*Folia Zool.* – 53(1): 87–98 (2004)

# Spawning movements of European grayling *Thymallus thymallus* in the River Aisne (Belgium)

Michaël OVIDIO*, Denis PARKINSON, Damien SONNY and Jean-Claude PHILIPPART

*University of Liège, Life Sciences Department, Laboratory of Fish Demography and Hydroecology, 10 Chemin de la Justice, B-4500 Tihange, Belgium; *e-mail: m.ovidio@ulg.ac.be*

Received 20 February 2003; Accepted 15 March 2004

A b s t r a c t . In three consecutive years (1998 to 2000), 20 adult grayling *Thymallus thymallus* (L.) (FL ± SD: 326 ± 43 mm) were radio-tracked during *circum* reproduction period (February to May) in the River Aisne, Belgium. Before the spawning period, grayling remained consistently in the pool-riffle sequence in which they had been captured. Pre-spawning migration time extended from 7 to 29 March. Distances travelled during the spawning migration ranged from 70 to 4980 m (mean ± S.E.: 1234 ± 328 m). Spawning migrations started under conditions of decreasing water level and increasing water temperature in a thermal range (daily mean T°) from 5 to 8 °C. Spawners remained from 1 to 31 days (mean ± S.D.: 10.4 ± 9.8 days) at the spawning grounds and performed a post-spawning homing from 28 March to 18 April in decreasing water flow and in a thermal range (daily mean T°) from 7 to 11 °C. This study demonstrates that migration patterns of grayling are similar between years, but with a timing adjusted as a response to annual variations of the hydroclimatic conditions.

**Key words**: fish-telemetry, home-range, River Meuse, migrations, between-year variation

## Introduction

In the 1970s, the European grayling *Thymallus thymallus* (L.), (family Thymallidae) was classified as a highly vulnerable fish species (Appendix III, Bern Convention, Council of Europe, 1979). Its biotopes have been severely damaged by human activities since the early nineteenth century and many populations have been reduced throughout Europe (P h i l i p p a r t & V r a n k e n 1983, M a l l e t et al. 2000). Currently, there is an increasing need to conserve and enhance grayling populations by stocking and habitat restoration (N y k ä n e n et al. 2001). However, effective management programmes cannot be planned without an understanding of the biological requirements of the species throughout its life cycle.

Most studies on the European grayling started in the last twenty years. The general life cycle was described by N o r t h c o t e (1995) and studies on habitat preferences were well documented (G ö n c z i 1989, S e m p e s k i & G a u d i n , 1995a,1995b, N y k ä n e n et al. 2001), including habitat modelling for different age-classes (M a l l e t et al. 2000). The intragravel life of embryos until emergence was studied by D ' H u l s t è r e & P h i l i p p a r t (1982), B a r d o n n e t & G a u d i n (1990a, 1990b), B a r d o n n e t et al. (1993) and P a r k i n s o n et al. (1999). F a b r i c i u s & G u s t a f s o n (1955), P e r s a t & Z a k h a r i a (1992), P o n c i n (1996), D a r c h a m b e a u & P o n c i n (1997) studied reproductive behaviour and H a u g e n & R y g g (1996) the food composition.

Data on migrations and mobility patterns of *Thymallus* sp. are scarce. The first studies were performed in lakes, i.e. on *Thymallus articus* (W i t k o w s k i & K o w a l e w s k i

1988, Beauchamps 1990), and on *T. thymallus* (Kristiansen & Døving 1996), and were based essentially on mark-recapture methods. Recently, detailed studies of individual behaviour have been undertaken in watercourses using radio-telemetry (Parkinson et al. 1999b, Meyer 2001, Nykänen et al. 2001). These studies, on a single year basis, provided new information on the species's diel activity patterns, the extent of its spawning migrations, the relationships with environmental variables, and habitat use by individual fish.

The aim of the present study, which builds on a preliminary study by Parkinson et al. 1999b was to analyse the *circum* reproduction movements of the European grayling in the River Aisne over three consecutive years in order to test whether their spawning mobility was related to various environmental conditions.

## Study Area

The River Aisne is a typical and relatively undisturbed salmonid brook (a tributary of the R. Ourthe) in the Belgian Ardenne. The Aisne, which flows into the River Ourthe (River Meuse basin) at Bomal-sur-Ourthe (Fig. 1), is 35-km long (sub-basin: 184 $km^2$) and has a mean annual discharge of 2.4 $m^3 s^{-1}$ (data from 1976 to 1986). It has a mean slope of 2.78 % and a mean width of about 10 m in the lower course. Mean annual water temperature averages 9.4° C (min. and max.: 0–19°C; records from 1988 to 2000). In the lower part of the Aisne, the fish assemblage is typical of the trout/grayling zones (Huet 1949) and is essentially composed of grayling (60.9% of the biomass) and brown trout *Salmo trutta* (36.5 % of the biomass) and small-bodied species (bullhead *Cottus gobio*, river lamprey *Lampetra planeri*,

**Table 1.** Characteristics of the grayling radio-tagged prior to spawning in the River Aisne between 1998 and 2000. Tag ratio is: tag weight/fish body weight. (see Fig. 1 for capture site locations).

| Fish code | Fork length (mm) | Body weight (g) | Sex | Date of capture | Capture Site | Tag Ratio (%) |
|---|---|---|---|---|---|---|
| M1 | 388 | 689 | M | 27 Feb.1998 | A | 0.77 |
| M2 | 383 | 619 | M | 27 Feb.1998 | A | 0.89 |
| M3 | 326 | 394 | M | 27 Feb.1998 | A | 1.40 |
| M4 | 323 | 394 | M | 27 Feb.1998 | A | 1.40 |
| F5 | 339 | 514 | F | 27 Feb.1998 | A | 1.07 |
| F6 | 324 | 428 | F | 27 Feb.1998 | A | 1.31 |
| F7 | 345 | 375 | F | 11 Mar.1999 | A | 1.57 |
| M8 | 348 | 373 | M | 11 Mar.1999 | A | 1.58 |
| F9 | 299 | 298 | F | 11 Mar.1999 | A | 1.98 |
| M10 | 323 | 336 | M | 11 Mar.1999 | A | 1.76 |
| M11 | 303 | 302 | M | 11 Mar.1999 | A | 1.95 |
| M12 | 300 | 280 | M | 11 Mar.1999 | A | 2.11 |
| F13 | 311 | 344 | F | 21 Mar.1999 | B | 1.92 |
| M14 | 322 | 294 | M | 21 Mar. 1999 | B | 2.24 |
| M15 | 455 | 349 | M | 29 Feb.2000 | C | 1.14 |
| F16 | 275 | 218 | F | 29 Feb.2000 | C | 1.83 |
| F17 | 272 | 216 | F | 29 Feb.2000 | C | 1.85 |
| M18 | 291 | 261 | M | 29 Feb.2000 | C | 1.53 |
| M19 | 280 | 227 | M | 29 Feb.2000 | B | 1.76 |
| M20 | 316 | 315 | M | 29 Feb.2000 | B | 1.26 |

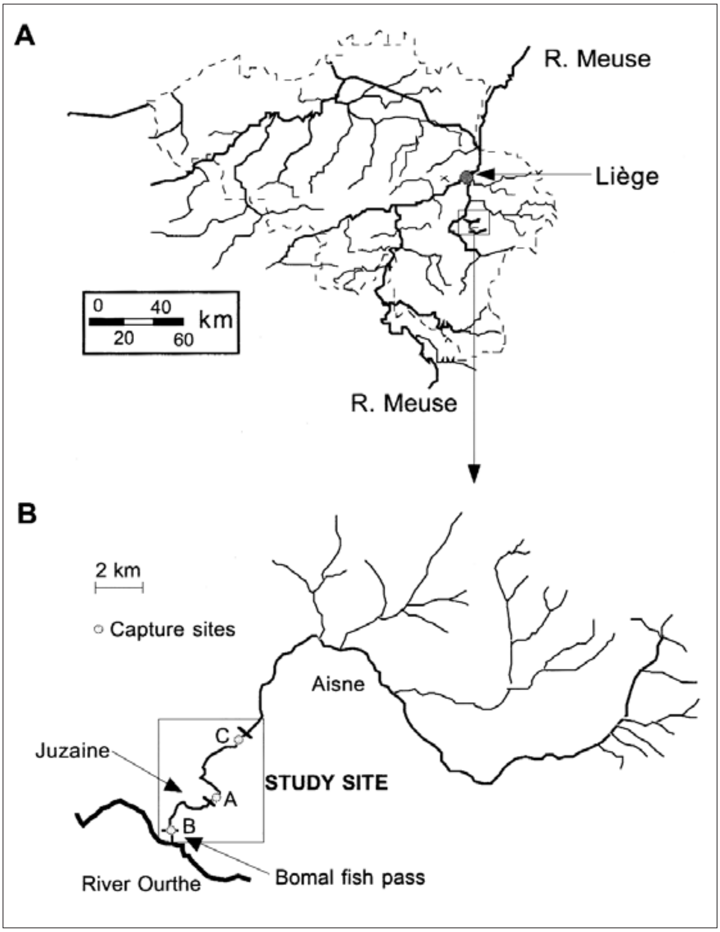


**Fig. 1.** (A) Location of the River Aisne sub-basin in Belgium. (B) The Aisne stream sub-basin, transverse bars represent weirs and dam that may interfere with the free circulation of fish.

European minnow *Phoxinus phoxinus*). The study area contains several small weirs (0.77 to 0.98 m high), which do not interfere with the upstream movements of brown trout (O v i d i o et al. 1998, O v i d i o 1999, O v i d i o & P h i l i p p a r t 2002), and were deemed to cause no major obstruction to the upstream migrations of grayling individuals (O v i d i o & P h i l i p p a r t 2002).

## Material and Methods

Between 27 February 1998 and 21 March 2000, 16 grayling (Table 1) were captured by electrofishing in various parts of the study area (Fig. 1) and additional 4 migrants from the River Ourthe or lower Aisne were captured in the fish pass at Bomal weir (capture site C, Fig.1). After submersion of the fish in a solution of 2-phenoxy-ethanol (0.2 ml $l^{-1}$), a radio transmitter (40 MHz, internal coil antenna, 3.9 to 6.0 g in air, ATS Inc.) was implanted into their body cavity through a midventral incision (before the papilla), which was subsequently closed by two or three separate stitches using sterile 3–0 catgut on 16-mm triangular cutting (Parkinson et al. 1999). Inspection of the gonads during tagging confirmed that all individuals were mature. The tag ratio (tag weight/fish body weight) in the air was always <2.24% and was considered to cause no major impairment of fish performance (Parkinson et al. 1999). In order to avoid any adverse effect of long-term post-operation care on their behaviour, the fish were released at their exact capture site as soon as they had recovered their equilibrium and showed spontaneous swimming activity (about 5 min after surgery).

The grayling were located with an accuracy of 5 to 10 $m^2$ by bi-angulation (Fieldmaster receiver and loop antenna; ATS Inc.) during daylight hours. In 1998 and 1999, grayling were located at least 6 times a week during the migrations associated with spawning, and, from 2 to 3 times a week after the spawning period. In 2000, the fish were located at least 6 times a week during the entire tracking period. Visual observations were used to detect spawning activity of tagged and non-tagged fish in the stream. Water temperature was monitored every 30 min by a data logger (TidBit , Onset Computer Corp.) located in Juzaine (Fig. 1). Hourly and daily data on river discharge and water level were provided by a gauging station in Juzaine (Data from DGRNE – Division de l'Eau).

Longitudinal movements were determined to the nearest 10 m using a decametre in the field. As the fish were not always located every day and at the same positioning frequency from one year to another, relationships between environmental variables and movements were not performed by statistical analyses, so as to avoid methodological bias (Ovidio et al. 2000). Non-parametrical tests and contingency tables were used to compare male and female resident time on spawning grounds and mean distances travelled among years and seasons.

**Results**

During the pre-spawning period, the home range of the grayling extended from 10 to 950 m (mean ± S.E.: 258±65.28) and varied substantially between individuals, seasons and years (Figs 2, 3 and 4). During this period, grayling remained most of the time in the pool-riffle sequence at which they had been captured but sometimes moved over longer distances during increasing water flow. In early March 1998 (Fig. 2), M2 moved about 1 km upstream during an increase of water temperature and water flow, then downstream again, and settled 500 m upstream of its capture place. In 2000 (Fig. 4), three days after tagging, an important flood was associated with a downstream movement of most individuals.

When considering the three tracking sessions (Figs 2, 3 and 4), migrations started between 7 and 29 March (18 to 29 March 1998, 20 to 28 March 1999 and 7 to 20 March 2000). Distances travelled during the spawning migration ranged from 70 to 4980 m (mean ± S.E.: 1234 ± 328, Figs 2–4). There was no relationship between the size of the individuals and the distance travelled during migration. M4 in 1998 spawned downstream its capture site (Fig. 2) but moved after spawning in late March. F13 and M20 rapidly moved downstream in direction of the River Ourthe just after their captures at Bomal fish pass (Figs 3 and 4). This can be a post-tagging stress or a rapid post-spawning homing within the River Ourthe. In 1999 and 2000, F7 and M18 stayed near their capture site during the entire tracking period and no spawning grounds were detected with their proximity.

Spawning migrations of the grayling captured by electric fishing in the Aisne started under conditions of decreasing water level and increasing water temperature in a thermal range (mean T°) from 5 to 8 °C (Figs 2–4). Females sometimes started moving before males

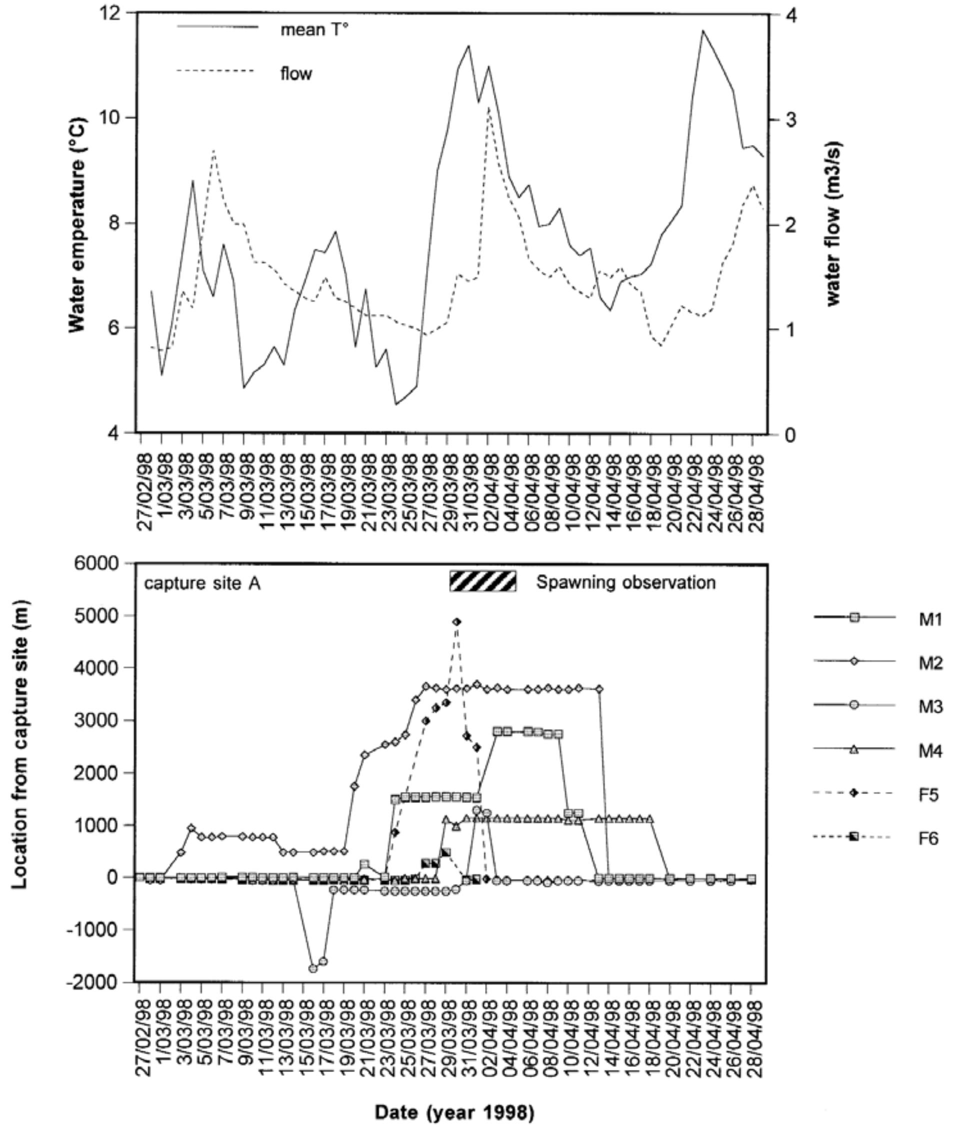


**Fig. 2.** Variations of water level and mean water temperature in the River Aisne during the study in 1998 (upper graph) and positions of the radio-tagged grayling (lower graph). Spawning observation concerned tagged and untagged graylings in the Aisne stream.

or at the same moment. In 1998, M1 and F5 started their spawning migration at the same time but reached different spawning areas. In 1999, F9 migrated on 26 March with M11 and reached the same spawning area. M8 and M10 migrated later. In 2000, males started their spawning migrations before females or at the same time.

From one year to another, males stayed for longer time on spawning grounds (no statistics due to small sample size). When grouping the 1998 to 2000 results, it appears that males stayed at the spawning grounds on average 12.2 ± 9.84 days (min.: 1 and max.

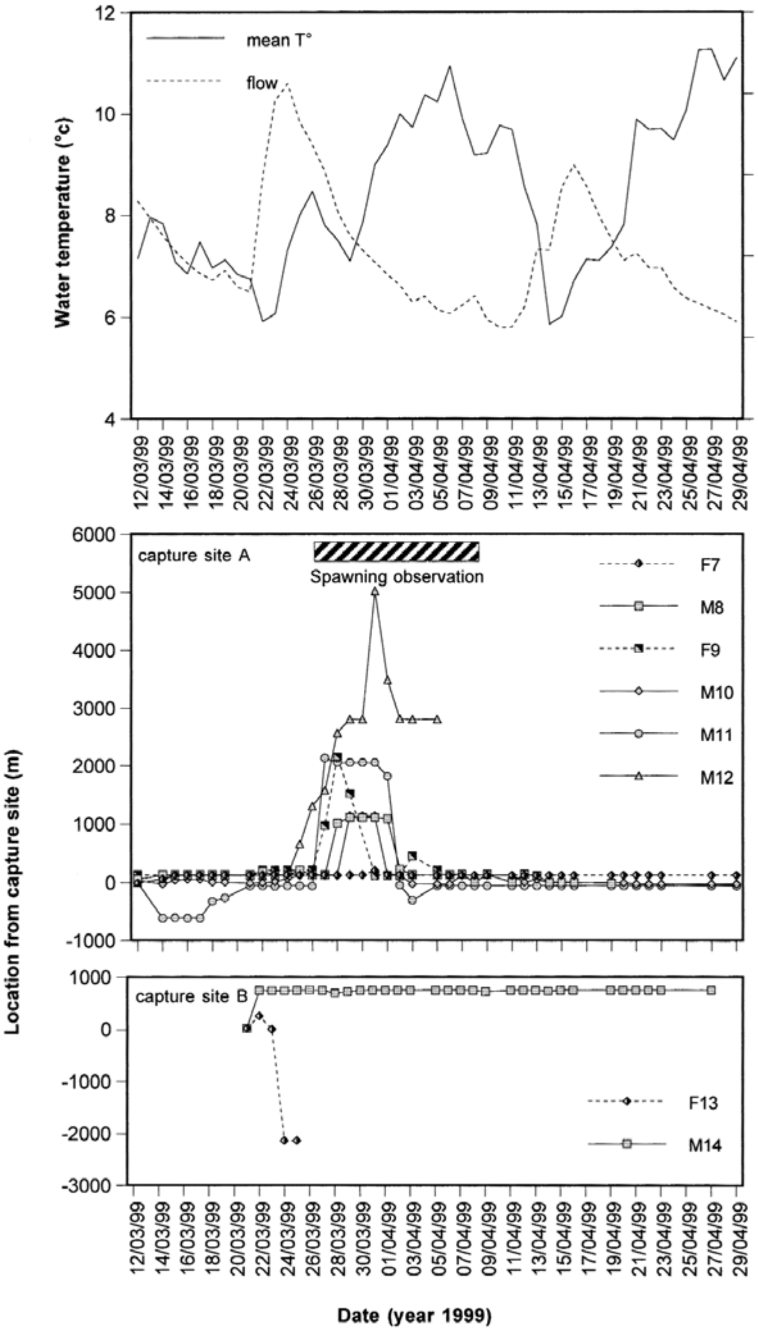


**Fig. 3.** Variations of water level and mean water temperature in the River Aisne during the study in 1999 (upper graph) and positions of the radio-tagged grayling (lower graph). Spawning observation concerned tagged and untagged graylings in the River Aisne stream.

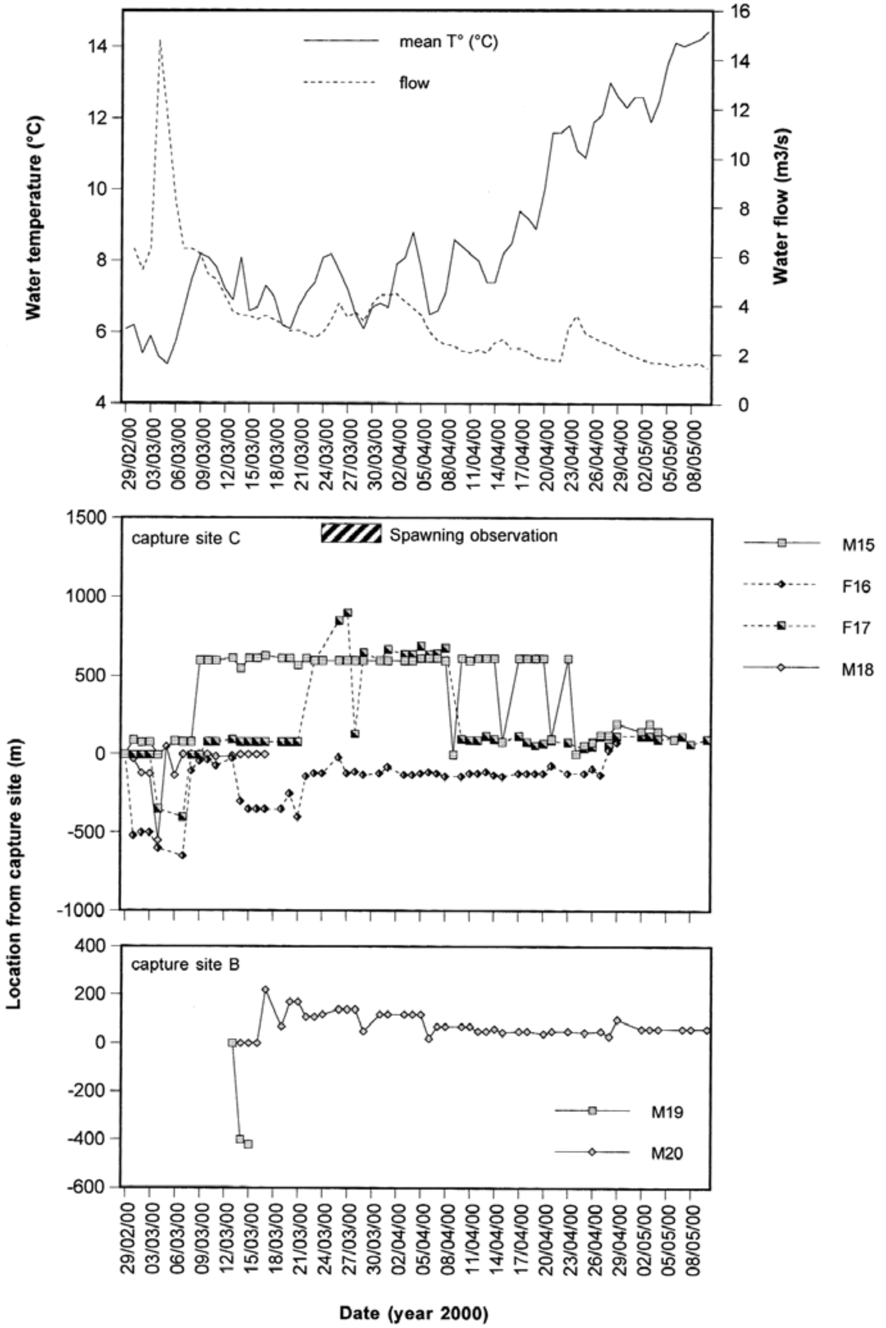


**Fig. 4.** Variations of water level and mean water temperature in the River Aisne during the study in 2000 (upper graph) and positions of the radio-tagged grayling (lower graph). Spawning observation concerned tagged and untagged graylings in the River Aisne.

18 days) and females 7.0 ± 7.6 days (min.: 2 and max.: 31 days), but the difference between the two sexes was not significant (Mann Whitney U test, $P = 0.46$; U = 17). From 1998 to 2000, grayling (both sexes combined) stayed 11.8 ± 9.9; 3.4 ± 1.5 and 19.0 ± 11.5 days respectively, on the spawning grounds, but the difference between the three years was not significant (Kruskal Wallis test; $P = 0.082$; H = 5.008; df = 2). From one year to another, different individuals used identical spawning sites.

In 1998 to 2000, spawning activity was observed between 23 March and 11 April (Figs 2–4) when water temperature was increasing in a thermal range (daily mean T°) from 7 to 11 °C. All the migrating grayling excepted M12 (lost during reproduction), M14 and M20, which stayed near their spawning grounds until the end of the transmitter battery life, returned to their capture site after spawning. Homing was completed within 24h, excepted for M1 and F5 that homed in 3 days. Post-spawning homing occurred from 28 March to 18 April in decreasing water flow and in a thermal range (daily mean T°) from 7 to 11 °C (Figs 2–4).

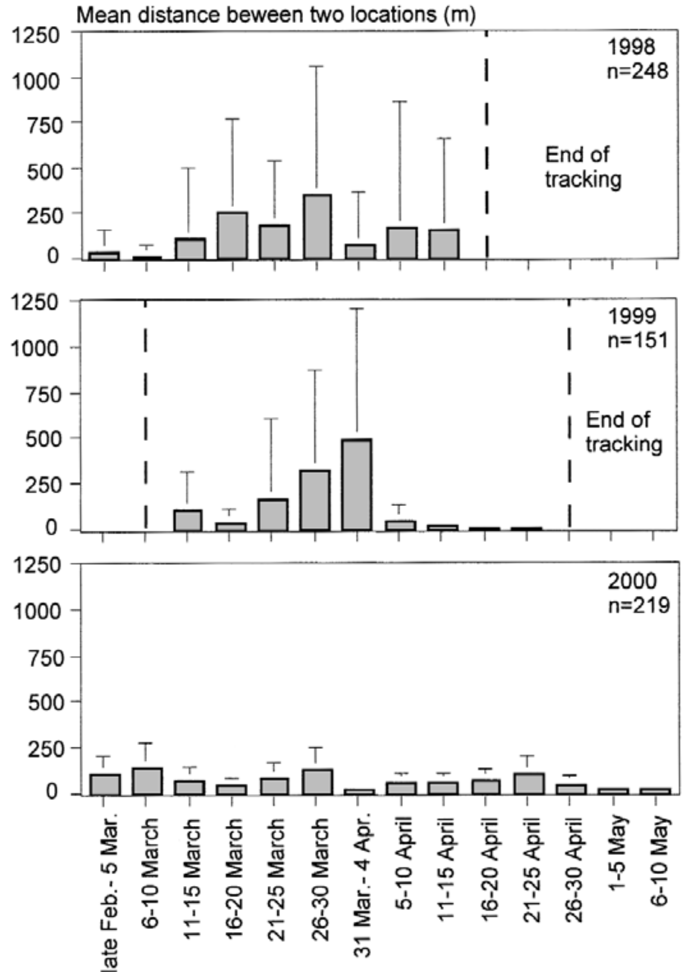


**Fig. 5.** Mean distance travelled between two locations by the grayling from late February to early May.

After post-reproduction homing, grayling generally stayed in the same pool-riffle sequence and showed similar behaviour to those observed before spawning. During this period, important rise of water flow is usually associated with displacements of fish. In 2000, M15 frequently travelled between two residences space-out 600 m apart.

For the mean distances travelled from late February to early May during 1998, 1999 and 2000 (Fig. 5), movement over 5-day periods during 11–15 March to 21–25 April was highly heterogeneous ($P < 0.0001$; $\chi^2 = 822.53$; df = 12) over the three years, indicating between year variability. In 1998 to 2000, mean distances travelled between two successive locations over the entire tracking period were 144.6 m, 150.8 m and 66.2 m, respectively. In 1998 and 1999, grayling accomplished significantly (Mann Whitney U test) longer movements than in 2000 (1998 vs 2000: $P < 0.01$; 1999 vs 2000: $P < 0.05$). No differences were observed between 1998 and 1999.

**Discussion**

The general activity cycle of the grayling during the *circum* reproduction period was quite similar between years in 1998, 1999 and 2000. During the pre- and post-spawning periods, grayling usually showed small-scale movements in the same pool-riffle sequence that mainly corresponded to alternate occupation of different residences. The fish displayed higher mobility patterns during their spawning migration (essentially upstream and as far as 4980 m) and rapidly homed to their established resting-places after reproduction. A similar pattern has been described for a grayling population in the River Ilmenau of Northern Germany (M e y e r 2001). In a large subarctic river, grayling were observed in late summer (13 August – 13 September) to remain mainly in the riffle-section, where they were captured, moving little between consecutive days. But, in autumn (2–30 October) they migrated to potential over-wintering places situated 0–14 km up- or downstream (N y k ä n e n et al. 2001).

During 2000 of our study, mean distances travelled by grayling in the Aisne were homogeneous through the entire tracking period. This could be due to the capture-tagging site being situated in the upper part of the grayling zone in 2000 and not in the middle part as in 1998 and 1999. Our observations also suggest a year-to-year heterogeneity in the precise timing of the movements. This demonstrates the behavioural plasticity of grayling originating from the same river, with a timing of movements adjusted as a response to annual variations of the hydroclimatic conditions.

Tracking sessions indicated that grayling usually started moving to their spawning grounds under conditions of increasing water temperature and decreasing water level (following a flood) in a daily mean thermal range from 5 to 8°C and during a period ranging from the 7 to 29 March. The scouring of the river substratum by the winter floods before the burying of eggs may be particularly advantageous for the development of the embryos (P a r k i n s o n et al. 1999a, 2001). Several tracked individuals, originating from the same shoal, usually started migrating on the same day towards common or different spawning grounds. This underlines the importance of particular environmental signals to enhance the migrations and demonstrates that the location of a spawning area is not exclusively determined by the geographic origin of the fish or by its belonging to a group of individuals.

In the River Ilmenau, grayling started their spawning migrations between 12 and 25 March 1991, and ascended the river at temperatures > 8°C (M e y e r 2001). In Scandinavian and Poland environments, grayling have been reported to start their migrations at 4–6 °C (Witkowski & Kowalewski 1988, Linløken 1993, Kristiansen & Døving 1996). The spawning migration of brown trout (*Salmo trutta*) in the River Aisne also took place when both water temperature and flow varied between consecutive days, in a precise thermal range (Ovidio et al. 1998). Reliance on a combination of stimuli is arguably a more efficient reproduction strategy than responding to a single cue which could occur on several occasions outsides the breeding seasons (Ovidio et al. 1998), and could make the fish lose its fitness. The phenomenon seems similar for the grayling. However, different populations are adapted to their peculiar environment and adequate stimuli to trigger migration may differ from one river to another.

Distances travelled by grayling in the River Aisne were shorter than those reported by Gustafson (1949), Witkowski & Kowalewski (1988), Linløken (1993) and Meyer (2001). This may result from a greater availability of suitable spawning grounds in the Aisne than in other rivers, which means that grayling are not require to move longer distances between feeding and spawning sites. Moreover, the grayling zone (Huet 1947) in the Aisne is only 12 km long. Brown trout in the Aisne have been observed to travel longer upstream distances than grayling (mean 8450 m), with frequent incursions into tributaries (Ovidio 1999), which grayling were never observed to make. Small weirs (height <98 cm) did not disturb grayling migrations. However, in larger rivers, impassable weirs appear to prevent the spawning migrations and must be regarded as a principal obstacle to the maintenance of grayling populations (Meyer 2001). The downstream movement of individual fish to the spawning grounds does not necessarily indicate the start of the spawning migration (Meyer 2001). For example, despite their verified maturity, four individuals we tagged were never observed to migrate in the Aisne. Captures of migrating grayling in the Bomal fish pass reveal the existence of movements from the main watercourse (the River Ourthe) to its tributaries, implying that intraspecific hybridisation can occur between the migrating population from the R. Ourthe and the resident population of the tributary. The use of individual coded visible implanted tags (NMT international) has revealed that some grayling (caught repeatedly in the fish trap of the lower Aisne (Philippart & Ovidio, unpublished results)) from the River Ourthe probably spawn in the river Aisne over successive years.

The three tracking sessions in the Aisne clearly indicated that different individuals usually used the same spawning grounds over several years. One spawning site was used during the three consecutive years and two others during two consecutive years. Other spawning grounds were only used once over years and this may sometimes be due to changes in the river bed after flood or spate events. This observation clearly stresses the need to detect the different spawning sites in the river and to establish a list of the areas that require protection so as to maintain natural recruitment by the species.

Most studies on grayling report that males arrive earlier than females on the spawning grounds, defend territories and court females coming from downstream (Fabricius & Gustafson 1955, Persat & Zakharia 1992, Poncin 1996, Parkinson et al. 1999b), but our observations in the Aisne indicate that females may sometimes start their migration before males. Meyers (2001) observed that some female grayling continued their ascent after they were observed spawning (possibly to spawn in an another site) and that males remained in the same spawning grounds for longer periods.

Grayling remain at the spawning grounds for a period of 1 to 31 days. We found no statistical differences in the time spent on spawning sites between males and females.

M e y e r (2001) observed presence on spawning grounds lasting from 18 to 32 days in the year 1991, whereas downstream movements immediately after spawning have been reported by M ü l l e r & K a r l s s o n (1983) and K r i s t i a n s e n & D ø v i n g (1996). Most individuals in the Aisne homed to the residence area where they were detected prior to spawning migration in one to three days. Post-reproductive homing was also observed by E b e r s t a l l e r et al. (1998) and M e y e r (2001). This behaviour may be considered as a return to an environment that can be optimally used because of its familiarity.

A c k n o w l e d g e m e n t s

This study was financially supported from the Ministry of Fisheries and Nature Conservation of Wallonia (D.G.R.N.E. and Direction of Non-navigable water courses), projects "Obstruction to Fish Migration" and "Meuse Salmon 2000" and is a contribution of the University of Liège (contract SSTC EV/12/31E-2003-2006) to the Belgian Federal Research Project "Fishguard". J.C. P h i l i p p a r t is a Research Associate from the Belgian F.N.R.S., D. P a r k i n s o n was a F.R.I.A. grant holder. The authors wish to thank G. R i m b a u d for field support and G.H. C o p p and an anonymous referee for constructive comments on an earlier version of the manuscript.

## LITERATURE

BARDONNET A. & GAUDIN P. 1990a: Diel pattern of first downstream post-emergence displacement in grayling, *Thymallus thymallus* (L., 1758). *J. Fish Biol. 37: 623–627.*

BARDONNET A. & GAUDIN P. 1990b: Effect of light during ontogeny on the expression of pattern of emergence of grayling fry, *Thymallus thymallus* (L 1758). *Bull. Fr. Pêch. Piscic. 317: 35–49.*

BARDONNET A., GAUDIN P. & THORPE J.E. 1993: Diel rhythm of emergence and of 1st displacement downstream in trout (*Salmo trutta*), Atlantic salmon (*Salmo salar*) and grayling (*Thymallus thymallus*). *J. Fish Biol. 43: 755–762.*

BEAUCHAMPS D.A. 1990: Movements, habitat use, and spawning strategies of Arctic grayling in a subalpine lake tributary. *Northwest Sci. 64: 195–207.*

Bern Convention 1979: Convention on the conservation of European wildlife and natural habitats. *Bern/Berne, Council of Europe, 19/09/1974.*

DARCHAMBEAU F. & PONCIN P. 1997: Field observations on the spawning behaviour of European grayling. *J. Fish Biol. 51: 1066–1068.*

D'HULSTÈRE D. & PHILIPPART J.-C. 1982: Observations sur le comportement d'éclosion et de post-éclosion chez l'ombre commun, *Thymallus thymallus* (L.). *Cah. Ethol. Appl. 2: 63–90.*

EBERSTALLER J., HINTERHOFER M. & PARASIEWICZ P. 1998: The effectiveness of two nature-like bypass channels in an upland Austrian river. In: Jungwirth M., Schmutz S. & Weiss S. (eds); Fish migration and fish bypass. *Blackwell Science Ltd, Oxford: 363–383.*

FABRICIUS E. & GUSTAFSON K.-J. 1955: Observations on the spawning behaviour of the grayling *Thymallus thymallus* (L.). *Rep. Inst. Freshwat. Res. Drottningholm 36: 75–103.*

GÖNCZI A.P. 1989: A study of physical parameters at the spawning sites of the European grayling (*Thymallus thymallus* L.). *Regul. Rivers, Res. Manag. 3: 221–224.*

GUSTAFSON K.-J. 1949: Movements and growth of the grayling. *Rep. Inst. Freshwat. Res. Drottningholm 29: 35–44.*

HAUGEN T. O. & RYGG T.A. 1996: Food- and habitat-segregation in sympatric grayling and brown trout. *J. Fish Biol. 49: 301–318.*

HUET M. 1949: Aperçu de la relation entre la pente et les populations piscicoles des eaux courantes. *Schweiz. Z. Hydrol. 11: 332–351.*

KRISTIANSEN H. & DØVING K.B. 1996: The migration of spawning stocks of grayling *Thymallus thymallus*, in lake Mjøsa, Norway. *Environ. Biol. Fish. 47: 43–50.*

LINLØKEN A. 1993: Efficiency of fishways and impact of dams on the migration of grayling and brown trout in the Glomma river system, south-eastern Norway. *Regul. Rivers, Res. Manag. 8: 145–153.*

MALLET J.P., LAMOUROUX N., SAGNES P. & PERSAT H. 2000: Habitat preferences of European grayling and brown trout in a medium size stream, the Ain river, France. *J. Fish Biol. 56: 1312–1326.*

MEYER L. 2001: Spawning migration of grayling *Thymallus thymallus* (L., 1758) in a Northern German Lowland river. *Arch. Hydrobiol. 152: 99–117.*

MEYER L., KRUSE S., KOLSTER H. & BRUNKEN H. 1998: Die Fichfauna im Einzugsgebiet der mittleren Ilmeneau. Fischökologische Untersuchungen zwischen Medingen und Lüneburg. *Fischökol. Aktuell 11: 11–31.*

MÜLLER K. & KARLSSON L. 1983: The biology of the grayling, *Thymallus thymallus* L. in coastal areas of the Bothnian sea. *Aquilo Ser. Zool. 22: 65–68.*

NORTHCOTE T.G. 1995: Comparative biology and management of Artctic and European grayling (Salmonidae, *Thymallus*). *Rev. Fish Biol. Fish. 5: 141–194.*

NYKÄNEN M. HUUSKO A. & MÄKI-PETÄYS A. 2001: Seasonal changes in the habitat use and movements of adult European grayling in a large subarctic river. *J. Fish Biol. 58: 506–519.*

OVIDIO M. 1999: Annual activity cycle of adult brown trout (*Salmo trutta* L.): a radio-telemetry study in a small stream of the Belgian Ardenne. *Bull. fr. Pêch. Piscic. 352: 1–18.*

OVIDIO M., BARAS E., GOFFAUX D., BIRTLES C. & PHILLIPART J.-C. 1998: Environmental unpredictability rules the autumn migrations of brown trout (*Salmo trutta*) in the Belgian Ardennes. *Hydrobiologia 371/372: 262–273.*

OVIDIO M., PHILIPPART J.-C. & BARAS E. 2000 : Methodological bias in home range and mobility estimates when locating radio-tagged trout, *Salmo trutta*, at different time intervals. *Aquat. Living Resour. 13: 449–454.*

OVIDIO M. & PHILIPPART J.-C. 2002: The impact of small physical obstacles on upstream movements of six species of fish. Synthesis of a five years telemetry study in the River Meuse Basin. *Hydrobiologia 483: 55–69.*

PARKINSON D., PETIT F., HOUBRECHT G. & PHILIPPART J.-C. 2001: Dynamique de modification de l'habitat physique de reproduction des pondeurs lithophiles sous gravier. Cas de deux frayères à ombres dans l'Aisne. *Bull. Soc. Géog. Liège 40: 41–55.*

PARKINSON D., PETIT F., PERPINIEN G. & PHILIPPART J.-C. 1999a: Habitats de reproduction des poissons et processus géomorphologiques dans les rivières à fond caillouteux: essai de synthèse et applications à quelques rivières du bassin de la Meuse. *Bull. Soc. Géog. Liège 36: 31–52.*

PARKINSON D., J.-C. PHILIPPART J.-C. & E. BARAS 1999b: A preliminary investigation of spawning migrations of grayling in a small stream as determined by radio-tracking. *J. Fish. Biol. 55: 172–182.*

PERSAT H. & ZAKHARIA M.E. 1992: The detection of reproductive activity of the grayling *Thymallus thymallus* (L. 1758) by passive listening. *Arch. Hydrobiol. 123: 469–477.*

PHILIPPART J.-C. & VRANKEN M. 1983: Atlas des Poissons de Wallonie, distribution, écologie, éthologie, pêche, conservation. *Cah. Ethol. Appl. 3: 395 pp.*

PONCIN P. 1996: A field observation on the influence of aggressive behaviour on mating success in the European grayling. *J. Fish Biol. 48: 802–804.*

SEMPESKI P. & GAUDIN P. 1995a: Habitat selection by grayling. I. Spawning habitat. *J. Fish Biol. 47: 256–265.*

SEMPESKI P. & GAUDIN P. 1995b: Habitat selection by grayling. Preliminary results on larval and juvenile daytime habitats. *J. Fish Biol. 47: 345–349.*

WITKOWSKI A. & KOWALEWSKI M. 1988: Migration and structure of spawning population of European grayling *Thymallus thymallus* (L.) in the Dunajec basin. *Arch. Hydrobiol. 112: 279–297.*