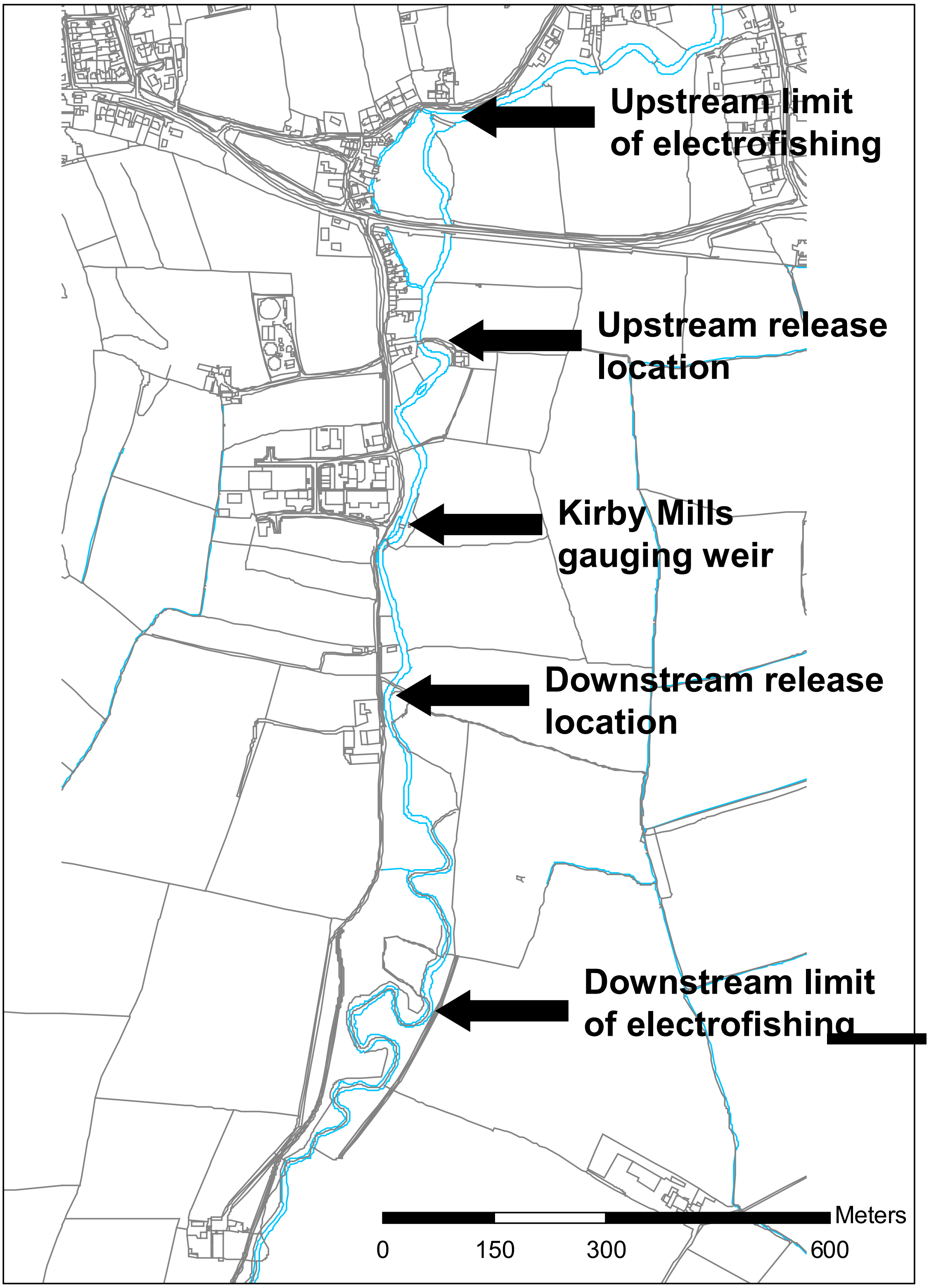

Figure 3.2 Map of River Dove study site showing weir site and sampling reaches.

3.3.3. Passive Integrated Transponder detector equipment

PIT arrays, based upon a modification of the design by Barbin Zydlewski *et al*. (2001), were installed in Costa Beck (*Fig. 3.3*) and the River Dove (*Fig. 3.4*) at the gauging weirs (NGR: SE774836 and SE704855, respectively). Each array had two antennae, one installed immediately upstream of the weir and the second downstream of the weir. It was thus possible to detect tagged fish moving over the weir and their direction of movement by the order of detections that occur subsequently at the two antennae.

At the Costa Beck site the upstream and downstream antennae were positioned approximately 5 m from the weir crest. At the Dove site, because of a deep pool immediately below the weir, the downstream antenna loop was positioned about 20 m downstream of the weir. The upstream antenna loop was positioned approximately 10 m upstream from the weir at the Dove site.

The dimensions of the antenna loops varied from 6 to 7.5 m wide and 0.4 to 1.0 m deep, depending on the dimensions of the river channel. Antenna loops were positioned to ensure that they conformed to the shape of the river channel so that all fish passing that location had to swim through the loop. The upper line of the loop was fixed in position by attaching it to a cord that ran across the surface of the river (*Fig. 3.3*), and the lower cable was buried just beneath the substrate with weights attached. The antenna was constructed using a single loop of 12-gauge insulated THHN multi-strand wire.

PIT detectors were constructed using commercially available radio-frequency identification systems (Texas Instruments TIRIS s-2000). The system (*Fig. 3.5*) consisted of a HDX reader module (TIRIS RI-RFM-008), operating at 134.2 kHz, connected to a control module (TIRIS RI-CTL_MB2A). The reader module was connected to an open loop inductor antenna that both generated an energising electromagnetic field and received transmitted signals from the tag. The reader circuit was set up with a charge time of 50 ms and a rest time of 50 ms so that tags that entered the antenna field for 100 ms were detected. Detection and logging efficiency were tested at the time of field installation, using several different tags, each attached to a pole that was passed through the loop. Tests across the whole river cross-section at each site and antenna gave detection efficiencies that typically exceeded 98 per cent. Such efficiencies are regarded as very good by comparison with other PIT systems, especially across such widths and depths (Lucas and Baras, 2000, 2001; Haro *et al*., 2001). Detection within the loops was tested weekly or more frequently throughout the study period. Records of detected tags were logged onto 32MB Compact Flash Cards. Data stored included tag number, time of record and antenna location. The information stored on the flash cards was downloaded regularly.

The PIT telemetry station at the Costa Beck site was powered by a 12 V, 110 Ah deep-cycle leisure battery, with additional power supplied from a solar panel (*Fig. 3.3*). Depending on weather conditions this provided 5 days or more continuous run time on a single charge. At the River Dove site the PIT station was powered by mains supply passed through a low noise, step-down transformer to provide 12 V DC current.

At the Costa Beck site the detection equipment operated from 23 July 2004 to 2 September 2004. There were two short periods in which technical difficulties caused the equipment to fail – these were from 09:16 to 18:20 on 25 July 2004 and between 10:17 3 August 2004 and 09:27 4 August 2004. Tagged fish that moved past the antennae during these periods would not have been recorded.

Figure 3.3 Costa Beck Crump gauging weir with PIT detection equipment. Arrows show: A, solar panel power supply; B, upstream antenna; C, downstream antenna.

Figure 3.4 Kirkby Mills Flat-V gauging weir on the River Dove during elevated flow conditions. Upstream antenna is about 20 m upstream of weir beneath trees (not visible), and downstream antenna is 5 m downstream from where photograph was taken.

At the River Dove site the detection equipment operated from 6 August 2004 to 17 October 2004. However, from 19:37 10 August 2004 to 18:30 11 August 2004 and from 08:55 12 August 2004 to 16:39 12 August 2004 exceptionally high flows caused temporary damage to the equipment. During these periods the PIT system was not operational and any tagged fish that moved past the antenna would not have been recorded.

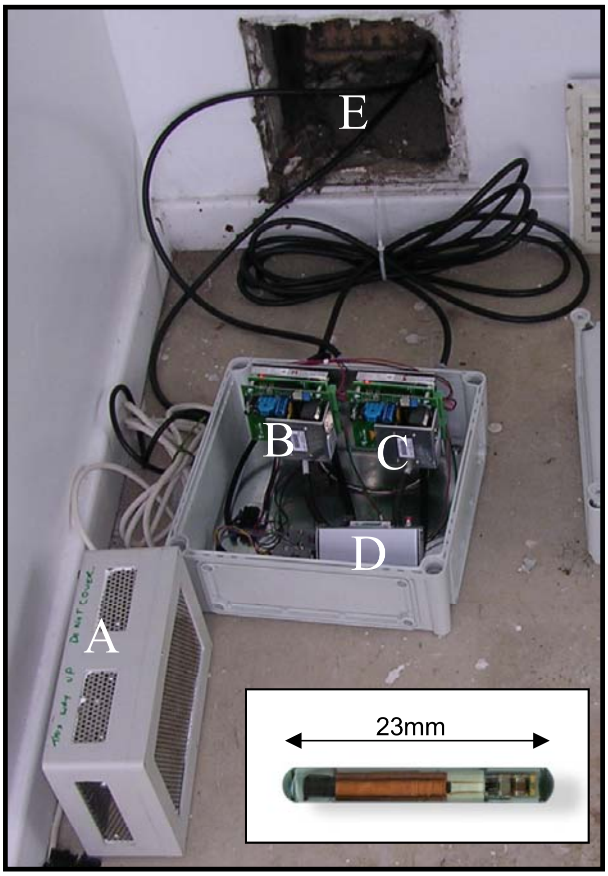

Figure 3.5 PIT telemetry station in River Dove gauging building: A, 240 V AC to 12 V DC power converter; B, downstream antenna reader–control module; C, upstream antenna reader–control module; D, flash card datalogger; E, cables passing to antenna. Inset, 23 mm biocompatible PIT tag.

3.4. Results

3.4.1. Costa Beck

Initially, the experimental plan was to capture grayling from downstream and upstream of the weir and translocate these upstream and downstream, respectively. In practice, it was only possible to capture grayling from upstream and transfer them downstream. Very few grayling were observed when electrofishing downstream of the weir. This appeared to be partly because of the low densities of grayling, but also deep water and weed growth greatly lowered fishing efficiency. Upstream of the weir a total of 57 grayling of a suitable tagging size were caught. The size ranged from a fork length of 174 mm to one of 330 mm (*Fig. 3.6*). Of the 57 tagged fish, 25 (44 per cent) were recorded moving upstream over the weir. A single fish was recorded at the lower detector, but not at the upper detector, so 96 per cent of fish regarded as attempting to traverse the weir succeeded in doing so. There was no significant difference between the size of homing fish and those that did not home (*t*-test, $P > 0.05$, *Fig. 3.6*). During the period of the experiment, discharge over the gauging weir remained very stable (*Fig. 3.7*) and so no plot of weir traversal in relation to discharge is presented. Most fish were recorded moving upstream over the weir only once, however eight of the grayling that initially moved upstream over the weir were recorded moving back downstream subsequently. Several of these made repeated movements over the weir during the course of the study. *Figures 3.8* and *3.9* provide examples of two of these fish. All fish logged at the upstream detector were logged previously at the downstream detector, which reflects the system's high detection efficiency.

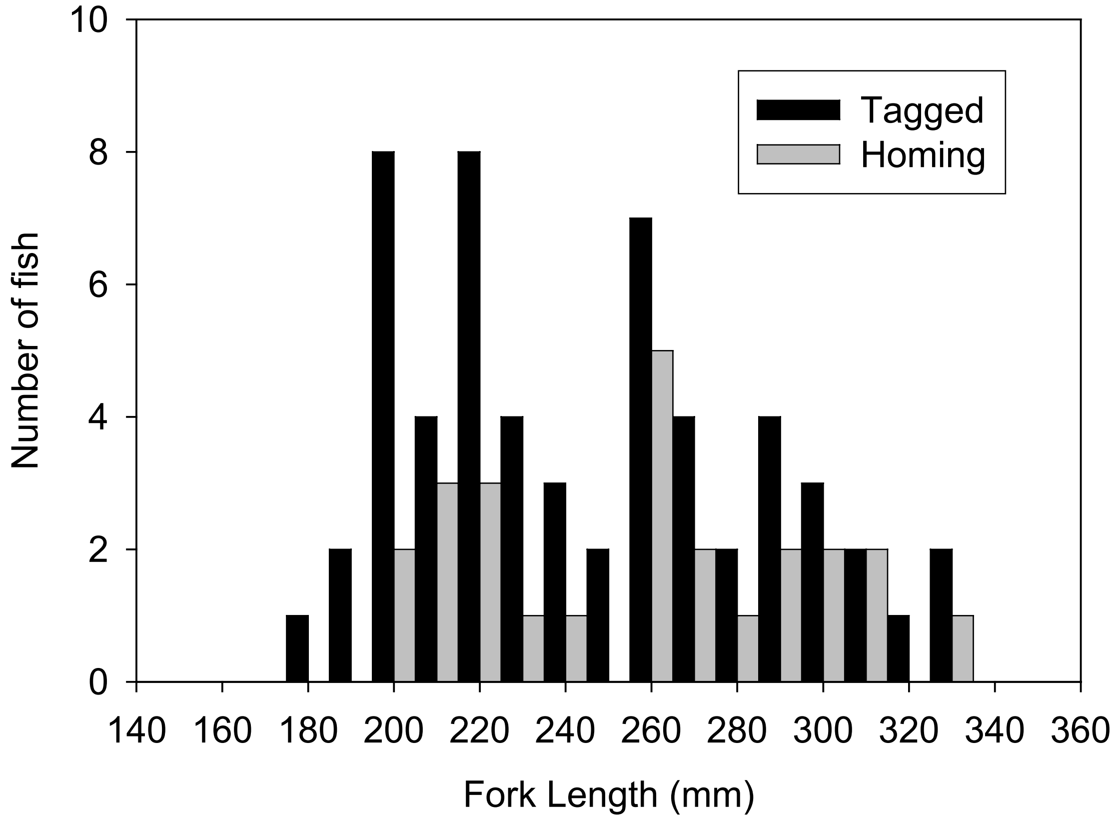

Figure 3.6 Size distribution of all PIT-tagged grayling in Costa Beck and size distribution of grayling that successfully passed upstream over the weir (that is commencing homing).

Following release (early evening 23 July 2004), the first grayling was recorded moving upstream over the weir on 25 July 2004. The pattern of first-recorded movements upstream by individual grayling is shown in *Figure 3.10*. Grayling frequently appeared to be moving in groups, since several fish at a time were recorded moving upstream in a short period, followed by a period of no activity. All grayling that ascended the weir did so within a week of tagging. The last record of a grayling moving upstream (excluding grayling that repeatedly moved up and down over the weir) was on 29 July 2004. The timing of movements upstream by grayling appeared to be random with respect to darkness, with no apparent pattern in the timing of movements (Rayleigh test, $z = 1.3608$, $n = 25$, $P > 0.05$; *Fig. 3.11*). The clustering of the times of movement reflects the observation that tagged grayling tended to move over the weir in groups. Although a greater proportion of adult grayling (>250 mm FL) homed compared with juvenile grayling (60:31.25 per cent), this was not significant (Chi-squared with Yates' correction = 2.03, $P > 0.05$).

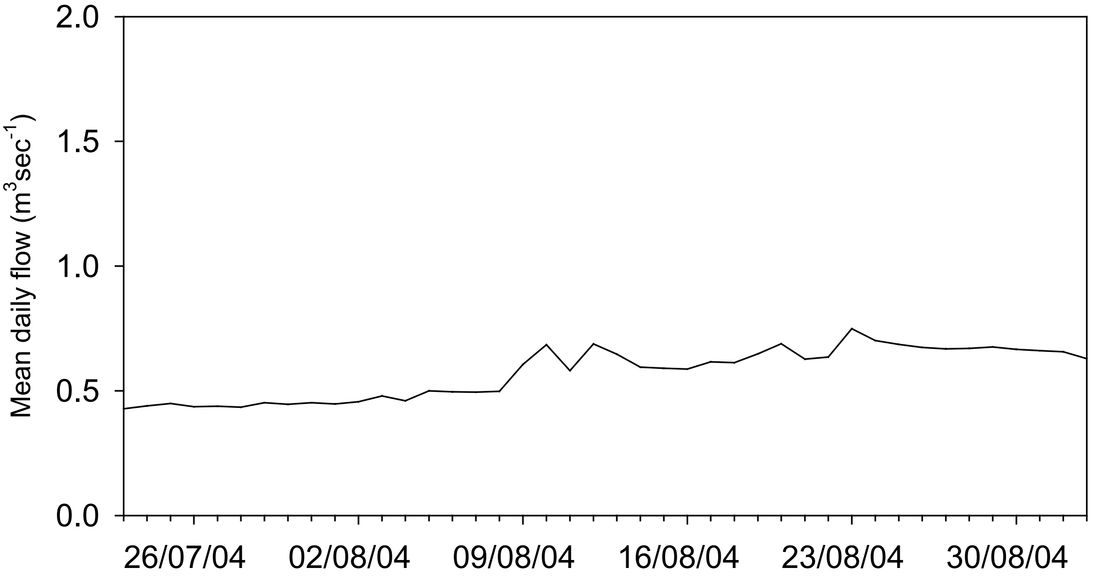

Figure 3.7 Mean daily flow at Costa Beck gauging station during study period.

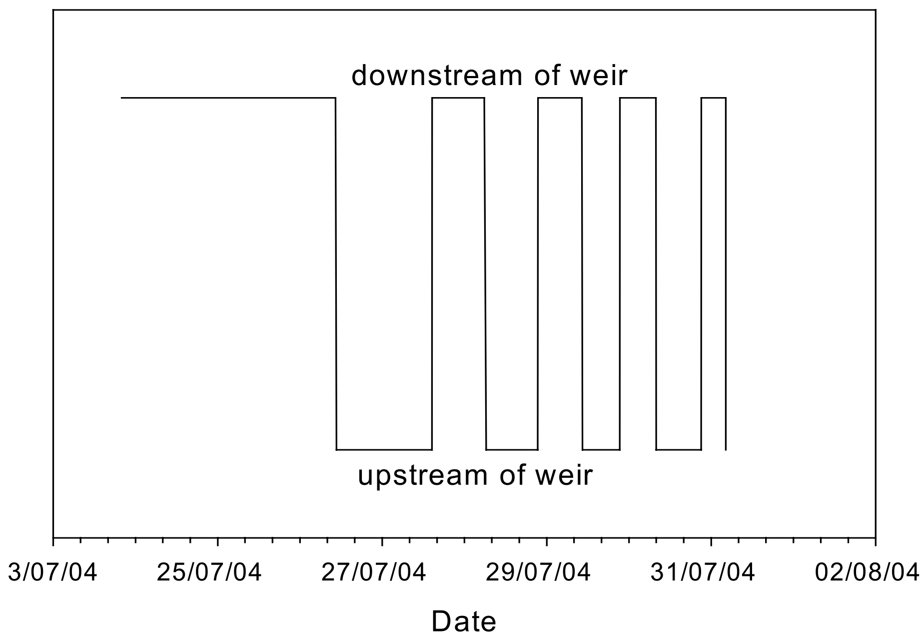

Figure 3.8 Movements of grayling PIT No. 127179157 (fork length 242 mm) over Costa Beck weir during the study.

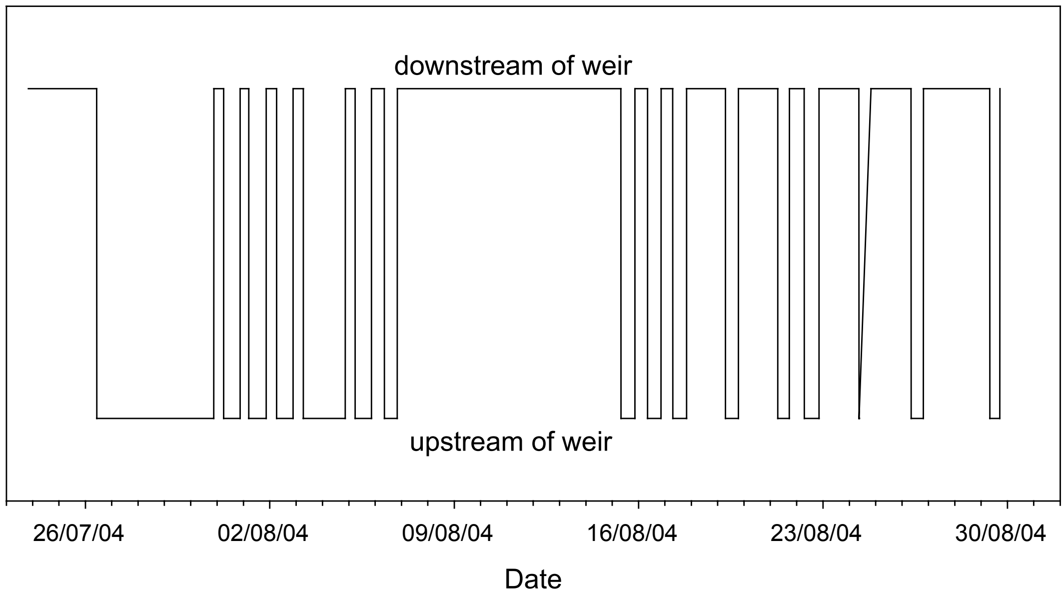

Figure 3.9 Movements of grayling PIT No. 127179153 (fork length 251 mm) over Costa Beck weir during the study.

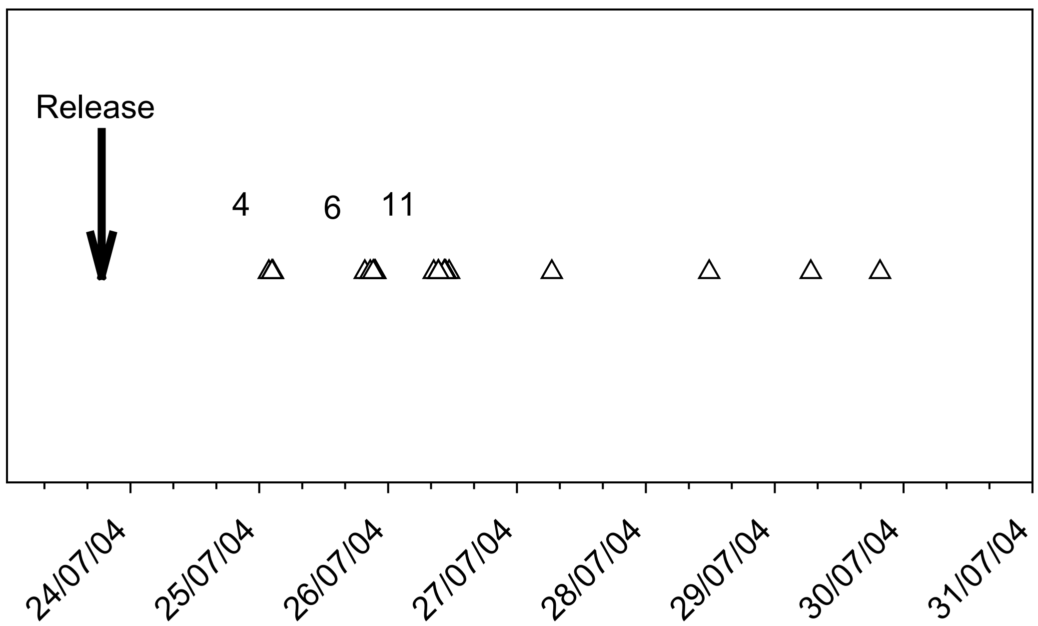

Figure 3.10 Timing of upstream movements (as first record per individual) over weir made by homing grayling. No fish moved upstream between 30 July and termination of the study on 2 September 2004.

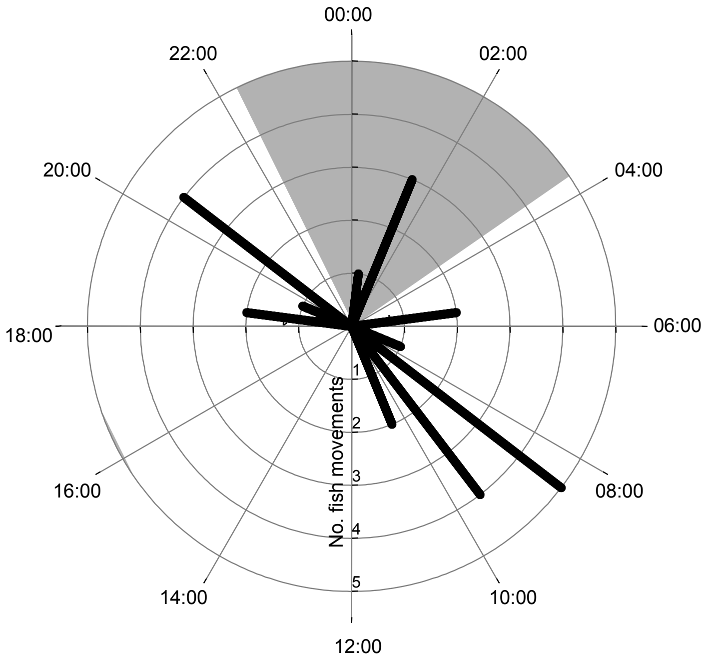

Figure 3.11 Rose diagram displaying time of day of movements (first records) by grayling that passed upstream over Costa Beck weir. The shaded area represents hours of darkness (sunset to sunrise). Passages of fish are pooled by the hour.

3.4.2. River Dove

In the River Dove, grayling and brown trout were caught in good numbers from above and below the gauging weir. A total of 74 grayling (35 caught downstream, 39 upstream) and 73 brown trout (40 caught downstream, 33 upstream) were retained and PIT tagged. The size distribution of tagged fish is shown in *Figures 3.12* and *3.13*. A high proportion of the grayling (69 per cent) released upstream moved downstream over the weir, while only a small number (13 per cent) of the grayling released downstream moved upstream. In contrast, the proportion of brown trout released downstream that moved upstream (64 per cent) was greater than the proportion of brown trout released upstream that moved downstream (20 per cent). The lowest proportion of fish that attempted to move over the weir and were ultimately successful were grayling released downstream of the weir (36 per cent), while the success rate in the other groups varied between 80 and 92 per cent (*Table 3.1*). An unsuccessful attempt was defined as when a fish was recorded at the antenna above or below the weir in the section in which the fish was released, but with no record of the fish at the other antenna.

Of the fish that successfully 'homed' to the section from which they originated, a small number were recorded moving over the weir more than once. Three trout were recorded making more than one movement over the weir, one trout moved up over the weir then back down, one down then back up and one moved up, down and then back up. A single grayling was recorded as making more than one movement over the weir, moving upstream and back downstream twice during the study.

Table 3.1 Numbers of grayling and brown trout PIT-tagged and numbers 'homing' (passing weir to section of origin) or unsuccessfully attempting to home.

Species	*No. tagged*	*Caught*	*Released*	*'Homed'*	*Attempt*	*Per cent success*
Grayling	35	Downstream	Upstream	24	2	92
Grayling	39	Upstream	Downstream	5	9	36
Brown trout	40	Downstream	Upstream	8	2	80
Brown trout	33	Upstream	Downstream	21	4	84

Most movements of fish over the weir occurred in the fortnight following tagging and release of fish. This period coincided with unusually high flows after a dry period of stable flow (*Fig. 3.14*). The period of high flow was followed by dry weather and stable flow. The only fish recorded moving over the weir during this dry period were three brown trout that moved upstream (*Fig. 3.14*). Towards the end of the study period there was a second period of high flows, when four further fish, comprising two grayling and two brown trout, were recorded traversing the weir (*Fig. 3.14*).

There was no clear pattern in the time of day of movement over the weir for brown trout (Rayleigh test, $z = 0.209$, $n = 29$, $P > 0.05$; *Fig. 3.15*), but there appeared to be a tendency for movement at night by grayling (Rayleigh test, $z = 4.25$, $P < 0.05$; *Fig. 3.16*).

3.5. Discussion

The proportion of grayling translocated downstream that successfully ascended the 0.2 m high Crump weir on the Costa Beck (96 per cent) was much higher than the value of 36 per cent for the 0.5 m high Flat-V on the River Dove. Measured water velocities at the crest (*ca*. 1 m s^{-1}) of both weirs were similar, but higher on the face of the Flat-V than on the Crump (about 1.9-3.0 *vs* 1.7-1.8 m s^{-1}, respectively) and the distance of travel up the downstream face of the Dove weir was longer. Despite a water depth of approximately 0.09 m across the width of the Crump weir on the Costa Beck (barely the body depth of a 300 mm grayling), all but one grayling that attempted it ascended the weir successfully. Several fish did so on more than one occasion.

It would therefore appear that Flat-V gauging weirs (and perhaps also other types) with heights of 0.5 m or more are likely to be difficult for grayling to negotiate. By contrast, 84 per cent of brown trout that attempted to ascend the Flat-V gauging weir on the Dove did so, despite identical environmental conditions and a similar size range of fish. This could reflect better swimming performance in brown trout than in grayling, although such differences were not very evident in the work carried out by Clough *et al*. (2003), which was nevertheless compromised somewhat by the rather poor health of some of the grayling in that study. Moreover, Clough's tests were based on forced swimming, which may give different results to volitional swimming. Fish of either species would certainly have been able to approach the standing wave below the Flat-V weir at aerobic swimming speeds by using the slower water off the mid-line. The difference in successful upstream passage between trout and grayling may also reflect behavioural inhibition or confusion of grayling in attempting the ascent of such a weir. Flat-V weirs are characterised by the presence of large side eddies, either side of the main flow entering the stilling basin. Some species appear more easily confused in turbulent or eddying flows (Lucas and Baras, 2001; Larinier, 2002a, 2002b) and Flat-V weirs have been found to be an impediment to the movement of other rheophilic fish species (Lucas and Frear, 1997).

There appeared to be some influence of flow or related factors such as turbidity, on the tendency of brown trout and grayling to pass the gauging weir on the Dove (*Fig. 3.14*). However, because most movements occurred soon after release on Costa Beck, where flows were stable throughout the study, the activity during higher flows in the Dove may have occurred irrespective of flow. A detailed examination here of the effects of flow on passage at the Dove Flat-V weir is therefore not possible and would require further study.

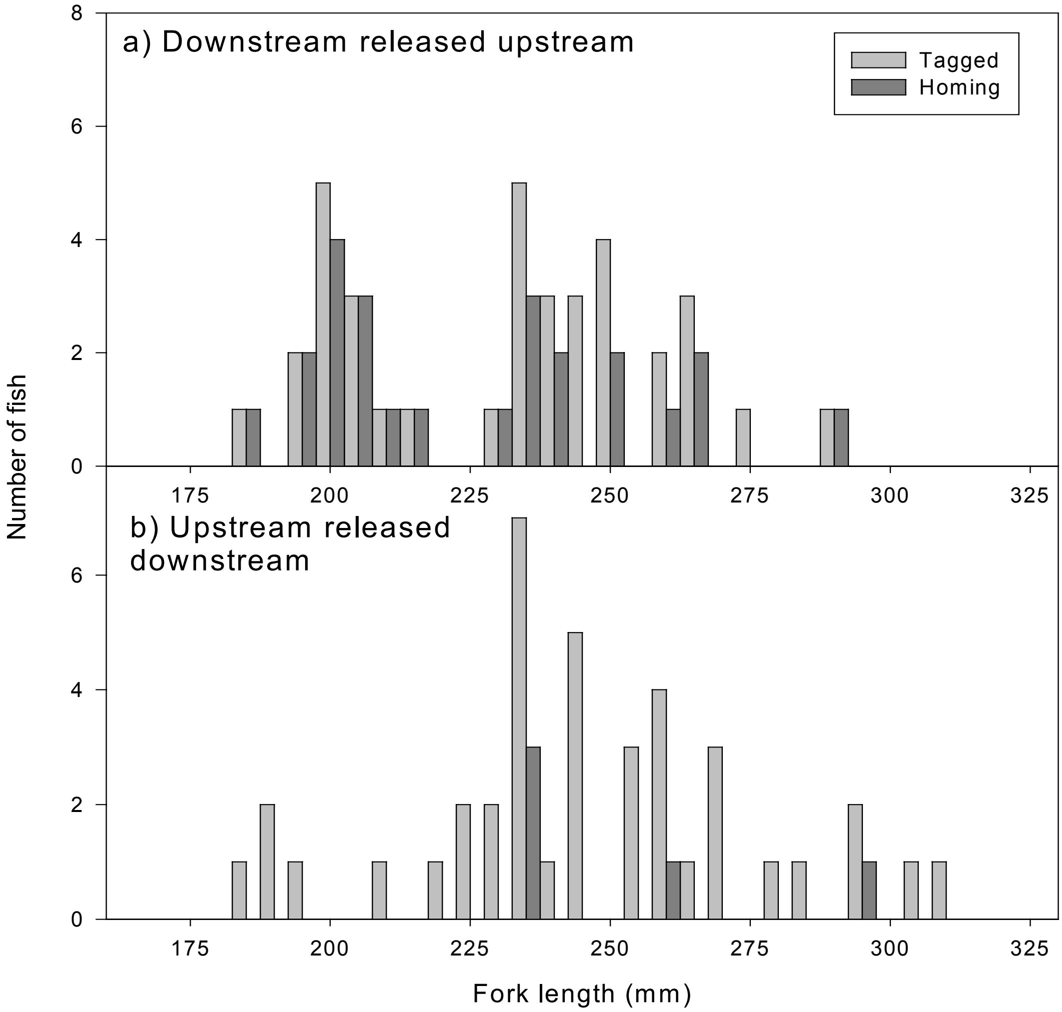

Figure 3.12 Size distribution of PIT-tagged grayling and those recorded moving over Kirkby Mills flow-gauging weir: (a) grayling captured downstream and released upstream of the weir, (b) grayling captured upstream and released downstream of the weir.

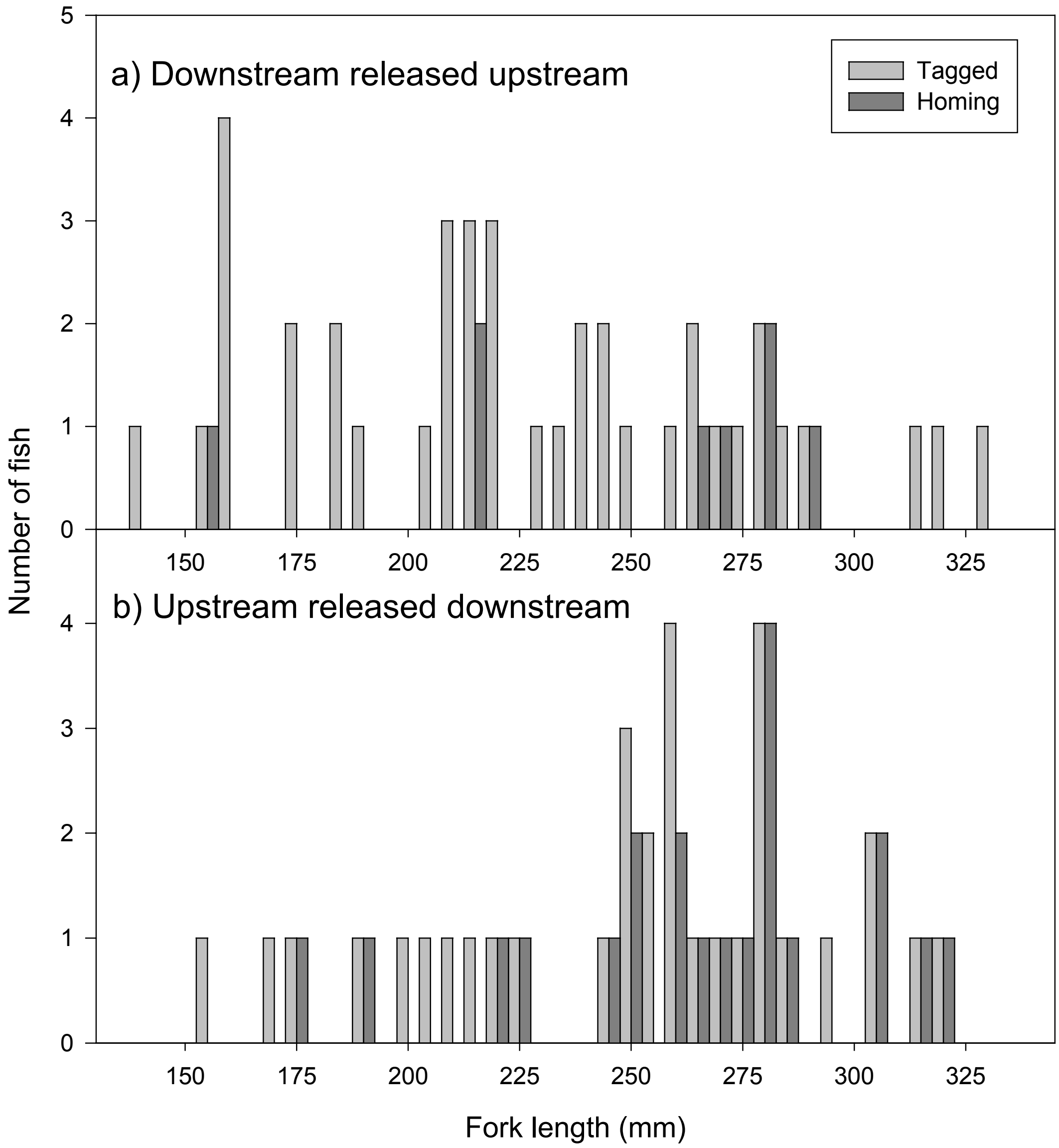

Figure 3.13 Size distribution of PIT-tagged brown trout and those recorded moving over Kirkby Mills flow-gauging weir: (a) brown trout captured downstream and released upstream of the weir, (b) brown trout captured upstream and released downstream of the weir.

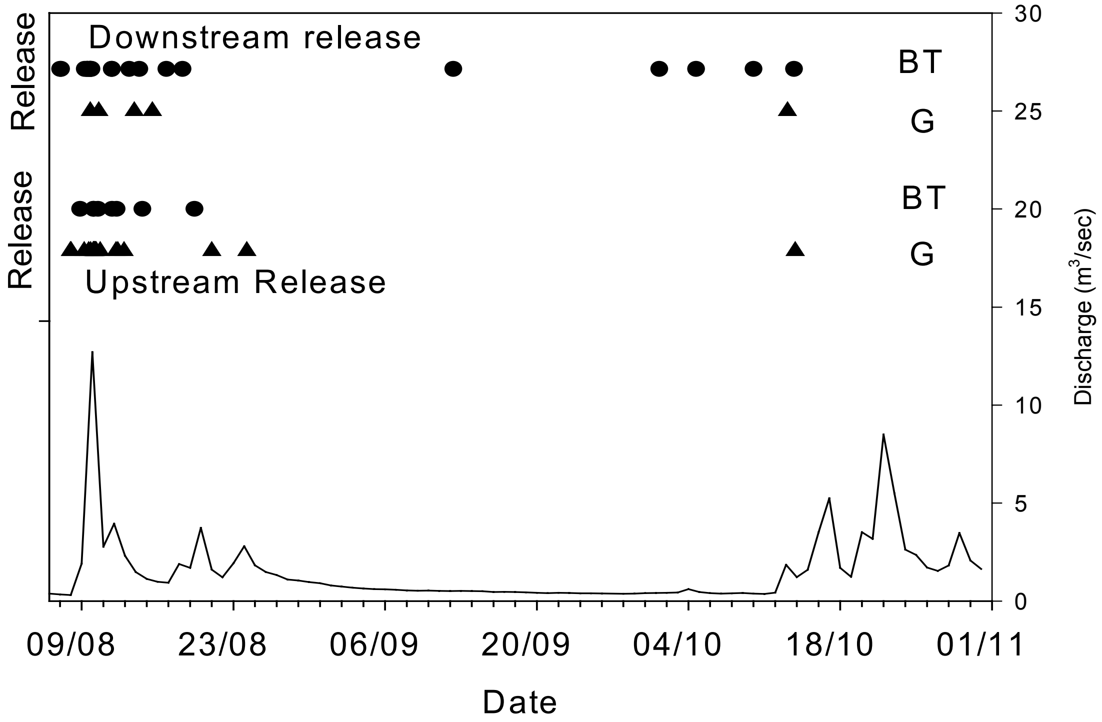

Figure 3.14 Timing of tagged grayling and brown trout passing over Kirkby Mills flow-gauging weir (first records for individuals) and daily mean discharge at Kirkby Mills, River Dove. BT, brown trout; G, grayling.

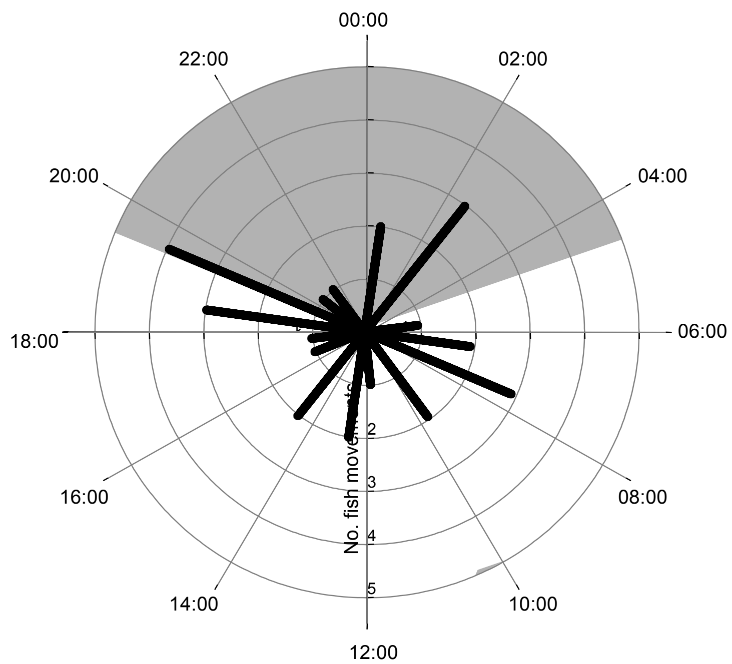

Figure 3.15 The time of day of movements made by brown trout over the weir at Kirkby Mills, River Dove. Passages are pooled by the hour. Shaded area shows hours of darkness (sunrise to sunset) at start of study.

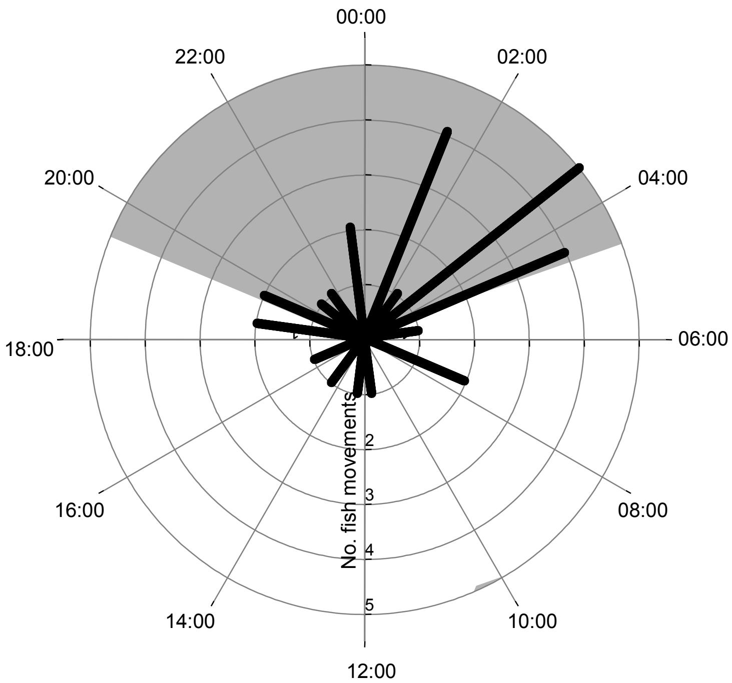

Figure 3.16 The time of day of movements made by grayling over the weir at Kirkby Mills, River Dove. Passages are pooled by the hour. Shaded area shows hours of darkness (sunrise to sunset) at start of study.

The proportions of tagged grayling detected while seeking to pass the gauging weirs were 36 per cent (Dove, released downstream), 44 per cent (Costa Beck, released downstream) and 74 per cent (Dove, released upstream). The proportions of tagged brown trout detected while seeking to pass the gauging weirs were 25 per cent (Dove, released upstream) and 76 per cent (Dove, released downstream). Interpretation of these data is limited by the lack of additional information on the movements of these fishes, for example from additional logging stations. Although technically feasible, additional fixed logging stations upstream and downstream were not set up because they could have influenced anglers' access (although only in very small areas), and would have required substantially more equipment and manpower. Incorporation of controls involving the release of fish back to their home areas also would have assisted interpretation, but was complicated by the limited availability of grayling on the Dove. The possibility of electric fishing the stretches to validate records was considered, but the stretches of river available were considerable and the fishing efficiency for grayling was rather low, especially in Costa Beck below the weir, so this was not attempted.

The proportion of grayling that attempted to move towards the upstream home section appears lower than that of brown trout, whereas, in contrast, for the Dove, the proportion of grayling moving downstream was greater than that for brown trout. It is possible that this may reflect a handling effect, with grayling being more sensitive than brown trout. However, the rapidity of return at Costa Beck, the aggregation of fish in small groups (rather characteristic of grayling behaviour and not evident in brown trout) and their passage through very shallow, fast water suggest that those grayling that did move upstream were behaving normally and were relatively unharmed by the capture and tagging process. It is also possible that movements of some fish were missed during the time that the equipment was not logging. Alternatively, it is possible that the local homing responses or capabilities of grayling are less than those of brown trout. Further experiments, with additional controls, would allow better interpretation of the spatial behaviour of grayling and brown trout and their passage at weirs.

In future studies it would be quite feasible to set additional PIT antennae at specific sites upstream and downstream in the locality of obstructions to obtain information of finer resolution on fish spatial behaviour. This could also include placement of antennae at the crest of the weir, at the centre and edges of the weir immediately downstream of the supercritical flow and in the stilling basin. Such antennae can be bolted on and have a narrow cross-section so would influence flow characteristics little, although agreement of those who manage hydrometric facilities would have to be obtained. It would also be possible to combine such equipment with video technology at sites where adequate visibility is available. The translocation method resulted in a short, intense period of attempted traversal of the weir, for grayling at least, which is ideal for experimental measurements of passage ability under different conditions. The ability to combine this with tagging and remote monitoring of relatively large numbers of fish, of a wide range of sizes and of several species in clear or turbid conditions, day or night, makes this approach to assessing fish passage and behaviour at flow-gauging weirs and other structures a very powerful one.

4. Conclusions and recommendations

Within the Rye, a small river, upriver migrations of grayling for spawning were common but not universal amongst tagged individuals. The extent of migration associated with spawning was generally less than that observed in continental European studies. Outside the spawning season, grayling in the Rye tended to adopt restricted home ranges, although in some cases the day-to-day movements of grayling were quite substantial. Extensive and erratic spatial behaviour was evident on the lowest section (A) of the Rye study reach in late winter 2004 and autumn to early winter 2004-2005. It is most likely to have resulted from avian predator avoidance, but possibly also from increased movement between habitat patches during changing discharge conditions.

Habitat use by adult grayling in the Rye changed between seasons, with radio-tagged fish from all sections selecting deeper, slower water with sand substratum during the two winter study periods. During the spawning season fish selected faster, shallower water with gravel, pebble and cobble substrate and tended to remain in similar habitat in the summer, but with greater use of overhead cover. There was some evidence that grayling in section A, which appeared to provide the least suitable habitat, used a wider range of habitats than those in sections B and C, but this may have been influenced by the greater abundance of avian predators in that section. In the Ure, outside the spawning season, several fish moved significant distances from a shallow glide to a deep, slow glide. The spacing of different available habitats is likely to dictate distances moved in order to access these. It is likely that in some British upland rivers, grayling will exhibit substantial autumn–winter movements to distinct overwintering areas.

The distinct differences in spatial behaviour within a single river reach are of very substantial interest in the context of the ecology of grayling, and stream fishes more generally, and deserve further attention. In an applied context, it seems very likely that this behaviour was associated with predator avoidance and there is increasing interest, through collaborative work by the Centre for Environment, Fisheries and Aquaculture Science (CEFAS) and the Environment Agency, to understand the role of fish behaviour and habitat use in avian fish predation. However, this study may be one of the first to provide information for a natural environmental setting. Similarly, this study demonstrated quite a strong motivation for rapid homing of grayling translocated downstream of their origin, which has pure and applied relevance to a better understanding of grayling ecology.

Other studies in continental Europe have found relatively localised home-ranging behaviour, though generally not as extreme as the very limited movement observed in a short summer study of English chalkstream (Lambourn) grayling by Martyn (2004). Taken together, the current study and others suggest a substantial degree of plasticity in the spatial behaviour of grayling in response to local environmental conditions. The adaptive pattern of seasonal movements by grayling in many rivers, which probably helps to enhance survival probability and sustain populations, especially in those rivers with variable flow and/or greater spatial dispersion of key habitats, needs careful consideration in local river management.

The current study suggests that attempts by adult grayling to ascend riverine obstacles during pre-spawning migrations may be more common than downstream movements over barriers at any time of the year. However, this may be a chance effect due to the small samples and limited periods of tracking individual grayling. Nevertheless, this may reflect an innate rheotaxic tendency in seeking spawning areas, which is of management significance. However, downstream movements of tagged adult grayling were observed during floods, even though not past barriers, and passive dispersal or displacement of young juveniles may also occur. These behaviour patterns suggest that movements along the river's longitudinal axis are likely to be relatively common and that access past potential barriers should be enabled. This is likely to be particularly important where key habitat types, for example spawning and nursery gravels, are widely separated, or for recolonisation of depleted regions upstream of barriers, particularly in rivers recovering from historic pollution or habitat degradation.

The current study was intended to include some measurement of habitat use by juvenile grayling, but pilot radio-tracking experiments were unsuccessful as several tags failed soon after release and several tags detached from the fish. Intentions to study summer microhabitat use by electric fishing and snorkelling failed because of frequent high water levels in summer 2004, while the promising technique of assessing microhabitat use of PIT-tagged grayling with concealed PIT loops in different microhabitats (Riley *et al*., 2003) was not undertaken due to time constraints. However, within the Rye, electric fishing of any type was found to be unsuitable for determining microhabitat use of grayling (by contrast to brown trout), because grayling were too sparsely distributed and easily disturbed to be collected effectively by 'point' fishing. Also, during upstream wading grayling were usually observed to travel many metres upstream before being stunned or rushing back downstream.

Available evidence from this study, supported by research elsewhere, suggests that many barriers across which brown trout can gain easy access may not be passed so easily by grayling. Specific evidence as to the low efficiency of grayling in passing even small Flat-V gauging stations in an upstream direction has been obtained in this study. These gauging stations are still a preferred option in small upland rivers and the Environment Agency should be very circumspect about the introduction of more of these where grayling are present. Careful assessment of the need for new obstructions, operation of existing structures and possible removal of potential barriers to movement should be considered in the context of grayling populations and other aquatic biota more generally. In the context of providing firmer advice here, it would be useful to test smaller Flat-V weirs than that considered here under a range of conditions to be better establish circumstances allowing relatively free passage.

Further research should be directed in several areas. Following the development here of an effective methodology for determining the passage efficiency and behaviour of grayling at barriers, further studies to examine these aspects at a variety of barriers and fishways would be highly illuminating, with direct and immediate management benefits. It appears likely that the behaviour, as well as swimming capacity, of grayling in response to flow patterns and structures is likely to be very important in determining whether they traverse a variety of types of barriers or utilise certain types of fishway. Understanding these processes is fundamental to improving fish access past barriers. The method developed, based upon utilising the homing response of translocated fish, showed that the response is rapid (most fish move within days), enabling effective data collection over a constrained period. It can also be combined with other techniques such as video recording at key sites. While radio-telemetry can also be used for the same approach and can gauge quite fine-scale approach behaviour to weirs day or night, the same can be achieved with PIT telemetry using small loops with low range, but for a much larger sample of a wider range of sizes, by virtue of its lower unit cost. The approach is also highly suited to multi-species applications for the same reason (Lucas *et al*., 1999), although non-salmonids may not exhibit such clear homing responses. This field-based experimental approach could also be integrated with more controlled measurements of fine-scale behaviour and passage of grayling and other species in laboratory flumes in a manner similar to that applied by Kemp *et al*. (2005), for which expertise and facilities are available at several UK institutes. This combination of field and laboratory approaches has great potential for developing a fundamental and generic approach to understanding how grayling and other species respond to different types of physical structures and environmental stimuli in terms of macro- and micro-scale behaviour. This would provide valuable applied information for enhancing fish access past barriers, but could also provide a new perspective to free-access enhancement. It is estimated that a one-year integrated study designed to better quantify the behaviour of grayling (and potentially other species too) at several types of gauging weir and fishways would cost approximately £50-60K (research staff at University, full economic cost (FEC)), or about two-thirds of this using a Masters research student. This study would run effectively as a small stand-alone project, but could link closely with ongoing Environment Agency research on hydrometrics and fish passage. Alternatively, a more fundamental and in-depth PhD-based 3-year study would cost about £110K at FEC. Research that incorporates PhD programmes now entails rigorous management and training, and with the right management is extremely reliable in terms of successful work-package completion.

Greater knowledge is needed concerning the seasonal habitat requirements and survival of juvenile grayling outside the summer period, for which there have been numerous published studies (see Section 1 of this report and Ibbotson *et al*., 2001). In rivers with high winter flows and substantial flow variation, it is likely that access to suitable habitats may be important for overwinter survival and growth and may represent a bottleneck to recruitment, especially in modified systems. Currently, little is known about movements, habitat use and survival of juvenile grayling outside of the summer season in Britain and Europe. Therefore, substantial effort should be placed upon understanding the seasonal habitat requirements of juvenile grayling, especially during autumn and winter, and how these influence survival, growth and space use, especially during autumn and winter. Field experiments and studies in semi-controlled flume environments would be highly informative here and would have the capacity to provide applied knowledge to habitat management, as well as the necessary functional ecological information. Such work would be highly worthwhile, but technically challenging. Flumes such as those at East Stoke and Almondbank could be highly appropriate facilities in which to determine the functional relationships between environmental factors and growth performance. In-stream experiments using mark–recapture of elastomer visible implant (EVI) or PIT-tagged juvenile grayling would enable local movement and survival in relation to environmental conditions to be determined. Comparisons between chalkstream and upland river environments would help to highlight similarities and likely critical periods or habitats. Habitat use work could be carried out under semi-controlled flume and uncontrolled natural conditions, the latter using snorkelling and/or a PIT telemetry approach based on that of Riley *et al*. (2003) using small PIT antennae concealed in bed habitat. It is expected that this study would take approximately 3 years, employing an experienced scientist nearly full time and, based on FEC, would cost about £170K, or if carried out by a PhD student would cost about £110K.

Following the current study, additional research concerning the space and habitat use of adult grayling in larger river systems (ideally including those subject to water discharge regulation) over the full annual cycle, if possible, may be informative and worthwhile if sufficient management needs are evident. Similarly, gaining a better understanding of the degree to which chalkstream grayling are highly sedentary (Martyn, 2004) throughout the year and whether they do need to access particular habitats under some circumstances may be worthwhile, if sufficient local management concerns are evident. However, these research areas are of less generic importance than the two projects identified above and should be considered as lower priorities. If carried out, radio-tracking and habitat measurement approaches would be appropriate, combined with complementary data, perhaps from mark–recapture or PIT telemetry. Each project would require 1.5-2 years to complete, including project start-up, a full year of field work and data analysis and report writing, and would cost £90-120K at FEC for a salaried research scientist, or somewhat less if mainly carried out by a research student.

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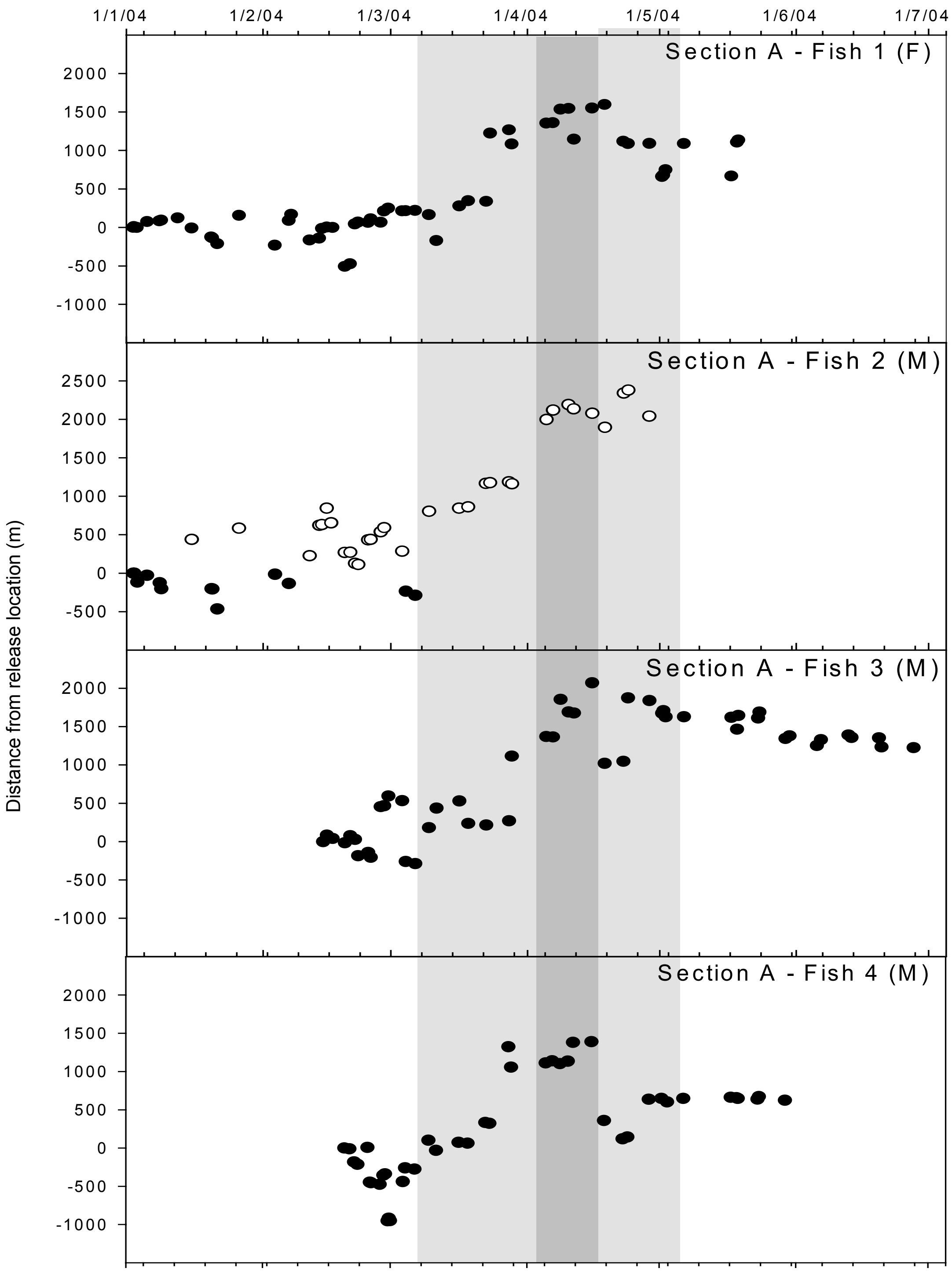
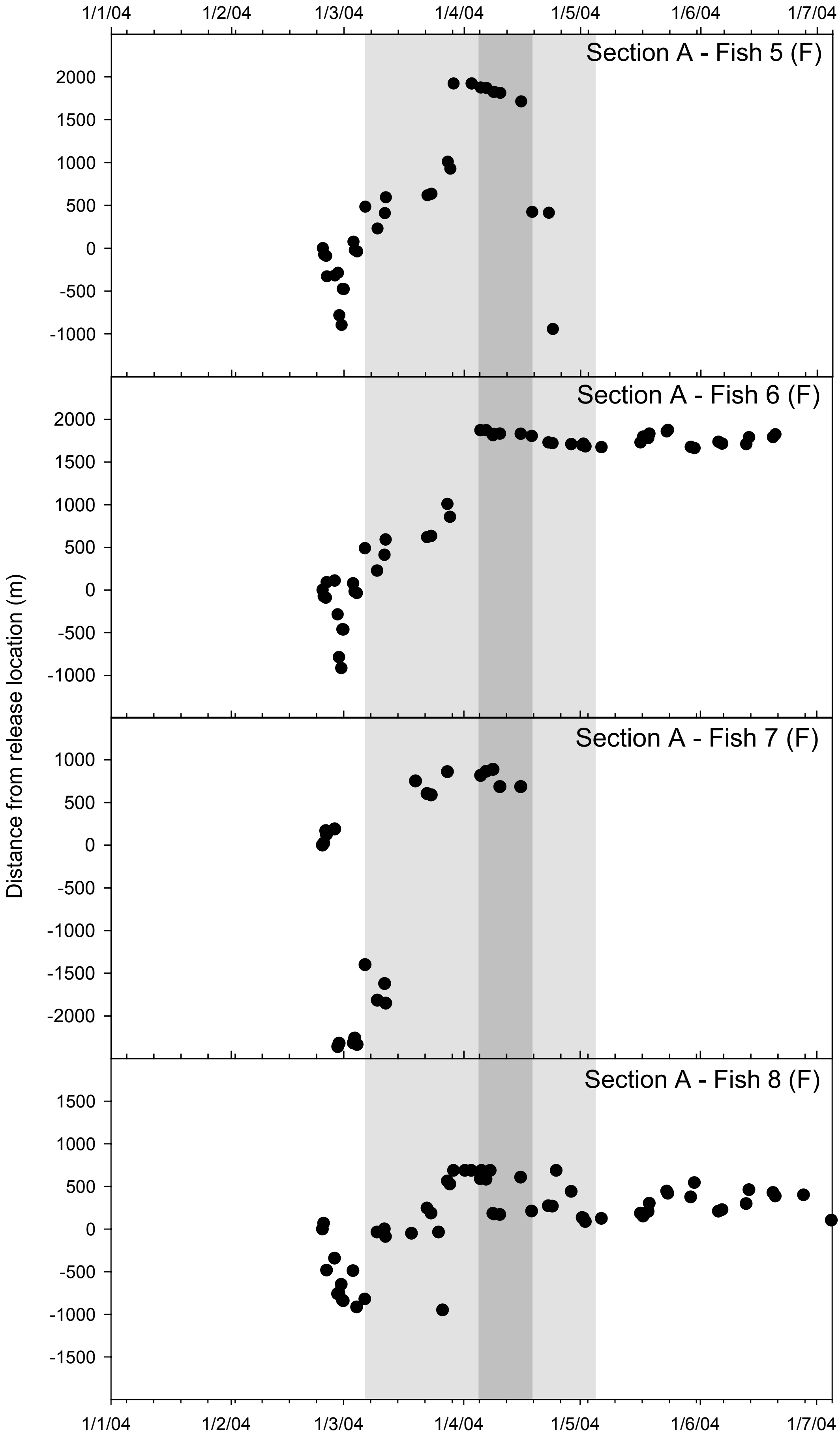
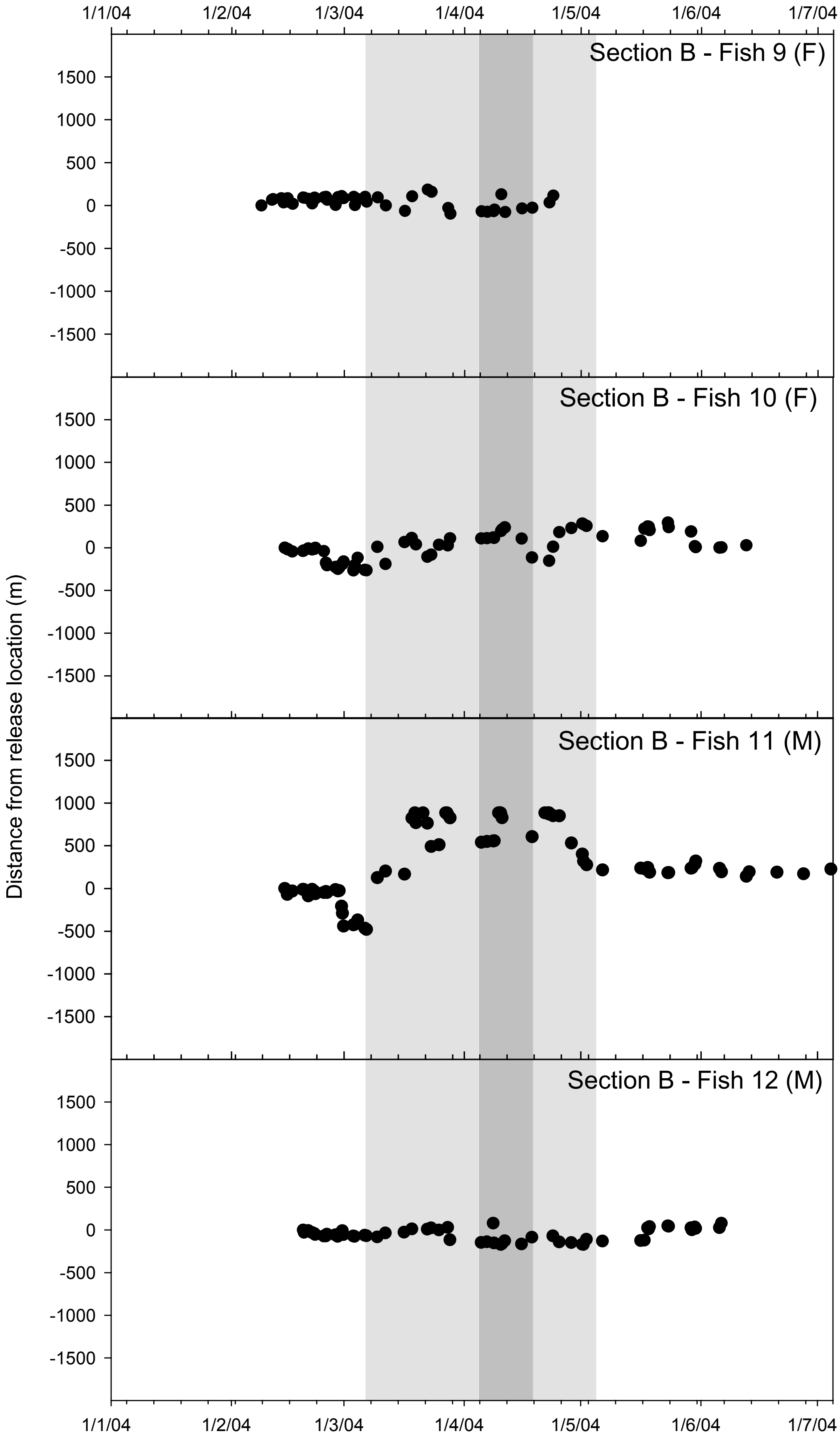
7. Appendices

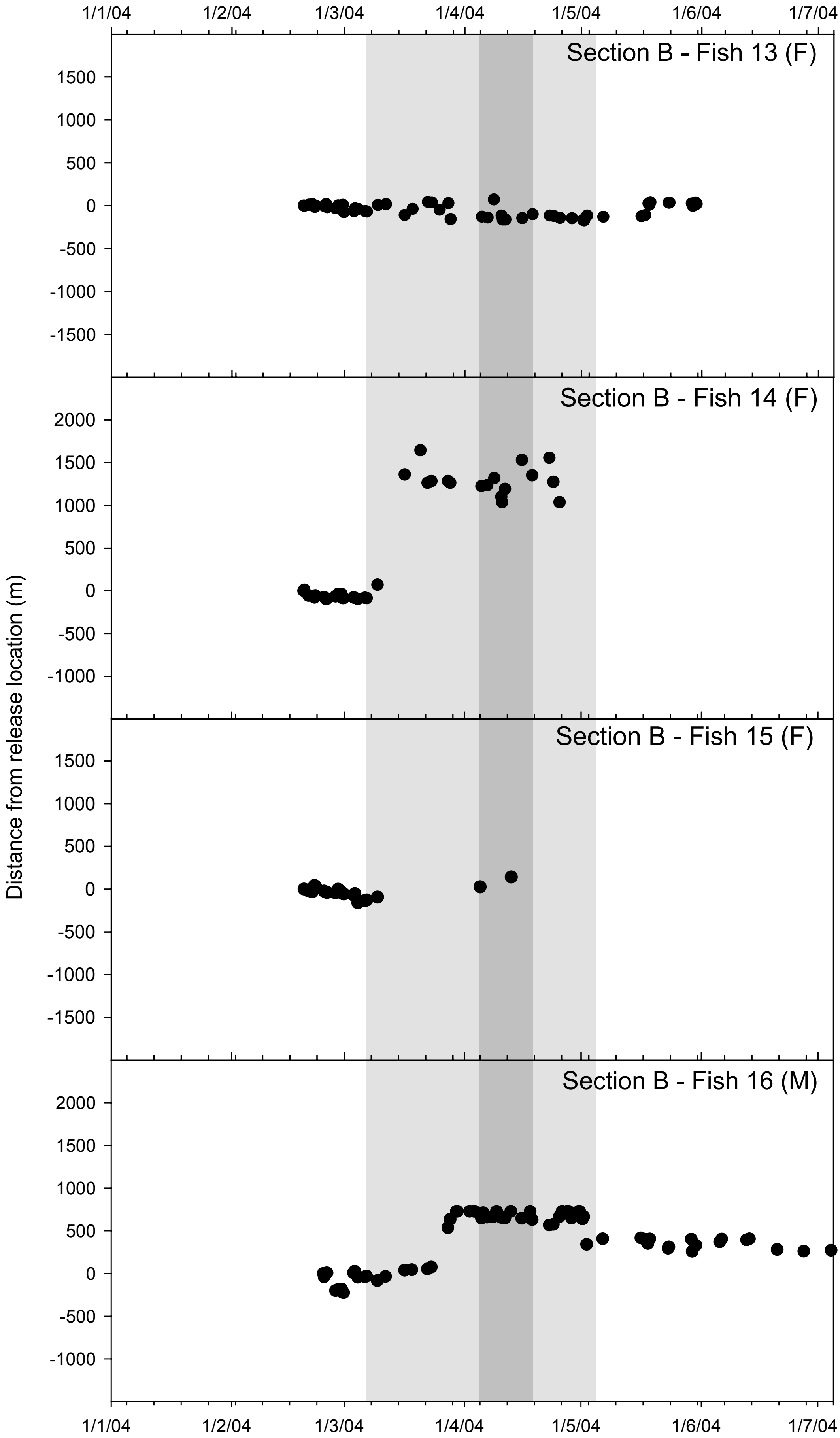
APPENDIX 1 Individual tracks of grayling radio-tagged in the Rye between 2 January and 6 March 2004. The dark grey bar identifies the period during which courtship and/or spawning was observed and the light grey bar identifies the period of pre-spawning and post-spawning migration (see text for details of method of determination).



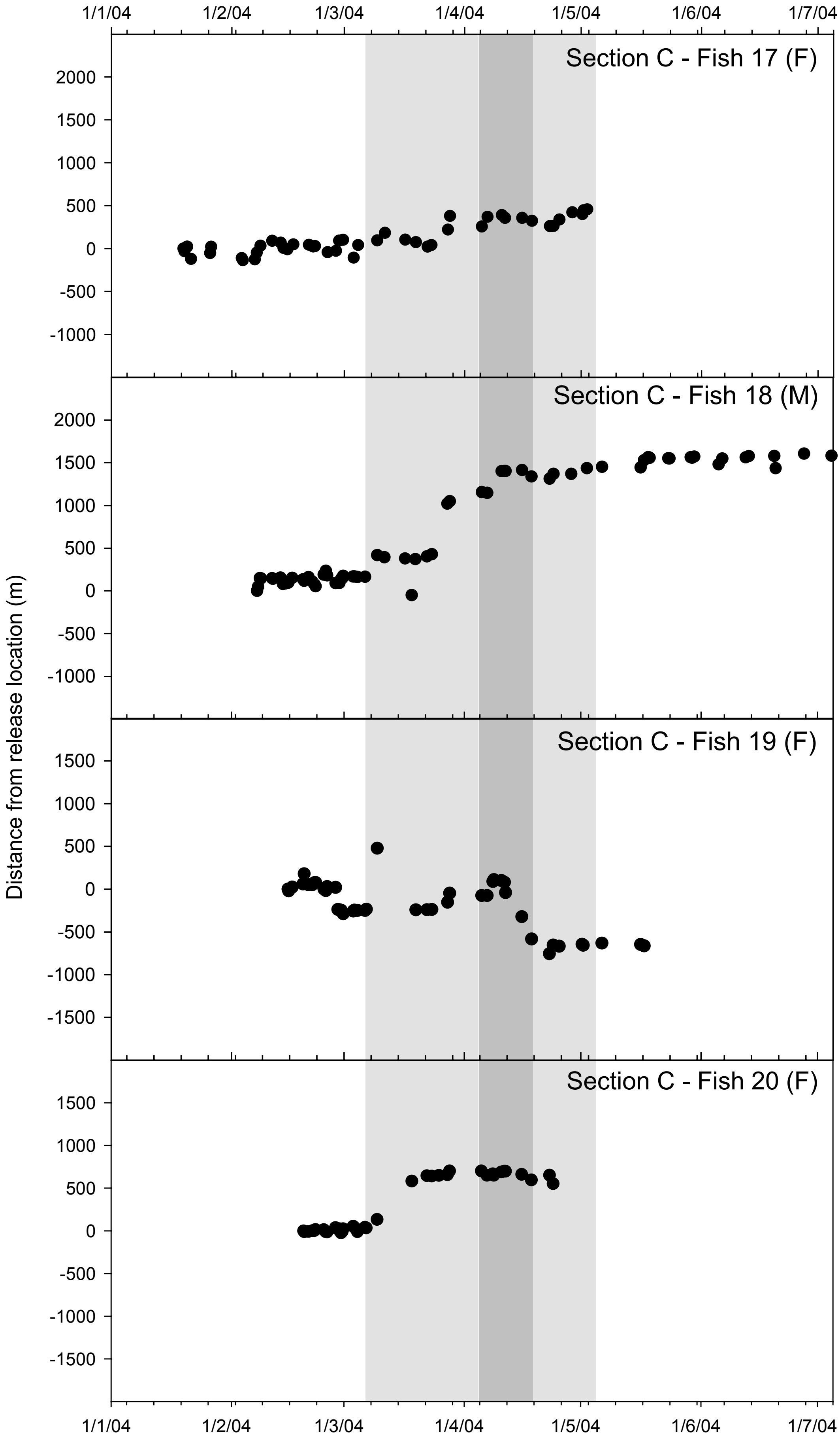

1/1/04
1/2/04
1/3/04
1/4/04
1/5/04
1/6/04
1/7/04
Section A - Fish 5 (F)
Section A - Fish 6 (F)
Section A - Fish 7 (F)
Section A - Fish 8 (F)
Distance from release location (m)
2000
1500
1000
500
0
-500
-1000
-1500
-2000



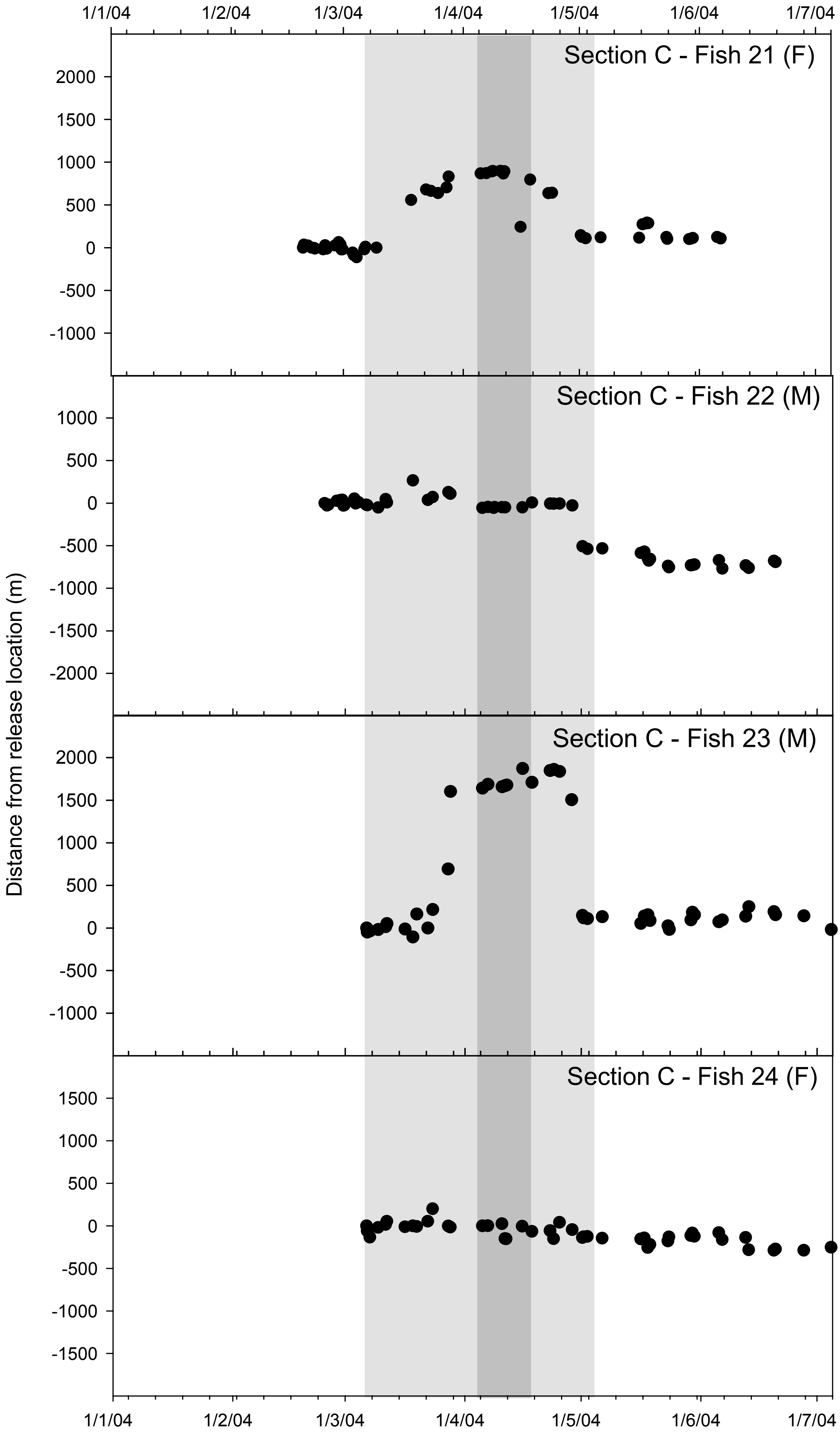
1/1/04
1/2/04
1/3/04
1/4/04
1/5/04
1/6/04
1/7/04
Section B - Fish 9 (F)
Section B - Fish 10 (F)
Section B - Fish 11 (M)
Section B - Fish 12 (M)
1500
1000
500
0
-500
-1000
-1500
Distance from release location (m)



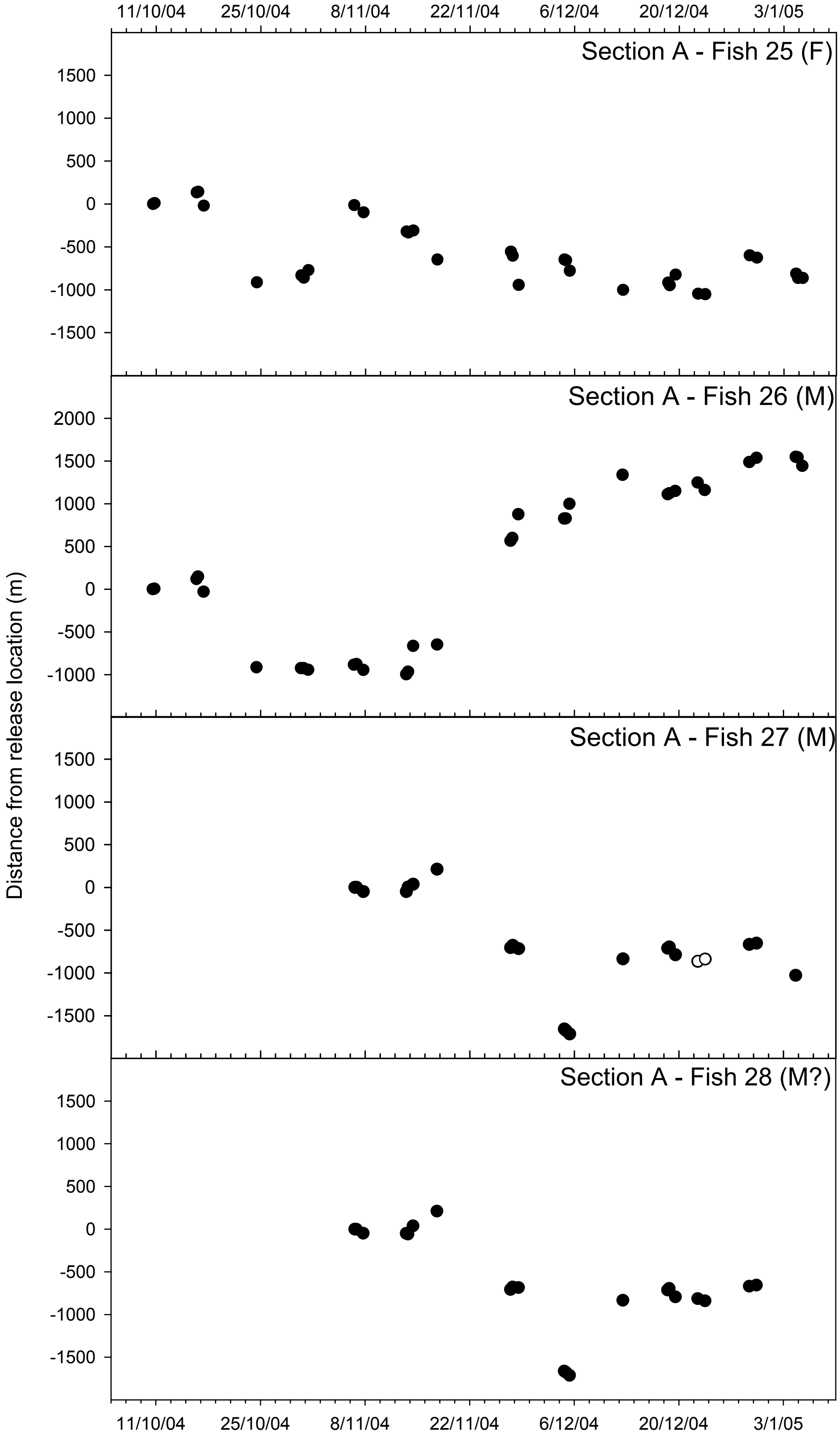
1/1/04
1/2/04
1/3/04
1/4/04
1/5/04
1/6/04
1/7/04
Section B - Fish 13 (F)
Section B - Fish 14 (F)
Section B - Fish 15 (F)
Section B - Fish 16 (M)
Distance from release location (m)
1500
1000
500
0
-500
-1000
-1500
2000

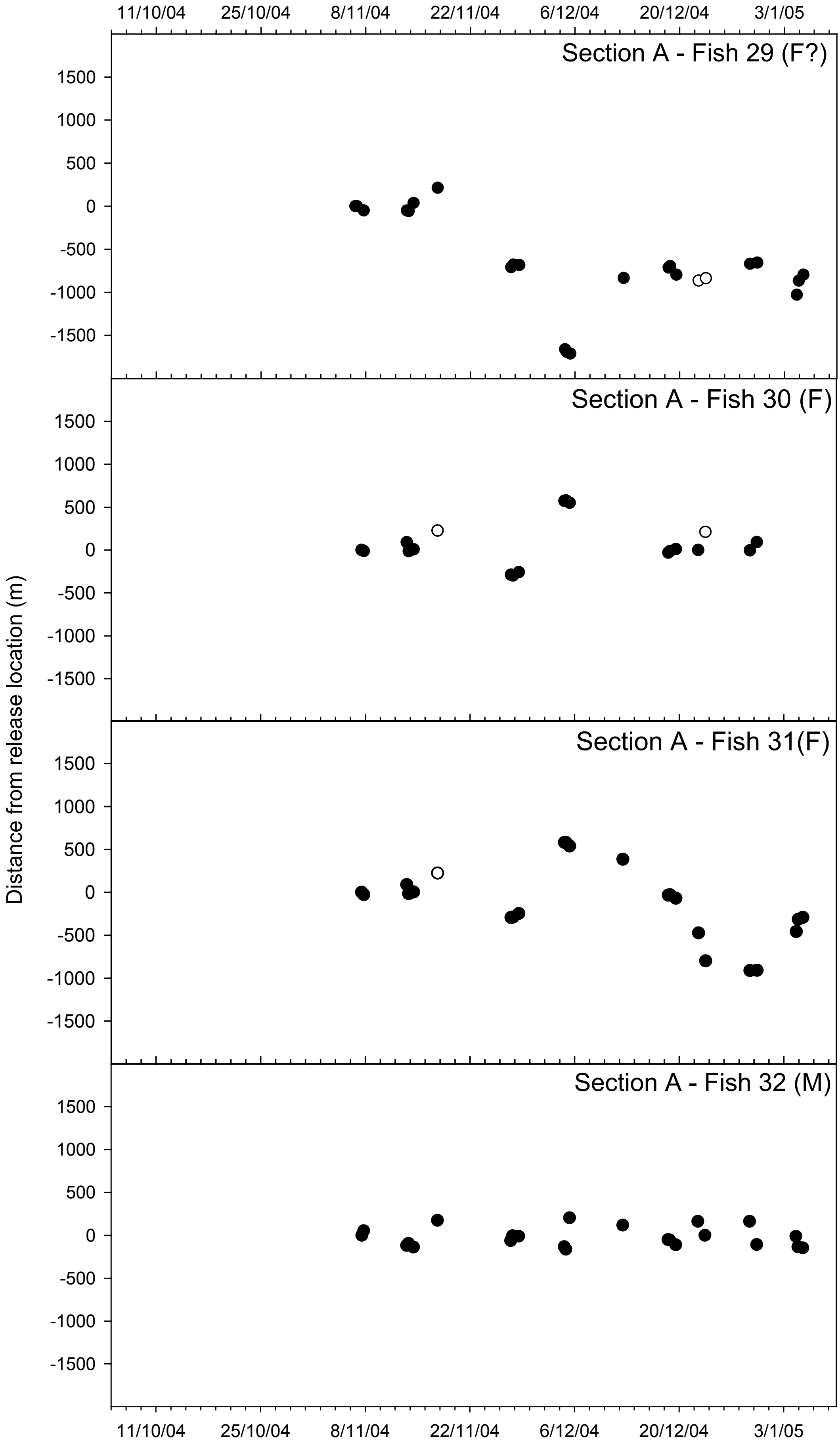


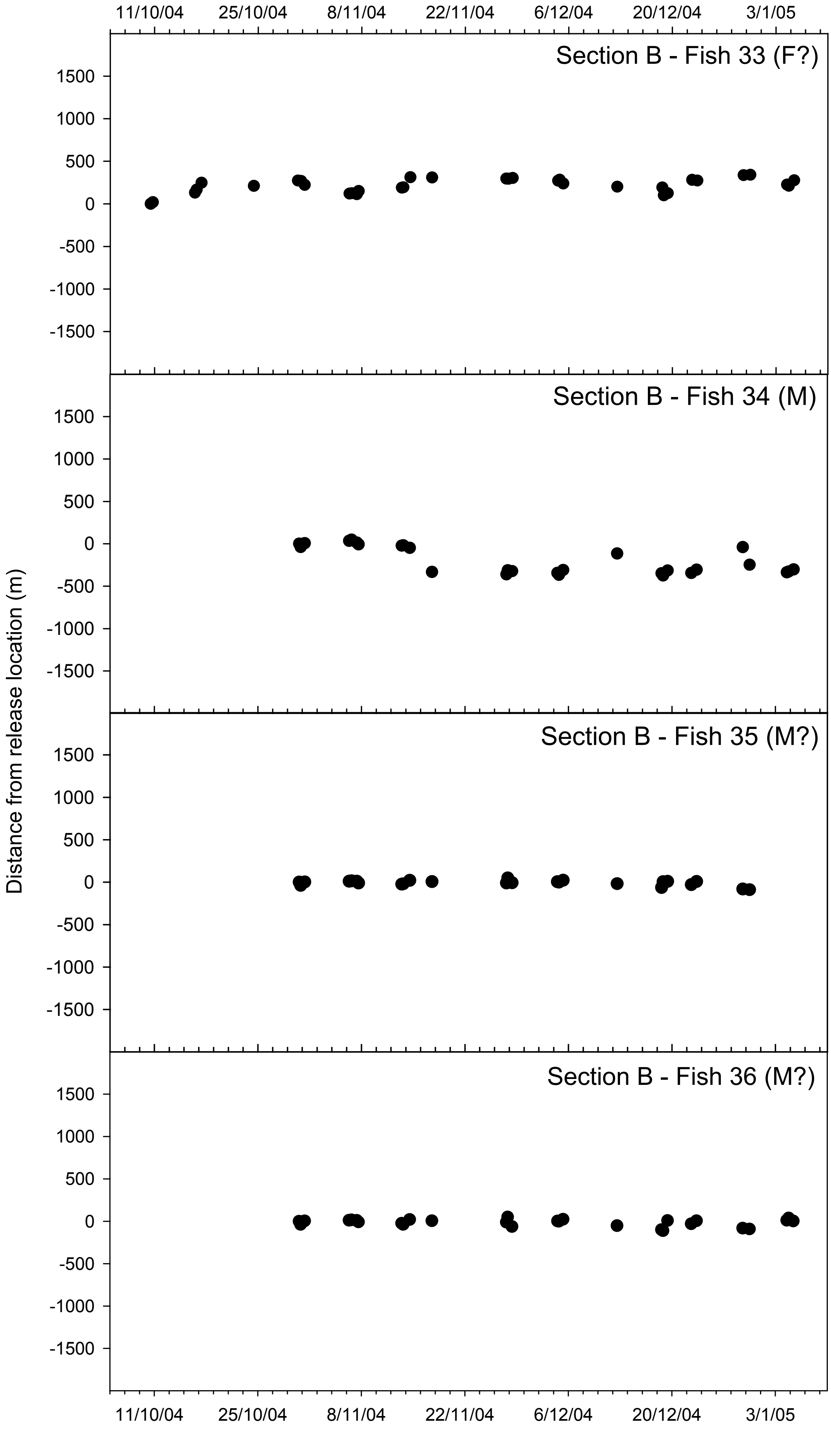
1/1/04
1/2/04
1/3/04
1/4/04
1/5/04
1/6/04
1/7/04
Section C - Fish 17 (F)
Section C - Fish 18 (M)
Section C - Fish 19 (F)
Section C - Fish 20 (F)
Distance from release location (m)
2000
1500
1000
500
0
-500
-1000
-1500

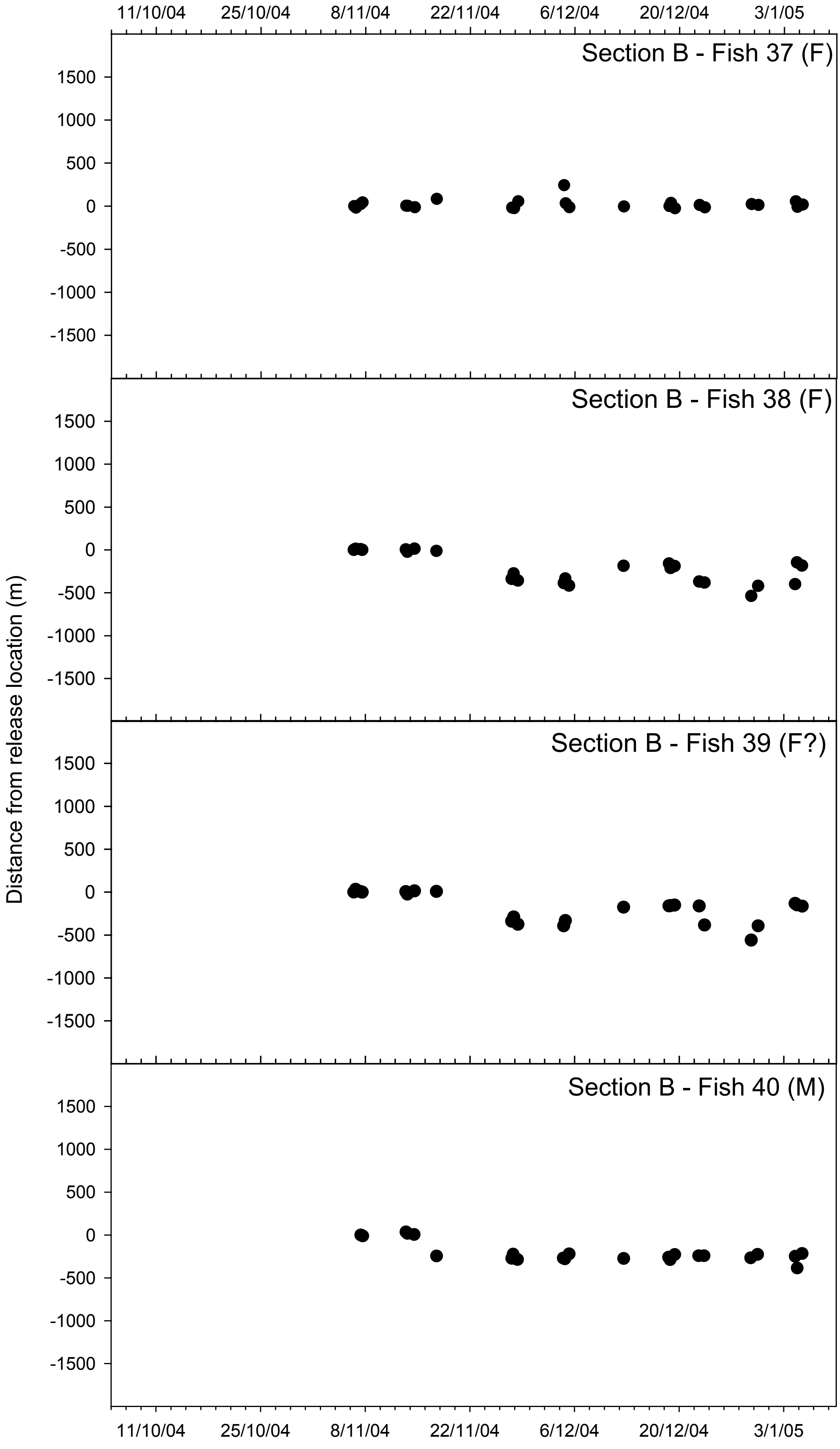

1/1/04
1/2/04
1/3/04
1/4/04
1/5/04
1/6/04
1/7/04
Section C - Fish 21 (F)
Section C - Fish 22 (M)
Section C - Fish 23 (M)
Section C - Fish 24 (F)
Distance from release location (m)

APPENDIX 2 Individual tracks of grayling radio-tagged in the Rye between 10 October and 7 November 2004. Solid symbols represent locations in the Rye, open symbols represent locations in the Dove.




11/10/04
25/10/04
8/11/04
22/11/04
6/12/04
20/12/04
3/1/05
Section A - Fish 29 (F?)
Section A - Fish 30 (F)
Section A - Fish 31(F)
Section A - Fish 32 (M)
1500
1000
500
0
-500
-1000
-1500
Distance from release location (m)


11/10/04
25/10/04
8/11/04
22/11/04
6/12/04
20/12/04
3/1/05
Section B - Fish 33 (F?)
Section B - Fish 34 (M)
Section B - Fish 35 (M?)
Section B - Fish 36 (M?)
1500
1000
500
0
-500
-1000
-1500
Distance from release location (m)


11/10/04
25/10/04
8/11/04
22/11/04
6/12/04
20/12/04
3/1/05
Section B - Fish 37 (F)
Section B - Fish 38 (F)
Section B - Fish 39 (F?)
Section B - Fish 40 (M)
Distance from release location (m)
1500
1000
500
0
-500
-1000
-1500

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