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## Reproductive migration of brown trout in a small Norwegian river studied by telemetry

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The movement of 34 large (39–73 cm standard length) brown trout *Salmo trutta* was monitored using radio telemetry for up to 74 days in Brumunda, a small Norwegian river (mean annual discharge  $3.3 \text{ m}^3 \text{ s}^{-1}$ ) flowing into the large Lake Mjøsa. The maximum range of movement in the river was 20 km. No clear relationships existed between individual movement and water discharge, temperature and barometric pressure. Brown trout migrated at all levels of water discharge. At low discharge ( $<2 \text{ m}^3 \text{ s}^{-1}$ ) movements were nocturnal. A weir 5.3 km from the outlet restricted ascending brown trout at low (*c.*  $6^\circ \text{C}$ ), but not at high (*c.*  $8^\circ \text{C}$ ) water temperatures. Spawning occurred in September to October and tagged individuals spent 2–51 days at the spawning sites. Mean migration speed from tagging to when the fish reached the spawning area, and from when they left the spawning areas and reached the lake was  $1.0$  and  $2.3 \text{ km day}^{-1}$ , respectively. All tagged brown trout that survived spawning returned to the lake after spawning.

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Key words: hydrology; migratory behaviour; radio telemetry; *Salmo trutta*; spawning migration.

### INTRODUCTION

The relationship between environmental factors and the migratory behaviour of fishes in rivers is complex, and several factors such as water discharge, temperature and light may affect the migration singly or together (Banks, 1969; Jonsson, 1991). Water discharge has frequently been reported to influence the upstream migration of salmonids (Banks, 1969), and freshets seem to trigger their upstream migration in rivers (Huntsman, 1948; Alabaster, 1970; Arnekleiv & Kraabøl, 1996; Jensen *et al.*, 1998). The importance of freshets, however, may be weaker in triggering movements after the fish has entered the river (Hellawell *et al.*, 1974; McKinnell *et al.*, 1994; Thorstad & Heggberget, 1998). In small river systems, movement in response to changes in water discharge can be regarded as an antipredator behaviour, as the predation risk is usually high

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during ontogenetic habitat shifts (Mather, 1998). Predation risk can further be reduced if the fishes move during night-time or during freshets when turbidity is high (Abrahams & Kattenfeld, 1997). As a consequence, fishes have been found to migrate upstream chiefly during twilight and dark periods, although daytime migration may be undertaken under special conditions such as during high flow (Jonsson, 1991).

Water temperature is a significant factor affecting important aspects in the life cycle of fishes such as growth (Brett, 1979), reproduction (Heggberget, 1988), and population dynamics (Friedland *et al.*, 2000). Moreover, as fishes are poikilotherms, water temperature also influences their migratory behaviour (Videler, 1993). In a recent study, Quinn & Adams (1996) showed that the timing of the spawning migration of American shad *Alosa sapidissima* (Wilson) and sockeye salmon *Oncorhynchus nerka* (Walbaum) changed differentially to a water temperature decrease of 1.8° C during the last 45 years. In studies conducted over considerably shorter time periods, the importance of water temperature influencing spawning migration seems to vary greatly. Daily variations in the upstream migratory behaviour of salmonids in the River Frome could not be correlated with changes in temperature (Hellawell *et al.*, 1974), whereas the ascent of anadromous brown trout *Salmo trutta* L. in the River Imsa was significantly affected by temperature (Jonsson & Jonsson, 2002). Salmonids restricted to freshwater habitats also demonstrate considerable variation in their displacement response to changes in water temperature, from being little affected (Clapp *et al.*, 1990) to being highly correlated (Davies & Sloane, 1987; Meyers *et al.*, 1992; Ovidio *et al.*, 1998). One reason for these discrepancies may be the duration of the spawning run. It may be expected that spawning runs of species performed over several months should be less correlated with daily fluctuations in environmental factors, than populations that undertake their spawning run over a few weeks. Moreover, fluctuations in environmental variables may have a larger effect in small than in large rivers (Jonsson, 1991).

Brown trout exhibit great variation in life history traits (Klemetsen *et al.*, 2003). Ontogenetic habitat shifts occur in populations performing migrations between spawning areas in running waters and feeding areas in rivers, lakes or at sea. As they mostly spawn in small streams, their movements until they reach their spawning area can easily be recorded. Changes in environmental conditions, such as water discharge due to rainfall, are faster in small streams compared to rivers, and behavioural responses in brown trout to such changes should accordingly be easier to detect. Thus, brown trout is an ideal model for studying migratory behaviour in detail in relation to changes in environmental conditions.

The ascent of sexually mature brown trout to their spawning areas in a small tributary of Lake Mjøsa, the largest lake in Norway, and their return to the lake after spawning were investigated in the present study. The small size of the river enabled detailed radio telemetry to be carried out in two consecutive years twice a day throughout the period the adults spent in the river. The following main questions were raised: (1) Do water discharge and temperature affect the upstream migration of brown trout after they have entered the river? (2) If so, what are the important cues, and when does the movement take place? (3) Are movements affected by time of entry and characteristics of the fish? It was expected that movements were positively correlated with discharge, negatively

correlated with temperature, and nocturnal in periods with low flow. Fish entering late were expected to demonstrate faster upstream migration than those entering early.

## MATERIALS AND METHODS

### STUDY AREA

The River Brumunda flows for 32 km in a south-westerly direction to discharge into Lake Mjøsa in the south-eastern part of Norway (Fig. 1). Brown trout in Brumunda can ascend 21 km to the Bergsbufallet waterfall at an altitude of 330 m above Lake Mjøsa (Fig. 2). In the uppermost stretch used by the brown trout, the River Brumunda is slow-flowing with gravel of small grain size. Further downstream the slope becomes steeper with large-sized gravel interrupted with deep pools of variable surface area. The pools are 2–4 m deep and vary between 100 and 500 m<sup>2</sup>. A weir, Spinneristreket, 5.3 km from the lake was built in the beginning of the 20th century to create an intake reservoir for a hydropower plant. This was shut down in 1950. Spinneristreket is unpassable for brown trout on the right river bank, whereas brown trout may pass at the left river bank. The catchment area of the River Brumunda is 221 km<sup>2</sup>. Extensive ditching in the drainage basin has resulted in rapid changes in the water discharge and increased turbidity in periods with heavy rainfall. Mean annual discharge at the outlet is 3.3 m<sup>3</sup> s<sup>-1</sup>, and the 95 percentile is estimated to be 0.2 m<sup>3</sup> s<sup>-1</sup>. The floods occurring on average once in a 10 and

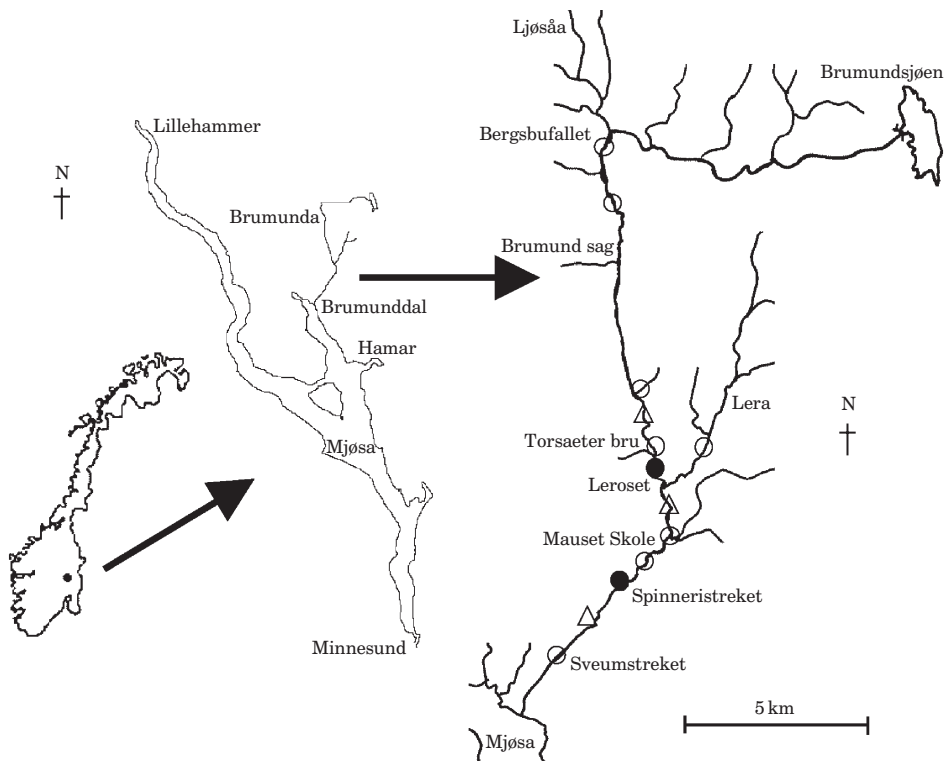


FIG. 1. The River Brumunda in south-eastern Norway with locations of special interest in the spawning run of the piscivorous brown trout population. Number and spawning site of radio-tagged spawners are indicated (○, 1; △, 2–5; ●, >5 fish).

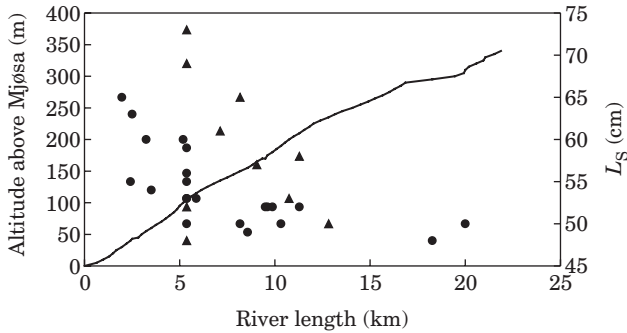


FIG. 2. The altitude of Brumunda in relation to its outlet into Lake Mjøsa, and standard lengths of radio-tagged mature female (●) and male (▲) brown trout at their spawning sites in Brumunda.

100 years period ( $Q_{10}$  and  $Q_{100}$ ) are estimated to be  $72$  and  $100 \text{ m}^3 \text{ s}^{-1}$ , respectively. Under normal conditions ( $Q < Q_{10}$ ) and the water is retained within the river channel.

The brown trout spawning in Brumunda is a migratory population utilizing Lake Mjøsa for feeding and overwintering. Six years of data (A. Rustadbakken, unpubl. data) show that most juveniles leave Brumunda at 3–4 years of age and 18–22 cm in standard length ( $L_S$ ) (range 2–7 years and 12–28 cm, respectively). In Lake Mjøsa, the juveniles achieve an annual increase in length of 10–14 cm, which is similar to the neighbouring brown trout population spawning in Gudbrandslågen (Aass *et al.*, 1989). Growth is significantly reduced after maturation, which occurs after 2–5 years (mean  $\pm$  s.d. =  $3.0 \pm 0.7$  years) in Lake Mjøsa, and few individuals become  $> 65$  cm.

## DATA RECORDING

In 1996 and 1997, a total of 34 brown trout were caught in a fish trap 1.9 km upstream of the outlet of the River Brumunda and tagged with radio transmitters (Table I). The radio transmitters (Model 16M, Model 7PN and Model 3PN, standard flat salmon transmitters, Advanced Telemetry System) were attached beside the dorsal fin (Mellas & Haynes, 1985). Sex and  $L_S$  were determined for each fish. The transmitters used in this study weighed between 10 and 27 g in air and 0.5–1.5% of the mass of the fish. During tagging, the fish were given a continuous supply of running water and the head was kept in darkness to keep them calm. The fish were released at the site of capture immediately after tagging. The tagged fish were 39–73 cm  $L_S$  (mean  $\pm$  s.d. =  $55.1 \pm 6.7$  cm). Of the 34 tagged brown trout, 10 females and seven males were tagged between 28 August and 2 October in 1996, and 13 females and four males between 2 September and 6 October in 1997. They were divided into two categories depending on when migration was initiated. Early migrants ( $n = 22$ ) entered the trap in August to September, and late migrants ( $n = 12$ ) entered the trap in October. Individual spawning migrations were divided into three phases (ascending, spawning and descending) based on the assumption that different environmental factors influence brown trout movement during the different phases. Spawning activity was observed visually for some of the tagged fish.

Each transmitter operated on a unique frequency (30–32 MHz) to ensure recognition of individual fish. The fish were tracked manually twice a day (0600 and 1800 hours) using a receiver coupled to a loop antenna from release until death or the fish left the river in November. Positions were mostly determined with an accuracy of 200–300 m. During the spawning period, positions were determined by a smaller dipole antenna with an accuracy of *c.* 50 m. Visual observations of some radio-tagged fish made the positioning even more accurate.

The individual spawning sites were defined as the area where upstream migration stopped and the downstream migration was initiated. The individual spawning periods

TABLE I. Characteristics of the radio-tagged brown trout on their spawning migration in the River Brumunda in 1996 and 1997. Tagging date, Julian/standard day; migration length, the distance between the lake and the uppermost observed position of individual fish

| Fish number | Tagging date | Sex | $L_S$ (cm) | Migration length (km) | Migration speed ( $\text{km h}^{-1}$ ) |            | Day (Julian) left Brumunda |
|-------------|--------------|-----|------------|-----------------------|--|------------|----------------------------|
|             |              |     |            |                       | Upstream                               | Downstream |                            |
| 1           | 240/28.08.96 | f   | 49         | 8.5                   | 0.3                                    | 2.6        | 273                        |
| 2           | 240/28.08.96 | f   | 55         | 2.5                   | 0.1                                    | 2.3        | 280                        |
| 3           | 240/28.08.96 | f   | 52         | 9.8                   | 0.3                                    | 0.7        | 291                        |
| 4           | 240/28.08.96 | f   | 58         |                       |  |            |                            |
| 5           | 240/28.08.96 | m   | 61         | 7.3                   | 2.1                                    | 0.9        | 301                        |
| 6           | 240/28.08.96 | m   | 48         | 5.3                   | 0.5                                    | 1.1        | 294                        |
| 7           | 240/28.08.96 | m   | 39         |                       |  |            |                            |
| 8           | 268/25.09.96 | f   | 53         | 5.3                   | 1.1                                    | 0.7        | 283                        |
| 9           | 268/25.09.96 | f   | 55         | 5.3                   | 0.9                                    | 0.9        | 282                        |
| 10          | 268/25.09.96 | f   | 50         | 5.3                   | 1.1                                    | 2.7        | 282                        |
| 11          | 268/25.09.96 | m   | 57         | 9.1                   | 1.3                                    | 2.8        | 292                        |
| 12          | 275/02.10.96 | m   | 73         | 5.3                   | 2.2                                    |            |                            |
| 13          | 275/02.10.96 | m   | 65         | 8.3                   | 0.4                                    | 1.7        | 309                        |
| 14          | 275/02.10.96 | f   | 65         | 1.9                   |  | 1.9        | 293                        |
| 15          | 275/02.10.96 | m   | 69         | 5.3                   | 1.4                                    | 2.6        | 300                        |
| 16          | 275/02.10.96 | f   | 54         | 3.5                   | 1.6                                    | 1.9        | 282                        |
| 17          | 275/02.10.96 | f   | 59         | 5.3                   | 1.0                                    | 1.0        | 297                        |
| 18          | 245/02.09.97 | m   | 58         | 11.4                  |  |            |                            |
| 19          | 245/02.09.97 | f   | 52         | 9.6                   | 0.2                                    | 3.1        | 289                        |
| 20          | 245/02.09.97 | f   | 53         | 5.9                   | 0.2                                    | 0.5        | 286                        |
| 21          | 245/02.09.97 | f   | 50         | 10.3                  | 0.2                                    | 5.2        | 293                        |
| 22          | 245/02.09.97 | f   | 50         | 20                    | 0.7                                    | 0.6        | 319                        |
| 23          | 245/02.09.97 | f   | 48         | 18.7                  | 1.6                                    | 9.3        | 275                        |
| 24          | 253/10.09.97 | m   | 52         | 5.3                   | 0.2                                    | 2.7        | 282                        |
| 25          | 253/10.09.97 | f   | 63         | 2.5                   | 0.5                                    | 2.5        | 275                        |
| 26          | 253/10.09.97 | f   | 56         | 5.3                   | 0.3                                    | 0.7        | 282                        |
| 27          | 253/10.09.97 | f   | 60         | 3.2                   | 1.3                                    | 3.2        | 275                        |
| 28          | 253/10.09.97 | f   | 53         | 5.3                   | 0.4                                    | 2.1        | 275                        |
| 29          | 279/06.10.97 | f   | 52         | 9.5                   | 0.6                                    |            |                            |
| 30          | 279/06.10.97 | f   | 60         | 5.2                   | 1.6                                    | 4.2        | 291                        |
| 31          | 279/06.10.97 | f   | 52         | 11.2                  | 1.7                                    |            |                            |
| 32          | 279/06.10.97 | f   | 50         | 8.2                   | 0.8                                    | 0.3        | 322                        |
| 33          | 279/06.10.97 | m   | 50         | 12.8                  | 1.3                                    | 2.9        | 292                        |
| 34          | 279/06.10.97 | m   | 53         | 10.8                  | 4.2                                    |            |                            |

were defined as the period spent at the spawning site, and was generally easy to define from evaluating the migration patterns.

Water temperature ( $T$ ) and discharge ( $Q$ ) were recorded daily at the fish trap (Fig. 3). Water discharge was usually  $<2 \text{ m}^3 \text{ s}^{-1}$  except in rainy periods. There was a decline in  $T$  from  $15\text{--}20^\circ \text{C}$  to *c.*  $2^\circ \text{C}$  during the study in both years. Barometric pressure ( $B$ ) was recorded at a research station 12 km south-east of the river outlet in 1996, and at the fish trap in 1997.  $B$  fluctuated between 970 and 1020 mb.

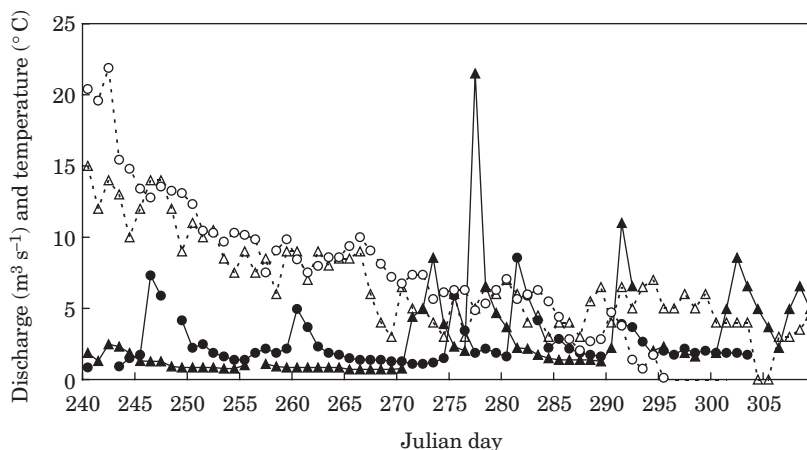


FIG. 3. Water discharge (●, ▲) and temperature (○, △) during the study period in 1996 (▲, △) and 1997 (●, ○). Julian day 244 = 1 September, 274 = 1 October and 305 = 1 November.

## STATISTICS

The data analysis and conclusions are based on fish that had entered Brumunda and were captured 1.9 km upstream the lake. This qualification is important as brown trout may respond differentially to environmental factors when entering the river compared to movements within the river.

Principal component analyses (PCA) were used to reduce the dependency among the three abiotic variables: barometric pressure, water discharge and temperature. The model was based on recordings at day  $x$ , and changes in the variables from day  $x - 1$  to day  $x$ . A  $\ln(Q + 1)$ -transformation was used to meet the assumption of a normal distribution. This resulted in six principal components, of which three were rejected because of an explanation level lower than the selected 15% (Table II). Individual movements were correlated with variables generated by the PCA.

Spearman rank ( $r_{sp}$ ) was used in the correlation analysis, the  $\chi^2$ -test was performed to test for differences in the female: male ratio, and Wilcoxon tests to elucidate differences between groups of fish length, tagging categories, migratory behaviour (migration

TABLE II. Principal component analyses (PCA) of three environmental variables (water discharge  $Q$ , water temperature  $T$ , barometric pressure  $B$ ) recorded at day  $x$  in Brumunda 1996–1997, and the change in these variables from day  $x - 1$  to day  $x$

|                       | Pc1   | Pc2   | Pc3   |
|-----------------------|-------|-------|-------|
| Eigenvalue            | 2.09  | 1.24  | 0.90  |
| Per cent of variation | 34.9  | 20.6  | 15.1  |
| Cumulative per cent   | 34.9  | 55.4  | 70.6  |
| Eigenvectors:         |       |       |       |
| $\ln(Q + 1)$          | 0.55  | -0.35 | 0.21  |
| $\Delta Q$            | 0.53  | 0.001 | 0.22  |
| $T$                   | 0.02  | 0.70  | -0.07 |
| $\Delta T$            | 0.25  | 0.40  | 0.67  |
| $B$                   | -0.48 | 0.18  | 0.44  |
| $\Delta B$            | -0.37 | -0.44 | 0.51  |

distance, speed and nocturnal activity), and duration of the different periods. Number of fish is given for each test unless the whole data set was used (Table I).

## RESULTS

There was no significant difference in the female:male ratio between years ( $\chi^2$ ,  $P=0.27$ ) or between categories of migrants ( $\chi^2$ ,  $P=0.39$ ). The  $L_S$  of tagged trout showed no significant relationship with years (Wilcoxon,  $P=0.9$ ), sexes ( $P=0.44$ ), or categories ( $P=0.09$ ).

The radio-tagged brown trout demonstrated considerable variation in migratory behaviour during their stay in Brumunda (Fig. 4). Some individuals migrated at distinct periods to reach spawning areas, whereas others migrated almost continuously to the spawning areas. The duration at the spawning site was pronounced in some fish but short in others. Postspawning migration was usually rapid. The environmental variables may affect brown trout differentially during these three phases, so they were treated separately. The mean  $\pm$  s.d. duration brown trout spent in Brumunda was  $30.5 \pm 16.1$  days (range 7–74 days,  $n=27$ ).

### UPSTREAM MIGRATION

Brown trout started their spawning run in Brumunda at water temperatures varying between 4 and 20°C. Most fish ( $n=31$ ) continued their ascent immediately after being captured and tagged. In 1996, three fish (numbers 2, 6 and 14) moved downstream after tagging, but they re-entered the trap within 5–30 days. Two fish (numbers 4 and 7) died during the study in 1996 due to angling, and a large male (number 12) died during downstream migration after being observed visually in spawning activity on several occasions. One fish (number

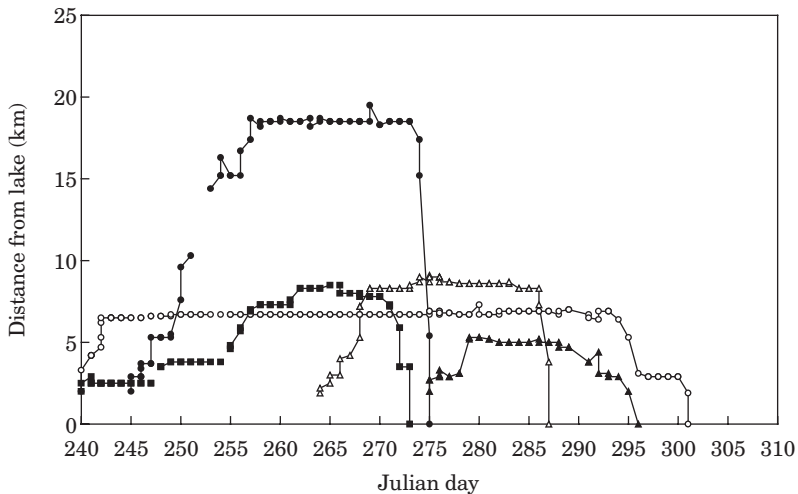


FIG. 4. Migratory movements of five [fish numbers: ■, 1 (female); ○, 5 (male); △, 11 (male); ▲, 17 (female); ●, 23 (female)] radio-tagged brown trout in Brumunda 1996–1997. Note that fish were tagged on different days.



18) was not positioned in the first week, and several periods without signals from this fish indicated transmitter malfunctioning. For the remaining fish, upstream migration, spawning location and downstream migration were recorded without specific problems.

The radio-tagged fish ascended a maximum of 20 km up the river (mean  $\pm$  s.d. =  $7.6 \pm 4.2$  km,  $n = 30$ ). There was no significant difference in upstream migrated distance between sexes (Wilcoxon,  $P = 0.27$ ) or between the two periods ( $P = 0.87$ ). The upstream migration distance was negatively correlated with  $L_S$  for both sexes, but significant only for females (Spearman rank,  $P < 0.001$ ,  $n = 22$ ) (Fig. 2). Two small females migrated almost all the way up to the unpassable Bergsbuffallet waterfall. With these two females omitted, the correlation was still negative but not significant.

Eleven radio-tagged fish stopped at the Spinneristreket, 16 fish passed the waterfall while five stopped their migration below this point. There was no significant difference in the female: male ratio between the fish that passed and those that stopped their upstream migration at the waterfall ( $\chi^2$ ,  $P = 0.95$ ). Fish passing Spinneristreket migrated at a significantly higher water temperature than those that stopped (Wilcoxon,  $P = 0.04$ ) (Fig. 5). There was no significant difference ( $P = 0.50$ ) in water discharge when fish passed and when fish stopped their migration at the weir.

The radio-tagged individuals took from 1 to 41 days (mean  $\pm$  s.d. =  $12.3 \pm 12.0$  days,  $n = 30$ ) on their upstream migration to the spawning areas. The mean individual upstream migration speed varied from  $0.08$  to  $4.15$  km day<sup>-1</sup>, with an overall mean  $\pm$  s.d. of  $1.0 \pm 0.9$  km day<sup>-1</sup> ( $n = 30$ ). The fastest upstream movement registered over a 24 h period was 5 km. There was no difference in upstream migration speed either between years (Wilcoxon,  $P = 0.53$ ) or sexes (Wilcoxon,  $P = 0.10$ ). Late migrants, however migrated significantly (Wilcoxon,  $P = 0.005$ ) faster ( $1.5 \pm 1.0$  km day<sup>-1</sup>,  $n = 11$ ) than early migrants ( $0.7 \pm 0.6$  km day<sup>-1</sup>,  $n = 19$ ). The upstream migration speed was not significantly correlated with body length ( $r_{sp} = 0.26$ ,  $P = 0.16$ ,  $n = 30$ ).

The individual movements between two registrations (morning and evening, and *vice versa*) were tested against the environmental variables measured on the

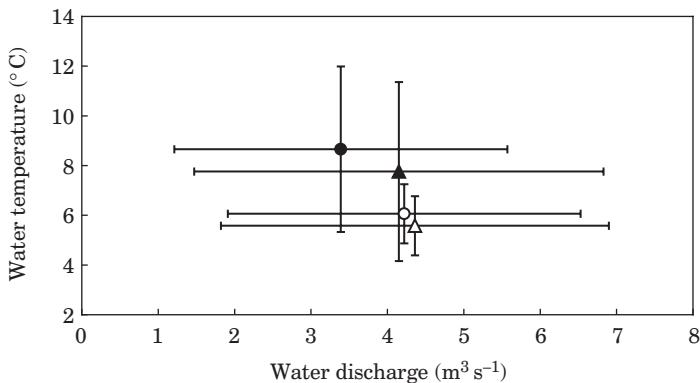


FIG. 5. Mean  $\pm$  s.d. water discharge and temperature when radio-tagged adult female (●,  $n = 10$ ; ○,  $n = 7$ ) and male (▲,  $n = 6$ ; △,  $n = 4$ ) brown trout stopped (○, △) and passed (●, ▲) the Spinneristreket weir in Brumunda during 1996 and 1997.

same day and the day before. Autocorrelation is a serious problem in such an analysis, and could lead to an invalid correlation between observed movements and measured environmental variables. The individual tests, however, showed overall weak correlations between observed within-river movements and the environmental variables represented by the three principal components pc1 (dominated by a  $Q$  effect), pc2 (dominated by a  $T$  effect) and pc3 (dominated by a  $B$  effect) (Table II). Only a significant effect of the pc1 component was found. Two individuals showed a significant correlation between their movements and pc1 measured the same day; one was positive (number 21;  $r_{sp} = 0.49$ ,  $P < 0.01$ ,  $n = 38$ ) and one was negative (number 23;  $r_{sp} = -0.84$ ,  $P = 0.04$ ,  $n = 6$ ). Two individuals showed a significant correlation between their movements and pc1 measured the day before; one was positive (number 21;  $r_{sp} = 0.42$ ,  $P = 0.01$ ,  $n = 37$ ) and one was negative (number 32;  $r_{sp} = -0.89$ ,  $P < 0.01$ ,  $n = 7$ ). Thus,  $Q$ ,  $T$  and  $B$  had only minor effects on the within-river movements of ascending brown trout in Brumunda.

A diurnal effect was found in migratory behaviour at low ( $< 2 \text{ m}^3 \text{ s}^{-1}$ ), but not at high ( $> 2 \text{ m}^3 \text{ s}^{-1}$ )  $Q$ . At low  $Q$ , the mean distance migrated was significantly ( $t$ -test,  $P = 0.003$ ) higher during night-time (mean  $\pm$  s.d. =  $0.56 \pm 0.5$  km,  $n = 25$ ) compared to daytime ( $0.3 \pm 0.5$  km,  $n = 25$ ). At high water discharge there was no significant ( $P = 0.26$ ) difference between movement during the night ( $0.4 \pm 0.4$  km,  $n = 22$ ) and day ( $0.3 \pm 0.3$  km,  $n = 22$ ).

## SPAWNING

Based on the focal observations, together with data on Brumunda brown trout at the local hatchery, the spawning in Brumunda takes place from mid-September to the end of October with highest intensity during the first half of October.

The individual spawning sites were distributed in the area from 1.9 to 20.0 km from the outlet, with the main areas at 2.0–5.3 km and 8.0–13.0 km from the outlet (Fig. 1). One fish (number 29) entered the Lera tributary, 9 km above Mjøsa. The radio tagged fish spent 2–51 days (mean  $\pm$  s.d. =  $10.8 \pm 9.6$  days,  $n = 29$ ) at their spawning sites. There was no significant difference in the duration at the spawning site between years (Wilcoxon,  $P = 0.79$ ), sexes ( $P = 0.87$ ), or periods ( $P = 0.85$ ).

## DOWNSTREAM MIGRATION

After spawning, 27 of the tagged fish started their descent back to Mjøsa. The radio-tagged individuals took on average (mean  $\pm$  s.d.)  $6.2 \pm 8.1$  days (range 1–33 days) on their downstream migration. There was no difference in the time of descent between years (Wilcoxon,  $P = 0.26$ ). Males started their descent later than the females ( $P = 0.005$ ), and late ascending migrants started their descent later than early ascending migrants ( $P = 0.001$ ). The mean individual migration speed downstream varied between  $0.25$  and  $9.25 \text{ km day}^{-1}$ , with an overall mean  $\pm$  s.d. of  $2.23 \pm 1.8 \text{ km day}^{-1}$  ( $n = 27$ ). There was no significant difference in downstream migration speed between years (Wilcoxon,  $P = 0.24$ ), sex ( $P = 0.60$ ), or between categories of migrants ( $P = 0.96$ ).

## DISCUSSION

Migratory behaviour of radio-tagged mature brown trout in the small river Brumunda was negligibly affected by water discharge, temperature and barometric pressure. At low water discharges, migration occurred during the night, and low temperatures restricted brown trout in passing a weir.

Telemetry studies increase the possibility of obtaining data on environmental factors affecting fish migrating upstream to their spawning areas. Handling and tagging may, however, influence the migratory behaviour. The transmitters weighing <1.5% of the fish, are not expected to have any significant effect on swimming performance or spawning activity of salmonids (Mellas & Haynes, 1985; Økland *et al.*, 1995; Arnekleiv & Kraabøl, 1996). Visual observations of several radio-tagged brown trout together with untagged fish during spawning also indicated that their behaviour did not differ. Moreover, 31 of the 34 fish tagged in the trap ascended further upstream immediately after release, and two of these were caught by anglers 2 h and 2 days after release. Thus, the observations strongly indicate that handling and tagging did not adversely affect fish behaviour.

The distance fishes have to migrate in rivers before they reach their spawning areas, could obviously influence the time of river entry. Populations of Atlantic salmon *Salmo salar* L. and *Oncorhynchus* sp. spawning in upper reaches enter earlier than populations with a shorter migration distance (Hawkins, 1987; Groot & Margolis, 1991), probably to reach their specific spawning areas in time. In Brumunda, however, no data indicate that time of river entry was associated with migration distance. The distance brown trout spawners migrate in Brumunda (maximum 20 km) is probably too short to affect time of entry. That no tagged brown trout migrated as far up as the Bergsbufallet (21 km) indicates that the brown trout belong to the migratory population and not to the resident population upstream of Bergsbufallet. Studies of salmonids above and below impassable waterfalls indicate insignificant intermingling resulting from downstream migration (Jonsson, 1982; Vourinen & Berg, 1989). Thus, immigration from the population above the waterfall has a minor effect on the results.

A weak negative trend between  $L_S$  and upstream migration distance was found in both sexes. There is no plausible explanation for this observation. River steepness could have an effect on the size distribution of females along the river. The rationale for this assumption is that gravel size is closely linked with water velocity (Novak, 1973), and larger substrata necessitate increasingly larger fish size to complete nest digging (Reiser & Bjornn, 1979; Ottaway *et al.*, 1981). An indication supporting this is that the smallest female tagged was observed spawning in areas with the lowest steepness and the finest substratum gravel. Similarly, Ovidio *et al.* (1998) found no correlation between brown trout size and migratory distance in their telemetry study of spawning fish. In large rivers with considerable longer migration distance, however, anadromous brown trout migrating to the head waters are larger than those migrating shorter distances (L'Abée-Lund, 1991).

After entering Brumunda, brown trout migrated both at high and low water flows, and there was no clear correlation between movement and hydraulic conditions. This was unexpected, as in small systems like Brumunda high

water discharge should be a more important stimulus for brown trout migrations than in larger systems. One reason for the observations may be that the amount of water is not a physical limitation for upstream migration. Similar behaviour was found in brown trout migrating in the neighbouring river, Gudbrandsdalslågen. When the fish had passed the outlet from a hydropower station, they migrated through coarse-grained riffle areas even at low ( $5 \text{ m}^3 \text{ s}^{-1}$ ; annual mean  $253 \text{ m}^3 \text{ s}^{-1}$ ) discharges (Arnekleiv & Kraabøl, 1996). Additionally, increased turbidity connected with rainfall may also have influenced the migration behaviour, and reduced the importance of water volume as an antipredator mechanism (Abrahams & Kattenfeld, 1997). On the other hand, low water discharge ( $<2 \text{ m}^3 \text{ s}^{-1}$ ) resulted in a shift towards nocturnal migration, which can be a result of innate antipredator behaviour. Nocturnal movement has frequently been documented in upstream migrating adult brown trout (Hellowell *et al.*, 1974; Clapp *et al.*, 1990; Ovidio *et al.*, 1998; Young, 1999), and in juvenile behaviour at low temperatures in rivers (Heggenes *et al.*, 1993). The lack of a relationship between upstream migration and hydraulic conditions in the present study is supported by other telemetry studies on brown trout (Evans, 1994) and the comparable cutthroat trout *Oncorhynchus clarki* (Richardson) (Brown & Mackay, 1995), but contradicts other telemetry studies of brown trout during their spawning migration (Clapp *et al.*, 1990; Meyers *et al.*, 1992; Ovidio, 1999). One plausible reason for this discrepancy in reaction norm to changes in discharge is the complexity in the patterns of movements of adult brown trout. Some of these studies were conducted in large rivers over an entire year cycle (Clapp *et al.*, 1990; Meyers *et al.*, 1992; Ovidio *et al.*, 1998; Ovidio, 1999), whereas others were restricted to distinct spawning run (Evans, 1994; Brown & Mackay, 1995; present study). As brown trout is a polymorphic species with distinct ontogenetic habitats shifts (Klemetsen *et al.*, 2003) connected both to individual development and seasonal rhythm, similarity in reaction norm to environmental variables over a year should not be expected. On the other hand all these studies, in common, focus on frequent recording of individuals throughout their prespawning, spawning and postspawning movements. Thus, they are not directly comparable to studies performed to describe the entrance of mature adult brown trout to a river for spawning (Rayner, 1942; Stuart, 1957; Davies & Sloane, 1987; Jensen & Aass, 1995; Jonsson & Jonsson, 2002). The latter studies have used point observations of fish sampled at physical obstacles, and related entrance of fish to environmental factors. One major difference between telemetry and point observations is that while telemetry reveals movement behaviour under natural conditions, point observations, chiefly carried out at the entrance of the river, may depend on specific conditions that trigger fishes to enter. These may not be identical with factors affecting movement further upstream. Smith & Smith (1997) highlighted the limitations of point observations of migration to identify environmental stimuli for migration in their study of Atlantic salmon entering the Aberdeenshire Dee in relation to effect of the tidal phase.

Fishes may depend on special hydraulic conditions to pass physical obstacles. As they are poikilotherms, cold water increases the problems of passing obstacles for ascending fishes (Jonsson, 1991). In Brumunda, 11 of the total 34 radio-tagged individuals stopped their upstream migration at the Spinneristreket.

Brown trout passing the weir experienced on average significantly higher water temperature than those that stopped their upstream migration at the weir, although a considerable overlap in temperature between those passing and those that stopped was evident. The mean temperature for brown trout ascending Spinneristreket was *c.* 8° C, and similar to that Ovidio & Philippart (2002) found for brown trout clearing obstacles in European rivers. This temperature has also been documented as essential in Atlantic salmon passing physical obstacles (Mills & Graesser, 1981, Jensen *et al.*, 1998) although no threshold temperature of migrating Atlantic salmon was found in the River Erne (Jackson & Howie, 1967). Similarities in water temperature requirements to ascend physical obstacles within and between closely related species indicate some general physiological requirements probably connected to swimming performance as this is greatly influenced by water temperature (Videler, 1993).

The exact migration speed in rivers is difficult to assess, as the migration may be discontinuous between two registrations. Estimation of mean migration speed between two registrations neglects any breaks. Moreover, the estimate of migration speed is related to distance on land and do not take into account any displacement due to water velocity. Despite the uncertainty in this estimate, the brown trout in Brumunda demonstrated considerable similarity in the mean and maximum migration speed with previous brown trout studies during their ascent to the spawning areas (Clapp *et al.*, 1990; Meyers *et al.*, 1992; Evans, 1994; Ovidio *et al.*, 1998; Ovidio, 1999). Moreover, the post-reproduction movement in brown trout seems in general to be rapid *c.* 5–9 km day<sup>-1</sup> (Meyers *et al.*, 1992; Ovidio *et al.*, 1998; Ovidio, 1999; this study). These migration characteristics indicate species-specific properties when the spawning run of brown trout has been initiated.

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