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Movements of Atlantic salmon migrating upstream through a fish-pass complex in Scotland

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Abstract – Movements of adult Atlantic salmon were tracked through a series of four fish passes and an impoundment on the River Conon system, Northern Scotland. Proportions of fish passing individual obstructions ranged from 63 to 100%. The cumulative effect was that only 4 of the 54 tagged fish reached the spawning areas. The fish were delayed for 1–41 days at a pool-and-overfall ladder and 1–52 days at a Borland fish lift. The fish swam through a 10 km long reservoir at $0.21–1.16\,km{\cdot}h^{-1}$. A total of 13 fish negotiated a 2.5 km long, 3 m diameter diversion tunnel through a mountain to their home river. High levels of electromyogram (EMG) activity were recorded during ascent of a pool-and-overfall fish ladder, indicating that high energy demanding burst swimming was required.

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Key words: salmon migration; fish-pass complex; radio telemetry; electromyogram telemetry

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Un resumen en español se incluye detrás del texto principal de este artículo.

Introduction

Atlantic salmon, *Salmo salar* L., migrating to their spawning grounds, may have to pass a range of natural and man-made obstacles including waterfalls, rapid flowing water, weirs and hydroelectric facilities. Several studies have used radio telemetry to investigate the behaviour of salmon migrating upstream and through fish passes (e.g., Hawkins & Smith 1986; Laughton 1989; Webb 1989; Gowans et al. 1999a,b). Telemetry of integrated muscle electromyograms (EMGi; Kaseloo et al. 1992; McKinley and Power 1992; Weatherley et al. 1996; Briggs & Post 1997) has been used to identify areas of difficult passage during fish migration (Hinch et al. 1996). EMGi can be used directly as an indicator of the intensity of fish activity (Kaseloo et al. 1992) and to evaluate fish-pass designs in relation to the swimming performance of the wild Atlantic salmon (Booth et al. 1997).

Hydroelectric schemes can incorporate several components which may constitute obstacles to migration (Mills 1989). Movements of salmon past dams may occur via fish passes. The efficacy of the pass, in part, determines the impact of the dam on the salmon population. Impoundments above the dams may affect the hydraulic, thermal and chemical characteristics of water, both upstream and downstream of the dam (Mills 1989). An absence of clear directional cues and modification of temperatures may affect salmon migration (Mills 1989). Diversion of water between catchments may interfere with migrations because olfactory cues from natal rivers may be transferred with the water and may lead fish the wrong way. Many hydroelectric schemes in Scotland include dams, impoundments and water transfers (Johnson 1988; Payne 1988), yet the cumulative effects of these structures and processes on upstream passage of fish has not been evaluated (Anonymous 1997). Even fairly small losses at each fish pass may result in large compounded losses throughout an obstructed system.

The present study investigated the return spawning migration of adult salmon to the River

Bran (a tributary of the River Conon), Ross-shire, Northern Scotland. This system has been extensively developed for hydroelectric generation and therefore salmon have to negotiate a series of fish passes and impoundments. They also experience water diversion from neighbouring catchments and are exposed to artificially-induced, wide ranges of daily flows (Mills 1989).

The aims of the study were to investigate: (i) the proportion of fish negotiating each pass and impoundment; (ii) the proportion of fish moving through a water diversion tunnel; (iii) the likely causes of fish mortality; (iv) rates of movements and survival of fish migrating through an impoundment; (v) muscle activities of fish negotiating a pool-and-overfall pass; and (vi) the cumulative impact of losses through the system.

Materials and methods

Study site

The Rriver Conon, Ross-shire, Northern Scotland, was developed for hydroelectric power generation between 1941 and 1961 (Payne 1988). The system includes more than 32 km of tunnels, 24 km of aqueducts, seven main dams and seven power stations (Fig. 1). The present study investigated the movements of salmon from the River Conon into the River Bran and, as became apparent, the River Meig. Prior to entering the study area, fish must negotiate Torr Achilty Dam (*c.* 6 km downstream of Luichart Power Station) via a Borland fish lift, the impoundment above the dam (Loch Achonachie) and the effects of power peaking (large variations in water flow) downstream of Luichart Power Station. Further upstream, Conon Falls fish ladder, Luichart Dam and Borland lift, Loch Luichart, Mossford, Grudie Bridge and Achanalt Power Stations, Achanalt dam and fish ladder, and Achanalt Barrage must all be negotiated by salmon returning to the River Bran (Fig. 1). The River Meig joins the River Conon *c.* 1 km downstream of Luichart Power Station. A Borland fish lift at Meig Dam provides a direct route by which salmon can migrate to spawning grounds above this structure.

Prior to the development of the River Conon system for hydroelectric generation, an impassable waterfall at Conon Falls meant that the River Bran was inaccessible to Atlantic salmon (Menzies 1928; Mills 1964). However, it was then agreed that the North of Scotland Hydroelectric Board would provide a means of fish passage at these falls and others at Achanalt to compensate for loss of habitat elsewhere in the Conon watershed. Stocking operations commenced on the River Bran in 1953 (Mills 1964), but trapping and tagging experiments revealed that very few smolts reached the bottom of Luichart Dam on

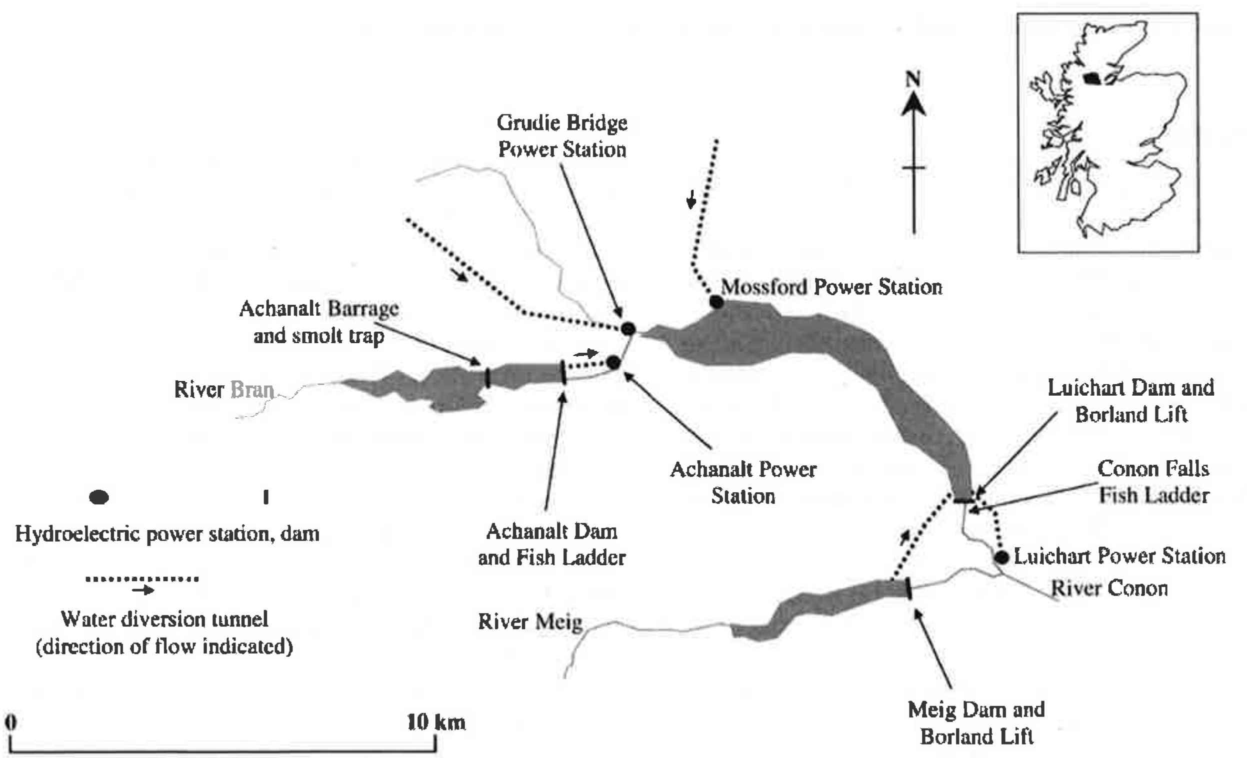

Fig. 1. The main study area on the River Conon, Northern Scotland, indicating the locations of the relevant hydroelectric structures and fish passes.

their way downstream (Mills 1964). Therefore, fry stocking was stopped in 1976. Juvenile stocking recommenced in 1992 in an effort to improve adult returns to the River Conon. In conjunction with this activity, a smolt trap was constructed at Achanalt Barrage (Fig. 1) in 1993, and in 1995, fish ladders at Conon Falls and Achanalt were rebuilt to enable adult salmon to pass upstream into the River Bran. Although suitable spawning habitat is available between Luichart Dam and Achanalt Barrage, no effective downstream fish passage facilities are available at this dam. Hence, the progeny of salmon spawning between Luichart dam and Achanalt Barrage are unable to migrate downstream to the sea.

Conon Falls fish ladder is a whole-river, pool-and-overfall pass with a total length of *c.* 275 m and height of *c.* 22 m. This equates to an overall gradient of 1 : 12.5, but short sections of the pass may be as steep as 1 : 4 and individual steps are as high as 0.8 m. In all, there are 37 pools in the ladder, three of which are large, relatively calm pools in which fish can rest during the ascent. Thus, the fish ladder is split into three major sections: the lower section (in which a fish trap was located), the middle section (between the release and 'resting' pools), and the upper section (from the 'resting pools' to the ladder exit). Flow was maintained at $1.05\,m^3{\cdot}s^{-1}$ between March and early November. For the remainder of the year (out with the main migratory season), water flow was reduced to $0.26\,m^3{\cdot}s^{-1}$.

Luichart Dam is located 120 m upstream from the top of Conon Falls fish ladder (Fig. 1). It is 218.8 m in length and 24.4 m in height. A Borland fish lift built into the dam provides a potential route of passage for fish upstream into Loch Luichart. Under normal flow conditions, all water passing downstream of the dam passes through this structure. The fish lift was programmed to carry out two lifting phases per day, one each in the morning and in the afternoon. Loch Luichart (Fig. 1) is 10 km long and stores water from the River Bran, water piped from other tributaries of the Conon via Mossford Power Station on the shore of the loch and from Loch Meig (Fig. 1). Grudie Bridge Power Station is situated *c.* 500 m upstream from the head of the loch at the confluence of the River Bran and the River Grudie (Fig. 1). Screens are fitted to prevent salmon from entering the tailraces of Mossford and Grudie Bridge power stations or from moving into River Grudie. Achanalt Power Station is a small run-of-the-river electricity generator which discharges into River Bran. It is situated 475 m upstream of the Grudie Bridge Power Station and *c.* 1 km above Loch Luichart (Fig. 1). Water is piped to the power station from Achanalt Dam, 200 m upstream (Fig. 1). A whole-river, pool-and-overfall fish pass provides a potential route for fish to migrate upstream of Achanalt Dam. The overall gradient of this ladder is 1 : 10 (length 200 m, height 20 m), and flow through the pass was maintained at $1.05\,m^3{\cdot}s^{-1}$.

Achanalt Barrage (Fig. 1) is located 800 m upstream of Achanalt Dam and is used to store water for Achanalt Power Station for short periods (Pyefinch & Mills 1963). The construction of this barrage raised the level of Loch a' Chuilinn by *c.* 1.5 m (Mills 1964). A small Borland lift is built into the barrage to provide a potential route for returning salmon to pass upstream. These fish may possibly also move upstream via sluice gates during high discharges.

Meig Dam was constructed to impound water from the River Meig for subsequent transfer to Loch Luichart via a 2.5 km long, 3 m diameter tunnel (Fig. 1; Payne 1988). Water flow through the tunnel is not regulated. The heights of Luichart and Meig Dams are such that the water level in Loch Meig is normally higher than that of Loch Luichart. Hence, the water flows into Loch Luichart; however, there are also periods of reverse flow. A Borland fish lift in Meig Dam provides a potential route for salmon migrating up the River Meig from its confluence with the River Conon. Under normal flow conditions, all water passing downstream of the dam passes through this structure. Fortuitously, in terms of this study, screens at Meig Dam designed to prevent emigrating smolts from entering this tunnel and normally left in place throughout the year were removed for maintenance during the 1996 study period, allowing unrestricted movement of fish. In 1996, the screens were also removed after the smolt run in 1997 to obtain conditions similar to 1996: to allow the passage of fish from the water diversion tunnel into Loch Meig.

Radio-tagging and tracking

Over the periods August–October 1996 and 1997, 54 adult Atlantic salmon (23 in 1996 and 31 in 1997) were captured during their ascent of Conon Falls fish ladder (Fig. 1) and were radio-tagged. With the exception of two fish captured during dewatering of the ladder in 1997 (to install telemetry equipment), all individuals were obtained from a trap in the lowermost section of the fish ladder. Tagged individuals comprised 25% ($n = 93$) in 1996 and 84% ($n = 37$) in 1997 of the total number of fish captured. The trap was checked periodically (three or more times daily). Fish were removed from the holding pen

(1.8 m × 1.2 m, water depth 0.9 m) by dip net and were transferred to a tank of fresh water for examination. Fish that showed signs of disease or physical damage were rejected for tagging, but were released upstream of the trap.

Each fish for radio-tagging was transferred to a tank of water containing an anaesthetic (Benzocaine, 40 mg·l^{-1}; Laird & Oswald 1975) and, once anaesthetised, a radio transmitter (Model TW3, Biotrack, UK; length, 52 mm; diameter, 16 mm; weight in air, 15 g) was gently inserted into its stomach. The radio transmitters used had internal coil antennae. Fish were also tagged externally, at the base of the dorsal fin, with a spaghetti tag to allow visual identification, and the fork length was measured. After tagging, fish were allowed to recover from anaesthesia in a tank of fresh water before being released upstream of the trap. Individual radio tags were identified from a combination of radio frequency (173.8–174.0 MHz) and pulse interval (600–2500 msec). The radio tags, and the tagging and tracking procedures have been outlined in detail elsewhere (e.g., McCleave et al. 1978; Hawkins and Smith 1986).

The locations of radio-tagged fish were determined both by manual bank-side tracking (daily in the vicinity of Conon Falls fish ladder and every 7–10 days elsewhere in the study area) and using automatic listening stations (ALSs) positioned throughout the river catchment. In 1996 and 1997, ALSs were deployed to monitor the movements of radio-tagged salmon in the uppermost chamber of Conon Falls fish ladder, the entrance to the tunnel leading to the Borland lift at Luichart Dam, at Grudie Bridge and Achanalt Power Stations and at Achanalt Dam (Fig. 1). A computer-controlled ALS (Biotrack, UK) was also installed at the top of the Borland lift at Luichart Dam to record the presence and exit of fish from this pass. In the light of the experience gained in 1996, additional radio-tracking equipment was utilised in 1997. A second ALS (Biotack, UK) was installed at Meig Dam throughout the 1997 study period to detect the movements of salmon into Loch Meig. The Meig–Luichart tunnel outfall (immediately above Luichart Dam) was also monitored for a short period of time in 1997 (8–13 September) to record the entry of salmon into the pipeline. The ALSs scanned through the range of tag frequencies at preset intervals (maximum 5 min between successive scans), and thus provided continuous records of presence and absence of each fish throughout the study. Where necessary, antennae reception zones were reduced either by means of in-line attenuation and/or detuned antennae or, as was the case with computer-controlled ALSs, by reducing antennae gain.

Data from both the years were combined to determine the proportion of fish that successfully negotiated each potential obstacle and the apparent delays recorded at these obstacles.

Electromyogram telemetry

Of the adult Atlantic salmon trapped during their ascent of Conon Falls fish ladder (Fig. 1) between August and October 1996 and 1997, 14 (9 in 1996 and 5 in 1997) were tagged with EMGi radio-transmitters (Lotek Engineering Inc., Newmarket, Ontario, Canada; length, 53 mm; diameter, 16 mm; weight in air, 18 g). Each tag comprised a pair of gold-tipped electrodes connected by wires to the main signal processing and radio transmitter unit. Prior to surgery, fish were transferred to a tank of anaesthetic (Benzocaine, 40 mg·l^{-1}; Laird & Oswald 1975). Once anaesthetised, a 3 cm incision was made on the ventral surface of the fish between the pelvic and the anal fins. The main body of the transmitter was sterilised in alcohol and pushed in through this incision and forward into the body cavity of the fish so that it rested above the pelvic girdle. The gold-tipped electrodes were inserted through the white muscle and upwards into the lateral red muscle using two 21-gauge rods (*c.* 2 mm diameter), so that the sensing tips of the electrodes lay *c.* 5 mm apart and immediately below the skin of the fish, close to the lateral line. The rods were then removed leaving the electrodes anchored within the muscle. The antenna wire was then coiled up and gently pushed into the body cavity of the fish. Finally, the incision was closed using three sutures (2/0 Ethicon silk). Surgery lasted for *c.* 5 min. The fork length of each fish was measured and a uniquely numbered spaghetti (Floy) tag was attached to allow visual identification. The fish were then placed in a tank of fresh water to recover from anaesthesia.

Once the tagging procedure was completed, the EMGi-tagged fish were transferred to a holding cage (length 1.2 m, width 0.6 m, height 0.6 m, water depth 0.5 m) that was placed in a large pool in the ladder upstream of the trap. EMGi-tagged fish were held overnight to ensure that the tagging was effective (i.e., an appropriate output was received from the transmitter) and that no adverse effects were apparent. The fish were then released.

Fish positions were determined by manual bank-side tracking, typically every 4–5 h during daylight hours. Signals from EMGi transmitters were received and stored by a microprocessor controlled ALS (SRX_400, Lotek, Ontario, Canada), and the data were downloaded to a PC each day. Downloading, which took *c.* 2 h to complete, was carried out during the hours of darkness when fish are least likely to ascend an obstacle such as Conon Falls fish ladder (Stuart 1962; Gowans et al. 1999a). EMGi activity was stored as a series of pulse intervals, and the reciprocal of this was used as an activity index (transmitter pulse rate in Hertz) before any further analysis was carried out. When no salmon were detected making upstream progress in the ladder, the receiver sampled the data from all the EMGi-tagged fish. When manual tracking revealed that a tagged fish was ascending the ladder, the receiver was adjusted to record only the data transmitted from this fish. In addition, the animal's movements up the ladder were monitored visually and by bank-side radio-tracking so that the recorded EMGi signal could later be related to observed activity and upstream progress.

Additional data

Water temperature was recorded at 30 min intervals in the uppermost chamber of Conon Falls fish ladder. Mean daily water temperature was 13.2 °C (range 8.6–17.1 °C) in 1996 and 12.7 °C (range 7.4–18.4 °C) in 1997. Mean flows in the River Bran upstream of Achanalt Barrage during the 1996 and 1997 study periods were 7.1 and 3.9 $m^3 \cdot s^{-1}$, respectively. Similarly, river flows in the River Meig upstream of Loch Meig were 6.3 and 3.4 $m^3 \cdot s^{-1}$, respectively.

Results

Radio-tracking

There was no significant difference between the mean fork lengths of radio-tagged fish in 1996 (mean 642 mm, range 555–835 mm) and 1997 (mean 658 mm, range 545–840 mm; $df = 51$; $t = -0.78$; $P = 0.44$) (Table 1). Fish weights were not recorded in 1996. In 1997, radio-tagged fish weighed 1250–4500 g (mean 2600 g; Table 1). The proportions of fish passing obstacles varied among structures (Table 2). Of the 54 radio-tagged salmon released in Conon Falls fish ladder, 39 individuals (72.2%) ascended the fish ladder. Of the others, four fish remained alive in the release pool, three fish moved back down the ladder, one of which died after becoming stranded in the rocks, while one later moved up the River Meig past Meig Dam, two fish were found dead or dying with symptoms of major fungal infection (*Saprolegnia* sp.) and four of the transmitters were recovered on the riverbank near the release pool. A further two fish began to ascend the Conon Falls fish ladder above the trap, but did not reach the top of the structure. One of these fish died after becoming stranded amongst the rocks, whilst the transmitter from the other fish was found on the riverbank. Mean time between release and ascent of the ladder was 9.9 days (range 1–41 days).

Of the 39 fish that ascended the Conon Falls fish ladder, one fish could not be tracked further because it regurgitated the radio-transmitter. A total of 24 of 38 radio-tagged salmon (63.2%) that approached the Borland lift at Luichart Dam ascended it (Table 2). Of those fish that failed, six remained between the ladder and the fish lift, three died with symptoms of major fungal infection (*Saprolegnia* sp.) and three radio tags were found on the riverbank. One fish moved back downstream beyond the fish ladder and the fate of the last fish was unknown (the radio-transmitter may have failed or the fish may have moved downstream out of the study area). All the fish that remained below the fish lift were detected at the entrance to the tunnel leading into the Borland lift, but none of them were recorded in the structure during a lifting phase. Fish remained between Conon Falls fish ladder and Luichart Dam (a distance of *c.* 110 m) for 1–52 days (mean 15.3 days) prior to ascent.

Of the 24 fish that entered Loch Luichart, 12 (50%) were detected at Grudie Bridge Power Station (Table 2). The remaining 12 fish were later recorded in the River Meig, having moved through the water diversion tunnel between Lochs Meig and Luichart. Thus, 100% of the fish passed through Loch Luichart. The time taken for fish to migrate through Loch Luichart from Luichart Dam to Grudie Bridge ranged from 8 h 50 min to 48 h 33 min (mean 25 h 36 min), corresponding to mean net swimming speeds of 0.21–1.16 $km \cdot h^{-1}$ (mean 0.51 $km \cdot h^{-1}$) or 0.10–0.53 $bL \cdot s^{-1}$ (mean 0.23 $bL \cdot s^{-1}$).

Of the 12 salmon detected at Grudie Bridge, 11 (92%) reached Achanalt Power Station (Table 2). The remaining fish moved back downstream of Grudie Bridge and was not detected there again. Of the 11 fish that moved upstream, 7 (64%) successfully ascended the fish ladder between Achanalt Power Station and the dam above it. A further two fish began ascent of the fish ladder, but did not reach the top of the structure: both transmitters were found on the riverbank. The other two salmon moved back downstream to Luichart Dam, and one of these fish later entered the River Meig. All seven fish that passed upstream through the Achanalt fish ladder were later detected at the Achanalt Barrage. Of these seven fish, four passed through the barrage and reached the spawning grounds located above this

Table 1. Details of adult Atlantic salmon radio-tagged on the River Conon 1996 and 1997.

Date of Tagging	Fork Length (mm)	Weight (g)	Furthest upstream location	Fate
07 August 1996	575		Release site	Transmitter recovered on riverbank
10 August 1996	625		Luichart Dam	Transmitter recovered on riverbank
04 October 1996	640		Luichart Dam	Transmitter recovered on riverbank
04 October 1996	630		River Meig	Entered Meig via water diversion tunnel
10 August 1996	615		Release site	Tag recovered on riverbank
03 October 1996	635		Achanalt Barrage	Did not pass beyond the barrage
10 August 1996	835		Luichart Dam	Remained downstream of dam
11 August 1996	555		River Bran	Passed upstream of all obstacles
03 October 1996	640		River Bran	Passed upstream of all obstacles
12 August 1996	790		Release site	Moved downstream of study area, entered River Meig via fish lift at Meig dam
12 August 1996	605		Achanalt Barrage	Fish lost, suspected transmitter failure
14 August 1996	595		Grudie Bridge PS	Fish remained downstream of power station
19 August 1996	630		Luichart Dam	Moved downstream of study area
19 August 1996	590		River Bran	Passed upstream of all obstacles
22 August 1996	625		Release site	Tag recovered on riverbank
22 August 1996	600		Achanalt Barrage	Did not pass beyond the barrage
23 August 1996	660		Release site	Found dead, *Saprolegnia* infection
26 August 1996	630		Luichart Dam	Remained downstream of dam
31 August 1996	630		River Meig	Entered Meig via water diversion tunnel
03 October 1996	615		River Bran	Passed upstream of all obstacles
31 August 1996	700		Luichart Dam	Found dead, *Saprolegnia* infection
01 October 1996	560		Release site	Moved downstream of study area
04 October 1996	790		Release site	Transmitter recovered on riverbank
14 August 1997	740	3500	River Meig	Entered Meig via water diversion tunnel
08 September 1997	790	4500	Achanalt Power Station	Moved downstream from Achanalt Power Station to Luichart Dam
16 September 1997	675	3000	River Meig	Entered Meig via water diversion tunnel
15 August 1997	660	2750	Release site	Moved downstream of study area, stranded among rocks, died
10 September 1997	610	2250	River Meig	Entered Meig via water diversion tunnel
04 October 1997	640	2750	River Meig	Entered Meig via water diversion tunnel
17 October 1997	650	2500	Conon Falls fish ladder	Transmitter recovered on riverbank alongside fish ladder
06 August 1997	655	2400	Release site	Remained near release site
06 August 1997	595	2100	River Meig	Entered Meig via water diversion tunnel
08 September 1997	790	3500	Luichart Dam	Remained downstream of dam
15 August 1997	545	1500	River Meig	Entered Meig via water diversion tunnel
16 August 1997			River Meig	Entered Meig via water diversion tunnel
08 September 1997	625	2300	Luichart Dam	Found dead, *Saprolegnia* infection
08 September 1997	840	4000	Release site	Remained near release site
09 September 1997	635	2400	River Meig	Entered Meig via water diversion tunnel
16 September 1997	740	3000	Achanaltfish ladder	Transmitter recovered on riverbank
11 September 1997	710	3100	Luichart Dam	Remained downstream of dam
27 September 1997	650	2700	Luichart Dam	Remained downstream of dam
15 September 1997	550	1500	Luichart Dam	Unknown
18 September 1997	635	2300	Unknown	Regurgitated transmitter prior to ascent of Conon Falls fish ladder (from PIT data)
15 September 1997	730	3300	River Meig	Entered Meig via water diversion tunnel
15 September 1997	635	2300	Achanalt fish ladder	Transmitter recovered on riverbank
19 September 1997	610	2200	Conon Falls fish ladder	Found dead after becoming stranded among rocks during ascent
16 September 1997	605	2100	River Meig	Entered Meig via water diversion tunnel, previously at Achanalt power station
16 September 1997	625	2000	Luichart Dam	Found dead, *Saprolegnia* infection
20 September 1997	670	3000	Luichart Dam	Remained downstream of dam
16 September 1997	545	1250	Release site	Remained near release site
16 September 1997	700	3200	River Meig	Entered Meig via water diversion tunnel
26 September 1997	625	2500	Release site	Found dead, *Saprolegnia* infection
02 October 1997	650	2500	Luichart Dam	Transmitter recovered on riverbank
02 October 1997	600	2000	Release site	Remained near release site

The furthest upstream locations and fates of each fish are noted.

Table 2. The proportions of radio-tagged salmon recorded passing upstream of structures associated with the hydroelectric power generation scheme on the River Conon, Northern Scotland.

Structure	Number of fish downstream of or entering the structure	Number of fish that passed beyond the structure	Percentage success	Cumulative percentage success
Conon Falls fish ladder	54	39	72.2	72.2
Luichart Dam and fish lift	38	24	63.2	45.6
Loch Luichart	24	24	100	45.6
Grudie Bridge Power Station	12	11	91.7	41.8
Achanalt Power Station, dam and fish ladder	11	7	63.6	26.6
Achanalt Barrage	6	4	66.7	17.7

structure, two fish remained below the barrage, while the remaining fish was lost, perhaps as a result of a transmitter failure. Excluding this fish, 66.7% of fish that approached the barrage successfully passed beyond it. It was not possible to determine whether the fish used the Borland fish lift or passed under one of the sluice gates in the barrage.

In summary, 4 of 54 (7.4%) radio-tagged salmon successfully passed beyond Achanalt Barrage. However, this figure includes fish that were lost during tracking (regurgitation or transmitter failure) and does not account for fish that moved into the River Meig from Loch Luichart. Excluding these fish, between 63.2 and 100% of the fish passed upstream beyond each individual obstacle and 17.7% of the fish that arrived at the Conon Falls fish ladder and were not known to be destined for the River Meig succeeded in reaching the spawning grounds (Table 2).

EMG telemetry

The mean fork length of the 13 EMGi-tagged fish was 638 mm (range 595–685 mm; Table 1). Fish weights were not recorded in 1996; in 1997, EMGi-tagged fish weighed 2200–2600 g (mean 2400 g; Table 3). Of these fish, four (31%) individuals were recorded ascending the Conon Falls fish ladder (two in 1996 and two in 1997). The proportions of fish moving upstream through the fish pass did not differ between the groups tagged with EMG and standard transmitters (Fisher's exact test, $P = 0.185$). The remaining nine fish either remained in the release pool throughout the study period (two fish), moved downstream out of the foot of the fish ladder (two fish), were found dead or dying with symptoms of major fungal infection (*Saprolegnia* sp., three fish) or the transmitters were recovered on the riverbank (two fish). Examination of the carcass of one of these latter fish suggested that it was removed from the river by an otter (*Lutra lutra* L.). Damage to this fish was similar to that observed in studies of otter predation by Carss et al. (1990).

The interval between tagging and the start of ascent of those fish that moved up the pass ranged from 1 to 28 days (mean 13 days). EMGi activity was successfully recorded from three of these fish (Fig. 2). The patterns of muscle activity recorded before, during and after the ascent, as determined by manual bank-side tracking, were broadly similar among the individuals (Fig. 3). All three fish were in the ladder at the onset of darkness, which was defined as the hours between evening civil twilight and morning civil twilight, and all three fish remained in the ladder overnight before completing ascent the following day. High levels of activity were recorded while the fish ascended the

Table 3. Details of adult Atlantic salmon radio-tagged with integrated muscle electromyograms (EMGi) transmitters on the River Conon 1996 and 1997.

Date of Capture	Fork Length (mm)	Weight (g)	Fate
07/08/96			Remained in release pool, tag found on riverbank
21/08/96	675		Ascended Conon Falls fish ladder 18/09/96
31/08/96	675		Remained in release pool, then tag found on riverbank
14/09/96	620		Found dead, *Saprolegnia* infection
02/10/96	595		Moved downstream out of study area
05/10/96	685		Ascended Conon Falls fish ladder 08/10/96, no EMGi data available
09/10/96	640		Remained in release pool
10/10/96	675		Moved downstream out of study area
15/09/97	610	2400	Found dead, *Saprolegnia* infection
15/09/97	660	2600	Ascended Conon Falls fish ladder 06/10/97
26/09/97	635	2400	Found dead, *Saprolegnia* infection
11/10/97	605	2200	Remained in release pool
15/10/97	650	2600	Ascended Conon Falls fish ladder 19/10/97

The fate of each fish is also given.

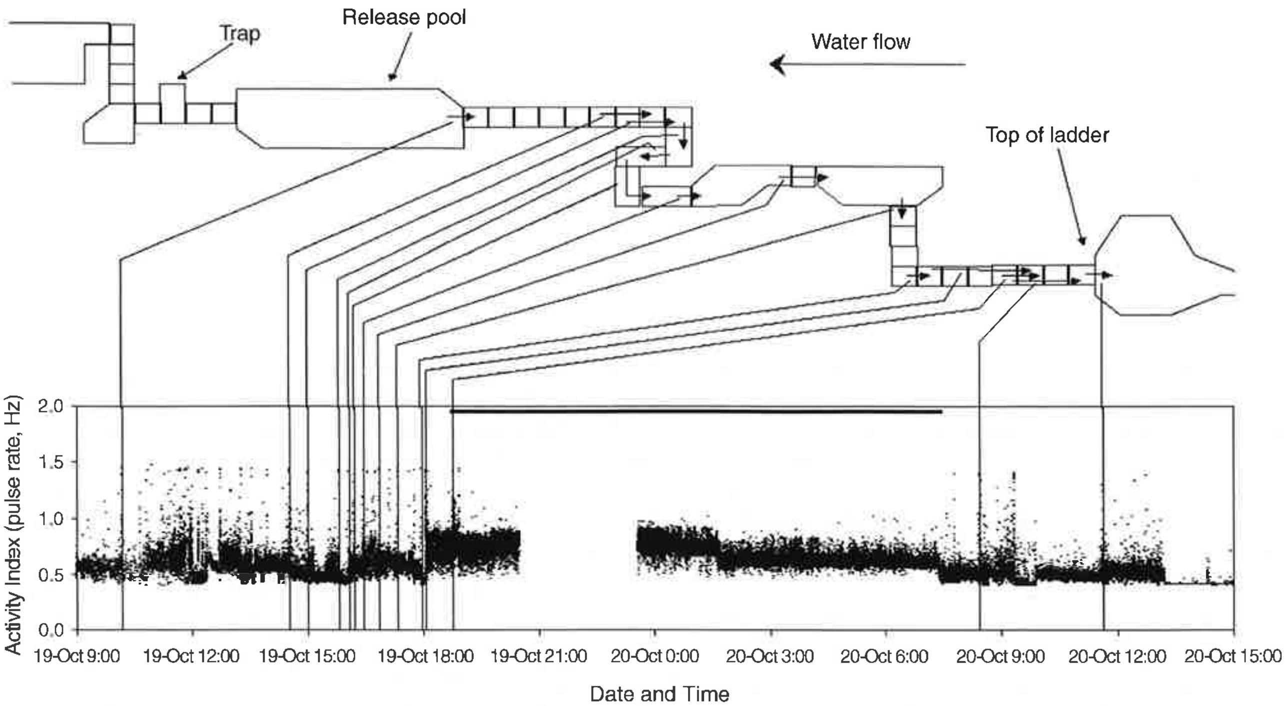

Fig. 2. Example of integrated muscle electromyograms (EMGi) response from an adult Atlantic salmon ascending Conon Falls fish ladder, River Conon. EMGi response is expressed as an activity index (EMGi transmitter rate in Hertz); each point on the scatter-plot represents a single EMGi pulse. Also shown is a schematic plan of the fish ladder with observed movements indicated. No recordings were made between approximately 20.30 and 23.30 hours, while the data logger was downloaded to the PC.

ladder, and in two fish, even higher levels were recorded when the fish remained in the ladder overnight. Both fish remained in turbulent sections of the fish ladder overnight, and although they initially attempted to continue moving up the structure after darkness, no net upstream progress was recorded. Lower levels of activity were recorded prior to and after ascent of the ladder, and occasionally during ascent (Fig. 2).

During active ascent of the ladder, bursts of EMGi activity coincided with observed bouts of activity (Fig. 2). During such episodes, the ascending fish were observed either trying, but failing, to pass upstream or succeeding in passing upstream into the next chamber. Typically, this would involve a burst of rapid swimming activity, during which rapid tail-beats or leaping behaviour was observed. In all three fish, the highest recorded bouts of EMGi activity were associated with attempts to pass upstream.

As mentioned above, one EMGi-tagged salmon was removed from Conon Falls fish ladder (Fig. 4). A period of high activity shortly after 3.00 hours on the morning of 26 August 1996 (Fig. 4), followed by a period in which no EMGi activity was recorded, suggests that this fish was caught and killed at this time. Interestingly, little else appears to have happened to this carcass over the next 4 h. A comparison of temperature data transmitted by the tag with that recorded in the fish pass, and combined with subsequent EMGi data, suggest that the consumption of the fish commenced at 8 A.M. At this time, the transmitted temperature fell sharply and EMGi activity increased (Fig. 4). This change in temperature is consistent with the transmitter having been removed from the carcass of the fish and exposed to air. Changes in the EMGi response at this time suggest that the transmitter electrodes may have been in direct contact with one another before they were sheared off.

Discussion

A proportion of the tagged salmon appeared to have entered the River Bran accidentally, and subsequently, corrected their migration pathway by swimming underground through a tunnel into the River Meig. When these fish were excluded from calculations, only 18% of fish caught in the Conon Falls fish trap passed to spawning grounds in the River Bran. The efficiencies of passage through different parts of the River Bran system varied greatly. There was no loss of fish moving through an impoundment, whereas only *c.* 63% of the approaching salmon passed each of the Borland lifts. A range of mortality agents was identified. Movements through a large impoundment

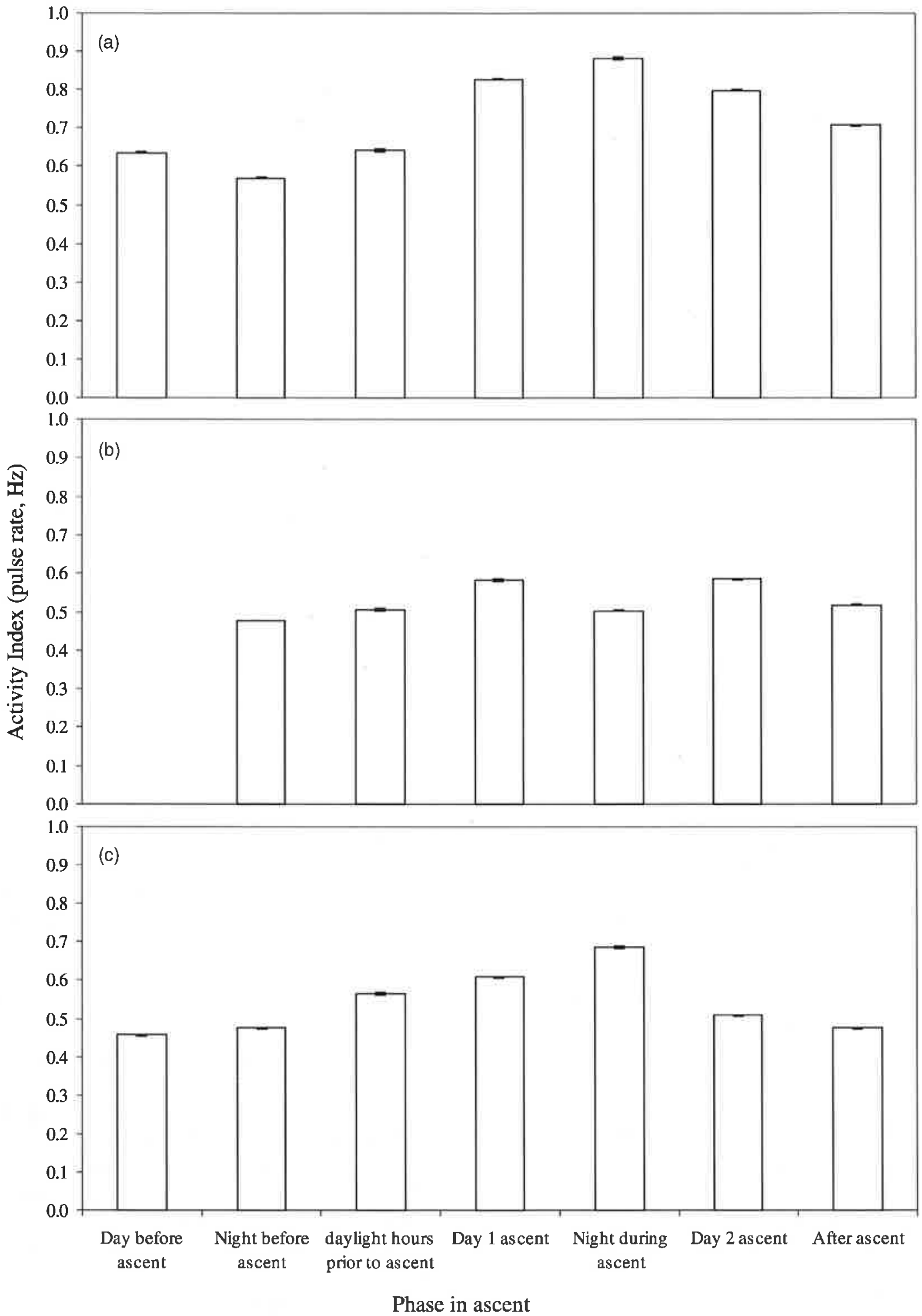

Fig. 3. Mean integrated muscle electromyograms (EMGi) response, with 95% confidence levels, recorded during each phase of the ascent of Conon Falls fish ladder, River Conon, by three EMGi-tagged adult Atlantic salmon (a, b and c). EMGi response is expressed as an activity index (EMGi transmitter rate in Hertz). The start- and end-points in each phase of the ascent were determined from manual, bank-side tracking.

were rapid, and delays encountered were inconsequential compared to those at fish passes. High muscle activities were observed in two of the three salmon in passes at night, indicating that a cessation of upstream movement did not necessarily equate with a reduction of energy expenditure when the fish were within a pool-and-overfall pass.

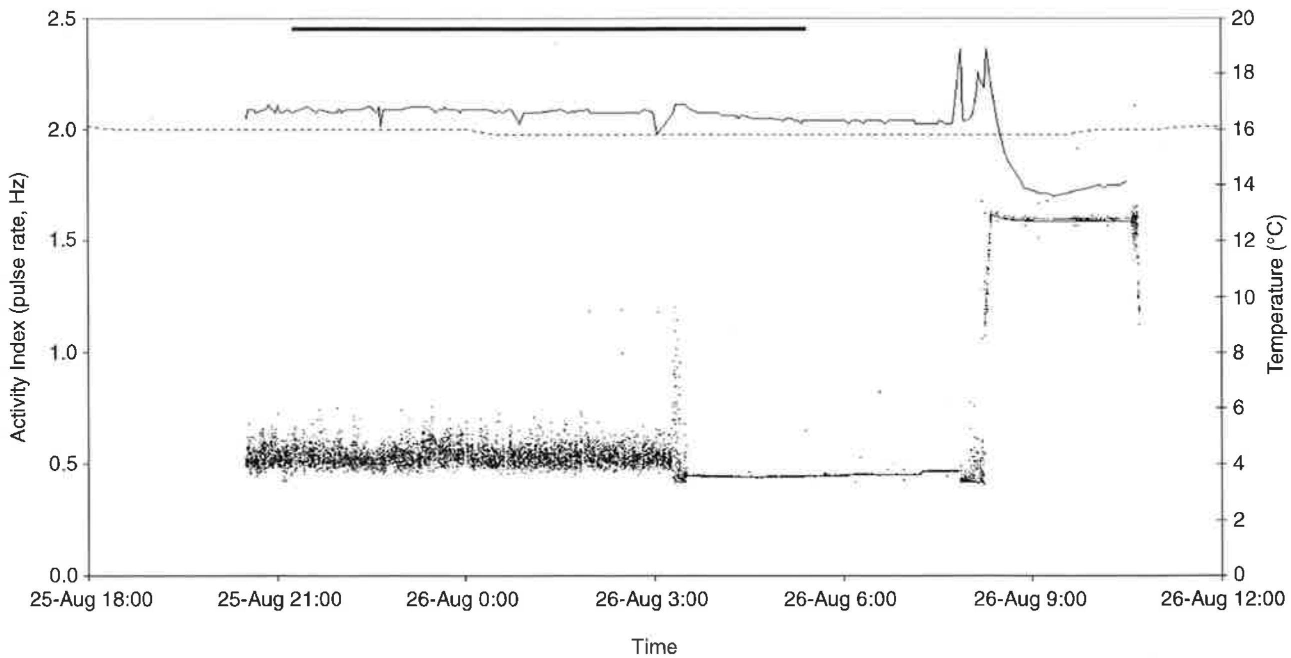

Fig. 4. Integrated muscle electromyograms (EMGi) response recorded from a wild, adult Atlantic salmon before, during and after capture by an otter, *Lutra lutra* (L.). Muscle actvity is expressed as activity index (EMGi transmitter rate in Hertz); each point on the scatter plot represents a single EMGi pulse. The heavy, solid line at the top of the plot indicates period of darkness (as defined by civil twilight), while the thinner, solid line represents temperature as determined by the EMGi transmitter. The thin, broken line represents water temperature as recorded at the top of the fish ladder. See text for a description of events.

Delays associated with the Conon Falls fish ladder and the Borland lift at Luichart Dam occurred over similar periods (1–40 and 1–52 days, respectively). Delays of adult Atlantic salmon prior to ascent of fish ladders have been recorded at Pitlochry Dam and elsewhere (Webb 1990; Laine 1995; Gowans et al. 1999a). Such delays may occur because fish enter a quiescent period in migration (Hawkins and Smith 1986; Gowans et al. 1999a,b) or because they are unwilling or unable to move through these fish passes immediately. Fish that remained in Conon Falls fish ladder or below Luichart Dam may also have been disinclined to continue up through these structures as they may have been destined for the River Meig, and had become confused by fluctuations in familiar olfactory cues from their native river. This may also explain why some fish moved back down the ladder after release. However, none of these fish that moved downstream was later recorded in the River Meig.

Salmon passed through the Meig–Luichart water diversion tunnel. Rodgers & Cane (1979) provided the only previous records of fish movements through a long tunnel (>1km), which was designed as part of a fish pass. Salmon do not appear capable of moving through highly turbulent fish ladders such as Conon Falls fish ladder at night (Stuart 1962; Gowans et al. 1999a), yet they moved through the Meig–Luichart pipeline in near total darkness. Presumably, the hydraulic conditions in this tunnel were conducive to easy migration. Returning adult salmon respond to home-stream odour (Hasler 1954; Hasler and Scholz 1983). It is likely that 'Meig' salmon were attracted up beyond the Meig/Conon confluence by high flow levels from Luichart Power Station (which contains some Meig water), and that these fish continued upstream through Luichart Dam before moving into the Meig via the water diversion tunnel. The presence of a smolt screen at the top of the tunnel would have prevented these fish from returning to their home spawning grounds.

Net swimming speeds recorded during migration through Loch Luichart (0.21–1.16 $km \cdot h^{-1}$) were of a similar range to those recorded during the migration of acoustically and radio-tagged salmon through Loch Faskally (0.18–1.36 $km \cdot h^{-1}$; Gowans et al. 1999b). This provides further evidence that adult anadromous Atlantic salmon can have little difficulty migrating through lakes and reservoirs.

Losses of fish below obstacles were attributed to a number of fates. At several of the obstacles in the study area, radio- or EMGi-tagged fish found dead or dying had major fungal infection (*Saprolegnia* sp.). This may have been a result of stress-related depression of the immune response (Mills 1989), perhaps associated with the accumulation of fish below obstacles. The capture, handling and tagging procedure would have caused acute stress. However, previous studies have used similar tagging procedures without observing sustained adverse effects (e.g., Hawkins and Smith 1986; Laughton 1989; Webb 1989; Gowans et al. 1999a). Prior to entering the study site, fish had already migrated past Torr Achilty Dam via a Borland fish lift, through a reservoir and past Luichart Power Station, where large variations in flow occur daily. A number of fish captured at Conon Falls fish ladder were rejected for tagging because they already showed signs of serious fungal infection when captured. It is possible that obstacles downstream of the study area had already affected long-term fish survival prior to their capture and tagging.

One EMGi-tagged salmon was recorded as it was being removed from Conon Falls fish ladder. The only salmon predators on the Conon system likely to kill fish in this way are otters (Hewson 1990). A further 11 transmitters (including two EMGi transmitters) were recovered on the banks of the river or fish passes, and it is likely that these fish were also removed from the river by otters. Carss et al. 1990) found that otters were more likely to kill healthy salmon than those infected heavily with *Saprolegnia*. Accumulation of fish below passes might have increased predation significantly by providing predictable, replenishing patches of high food density. Salmon naturally accumulate in pools on their upstream migrations, but they are then in a position to select the areas they use.

Few studies have investigated the causes of mortalities below potential obstacles. Webb (1990) found that 5 of the 11 radio-tagged salmon moved back downstream after encountering Pitlochry Dam, and suggested that these movements were associated with entry into the unscreened turbine draught tubes. Several fish in the present study moved downstream and were not recorded again, although one fish later ascended the River Meig via Meig Dam. A further two fish died after becoming stranded in rocks alongside the Conon Falls fish ladder. These findings highlight the importance of ensuring that fish passage facilities are constructed so that they are as easy as possible for fish to pass through.

In the present study, EMGi telemetry was used successfully to record the muscle activity of three adult Atlantic salmon as they ascended Conon Falls fish ladder. When compared to salmon tagged with simple location transmitters in the present study, relatively few EMGi-tagged fish successfully ascended the ladder. This may reflect the more invasive tagging technique used with the EMGi transmitters or it may reflect the low numbers of fish tagged. Although previous studies have noted no abnormal behaviour or movements in EMGi-tagged fish (Økland et al. 2000), the cumulative effect of this procedure with other factors outlined above may have affected the subsequent survival, behaviour and movements of the fish.

High levels of EMGi activity corresponded to episodes of high locomotory activity that were observed as fish attempted to move upstream through the fish pass. Maximum EMGi responses recorded during ladder ascent were higher than those recorded in laboratory experiments to establish the relationship between EMGi response and oxygen consumption in swimming fish (Booth et al. 1995; Hinch et al. 1996; Økland et al. 1997). This may be, in part, because of differences in EMGi responses between fish in laboratory studies that typically utilise swim-tubes and those from free-swimming fish, where it has been shown that even small movements or changes in posture can affect the EMGi (Økland et al. 2000). Such high activity levels may well indicate periods of white muscle activity (Hinch et al. 1996), resulting in an oxygen debt and a metabolic rate that may be as much as 40 times greater than at maximum sustained swimming rate (Puckett and Dill 1984).

As in previous studies (Stuart 1962; Gowans et al. 1999a), upstream movements by salmon in the pool-and-overfall fish pass were substantially reduced during darkness. Two of the EMGi-tagged fish remained in the steeper, turbulent sections of the fish ladder overnight. In both fish, mean levels of activity recorded at night were elevated, despite no net upstream movement. Oxygen consumption of wild Atlantic salmon increases linearly with EMGi activity index (as defined in the present study; Booth et al. 1995). Evidently, there were high energy costs for maintaining position against the flow in the fish pass at night. It seems that if fish are unable to pass through a ladder within one period of daylight, the rate of metabolism can remain high for prolonged periods, reducing the amount of energy available for further migration, spawning activity and/or gonads.

Studies of salmon migrating through areas of Scottish rivers free of hydroelectric development (Hawkins and Smith 1986; Laughton 1989; Webb 1989) have reported none of the types of mortality we observed. Few data are available with respect to the cumulative effects of a number of fish passes or other hydroelectric facilities on fish migration. Such studies often rely on the use of fish counting facilities at consecutive dams. For example, Liscom et al. (1985) describe the study of Junge & Carnegie (1976) in which 50% of chinook salmon (*Oncorhynchus tshawytscha* Walbaum) counted at Bonneville Dam on the Columbia

River were counted over Dalles Dam, and 78% of these fish were later counted over John Day Dam. Thus, between these three dams, a loss of 61% of fish occurred. Similarly, 62% of steelhead trout (*O. mykiss* Walbaum) were lost over the same distance. In the present study, similar losses were recorded between Conon Falls fish ladder and Achanalt Barrage. This study illustrates the scale of cumulative losses to Atlantic salmon migrating through fish pass complexes in Scotland and some of the likely mortality agents.

Resumen

1. Técnicas radio-telemétricas fueron utilizadas para rastrear los movimientos de 54 adultos de *Salmo salar* a través de exclusas tipo 'borland' y a traves de escalas de artesas en el río Connon al norte de Escocia. Este rio tiene dos afluentes principales superiores, los ríos Bran y Meig. El agua pasa entre los afluentes a través de un túnel construido en la montaña que separa las dos subcuencas (Fig. 1).
2. Una proporción de los peces que se aproximaron a cada paso fallaron en migrar río arriba de tal manera que la eficiencia, medida como el numero de peces que pasaron, varió entre 63 y 92% entre todos los pasos. El efecto acumulado de ineficiencias en las series de pasos resultó en que 17.7% de los peces marcados no conocidos ser del río Meig alcanzaron las áreas de puesta aguas arriba (Tabla 2). Los peces que se movieron a través de los pasos se demoraron 1–41 dias en las escalas y 1–52 dias en las exclusas.
3. Los peces que se movieron a través del lago Luichart, un lago de grandes dimensiones localizado entre secciones del río, lo hicieron a velocidades netas de natación de 0.21–1.16 km/h. De los 54 peces marcados, 13 nadaron a través del túnel que une los ríos Bran y Meig lo que sugiere que la transferencia de agua ha influido seriamente el comportamiento de 'homing'.
4. La actividad muscular de 3 salmones marcados con transmisores EMG fueron observados cuando se movían a través de las escalas. Todos estos individuos mostraron una alta demanda de energía durante el paso. Los mayores niveles medios de actividad fueron observados durante el anochecer incluso aunque la migración aguas arriba no progresó en este momento.

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