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Emigration patterns among trout, *Salmo trutta* (L.), kelts and smolts through spillways in a hydroelectric dam

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Abstract The emigration patterns among radio-tagged trout, *Salmo trutta* L., kelts (n = 41, total length: 60–90 cm) and smolts [n = 27, total body length (BL): 22–30 cm] in the regulated River Gudbrandsdalslågen, south-east Norway, were studied by investigating the influence of sex (kelts) and BL (kelts and smolts) on the timing of emigration. In total, 49% of the kelts emigrated towards the hydroelectric dam shortly after spawning, whilst 51% over-wintered. Female kelts were five times more likely to initiate autumn emigration, and eight times more likely to descend the spillways during the first release of surface water than males. Large individuals of both sexes descended earlier than smaller individuals. Larger smolts were more likely to descend during the first release of surface water than smaller smolts. To safeguard the emigration of iteroparous trout kelts and smolts, the spillways should release surface water both in autumn and spring to avoid selective forces during emigration through spillways.

KEYWORDS: emigration, iteroparity, spillways, telemetry, trout.

Introduction

During the life cycle of migratory brown (sea) trout, *Salmo trutta* (L.), downstream emigration from spawning and nursery areas occurs during two distinct periods: as kelts after spawning in autumn and as smolts in spring (Bendall, Moore & Quayle 2005; Arnekleiv, Kraabøl & Museth 2007). Several studies have documented bottlenecks of salmonid smolt runs in regulated and natural rivers (Jonsson & Ruud-Hansen 1985; Hvidsten, Jensen, Vivaas, Bakke & Heggberget 1995; Rivinoja 2005). However, little is known about selectivity imposed by hydroelectric spillways during the emigration of kelts and smolts in regulated rivers despite them possibly spawning repeatedly during their life cycle. Repeated spawners are an important component in many diadromous and inland potamodromous brown trout stocks (Aass, Sondrup-Nielsen & Brabrand 1989; L'Abée-Lund, Jonsson, Jensen, Sættem, Heggberget, Johnsen & Næsje 1989; Arnekleiv *et al*. 2007). In contrast to ascending spawners during summer and autumn, emigrating kelts and smolts encounter the hydro-electric facilities from the opposite direction. For this reason, the physical and biological nature of bottle-necks, threshold values for water discharge and

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individual motivational state concerning energy reserves relevant to pass obstructions may be quite different in this migratory phase compared with upstream migrating adult spawners. The ability to emigrate through run-of-river hydroelectric dams is of vital importance to maintain iteroparity, but may vary because of different design and whether release of surface water occur when emigrating trout is motivated and energetically able (Arnekleiv *et al.* 2007).

A major management issue in regulated rivers is the trade-off between the amount of production water through the turbines and release of spillwater through spillgates and sluiceways to provide adequate survival rates and population stability (e.g. Coutant & Whitney 2000; Larinier & Travade 2002; Johnson & Dauble 2006). Arnekleiv *et al.* (2007) demonstrated the importance of surface water release at Hunderfossen dam to provide effective downstream migrating route for brown trout kelts and hatchery-reared smolts. In this study, the influence of sex and body length (BL) on the emigration pattern among kelts leaving the spawning grounds and passing spillways were examined. The role of total BL of hatchery-reared smolts on the emigration pattern through spillways was also examined.

Study area

River Gudbrandsdalslågen (200 km) is the main tributary of Lake Mjøsa (363 km^2), the largest lake in Norway. About 65% of the 11 500 km^2 catchment

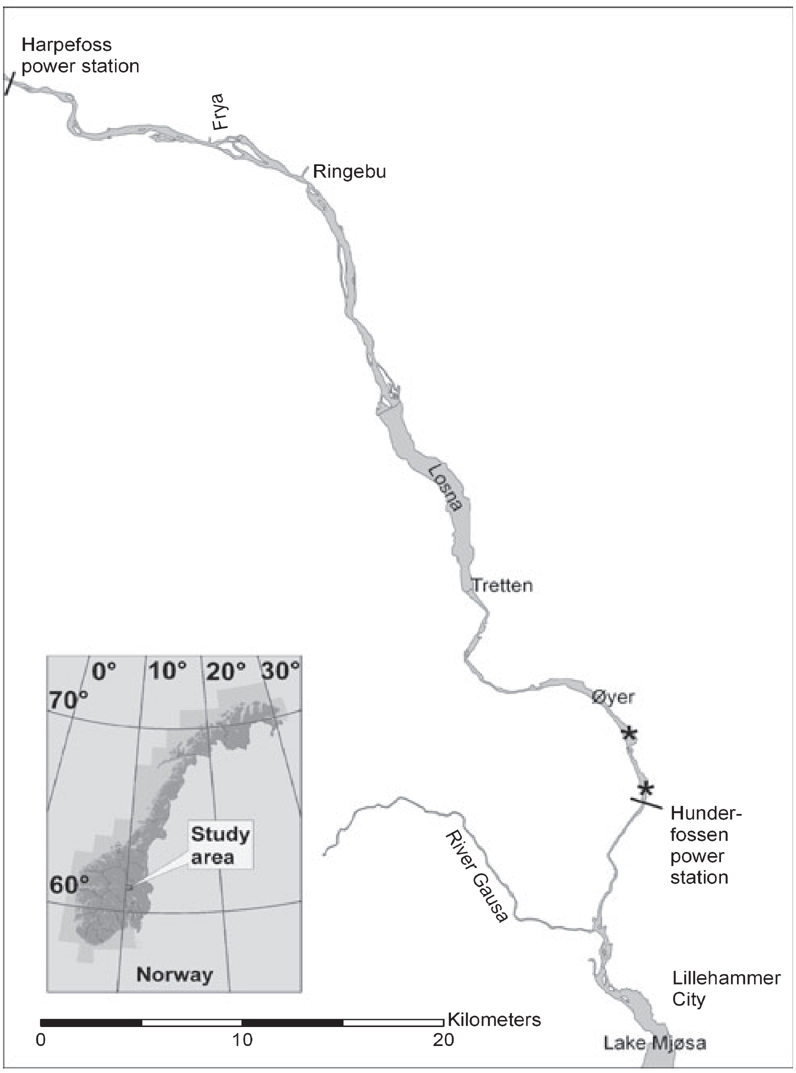

Figure 1. River Gudbrandsdalslågen from the outlet in Lake Mjøsa and the upper spawning ground at Harpefoss. Radio-tagged brown trout spawned at Øyer, Tretten, Ringebu, Frya and Harpefoss.

area is situated at altitudes above 1000 m. Two distinct annual flood periods induced by snow-melting are recognised: in May during lowland melting and in July to August when high summer temperatures and rainfall melt off glaciers and snow from the alpine areas. The mean annual water discharge in the river is about 350–400 m^3s^{-1}, but varies between 30 m^3s^{-1} in late winter and 2500 m^3s^{-1} during extreme summer spates.

The Hunderfossen Power Station is situated 15 km from the river outlet into Lake Mjøsa (Fig. 1). The power station was established in 1963 and abstracts up to 300 m^3s^{-1} of the total discharge as production water, which is returned to the river through a 4.4-km tunnel. Surplus water is released by several bottom and surface spillways along the dam, and upstream migration is facilitated through a compensation flow regime in the 4.4 km regulated river stretch and a fishway at the dam (Fig. 2).

The migrant large-sized (BL mean: 65–70 cm) and piscivorous brown trout population in River Gudbrandsdalslågen forage in Lake Mjøsa for 1–4 years before sexual maturation. Approximately 80% of the spawning grounds are located above the Hunderfossen dam (Arnekleiv & Kraabøl 1996). The hydroelectric development caused dramatic changes in commercial and recreational fisheries (Aass & Kraabøl 1999). Today, about 50% of the annual spawning stock is hatchery-reared trout (Jensen & Aass 1995).

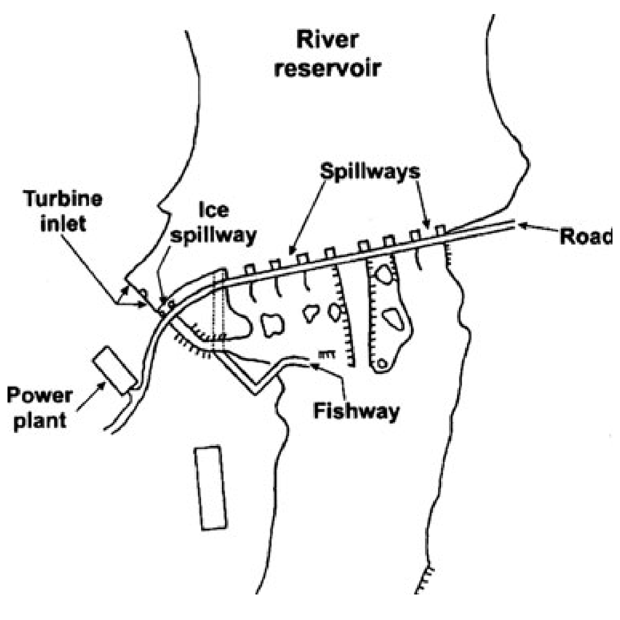

Figure 2. Schematic of the Hunderfossen dam and the different spillways, fishway and turbine inlet.

Material and methods

Three possible routes to pass the dam were identified: the turbines, the fishway and the spillways. Determination of individual passage routes was done by manual radio-tracking.

Radio-tagging of kelts

Emigration of brown trout kelts from the spawning and over-wintering areas above the Hunderfossen Power Station (Fig. 1) was studied in 1993–1994 (n = 16) and 1997–1998 (n = 25). In total, 41 brown trout (BL range = 60–91 cm, BL mean = 75.9 cm) were caught during upstream migration prior to spawning in the fishway and radio-tagged from July to late September in 1993 and 1997. Of these, 35 were tracked during spillgate passage, whereas three passed through the fishway and three died in the reservoir above the dam in April 1998. The latter six were excluded from the study of spillway passage. During the attachment of radio transmitters, the brown trout was placed in a partially covered, cylindrical tank filled with well-oxygenated water, and released at the fishway exit on the upper side of the Hunderfossen Power Station (Fig. 1). An ATS radio transmitter was externally attached to the adults (Model LS6 with Eiler activity, 142 MHz, expected longevity: 190–370 days), below the dorsal fin (see Thorstad, Økland & Finstad 2000; and Arnekleiv *et al.* 2007). The activity function was used to determine spawning activity and survival. The transmitters were either cylindrical or flat-shaped, and weighed between 16 and 27 g in air (0.5–1.5% of the body mass of the fish) and had outline dimensions of 48 mm length and 22 mm diameter (cylindrical) or $48 \times 25 \times 12$ mm (flat-shaped). Fish were tracked manually by using an ATS Receiver (model R2100) each day during spawning and emigration from spawning grounds and during spillwater release at Hunderfossen dam.

Radio-tagging of smolts

The downstream passage of smolts through the waterways at Hunderfossen dam was studied by radio-tagging 27 smolts (BL range = 22–30 cm, BL mean = 26.2 cm) from the local hatchery. All smolts (2 years old and F1-generation of native, wild stock) were tagged with external attached radio-transmitters (Model TXP-1, Televilt AB, Sweden, 142 MHz, expected longevity 60–84 days). The transmitters weighed 2.6 g in the air (< 1.3% of the smolt body mass with outline dimensions of $22 \times 10 \times 10$ mm). All smolts were released 5 km upstream the dam in Øyer (Fig. 1) on 14 May 1998 and tracked manually every 4 h each day and night during the experiments of surface water release (14–25 May, 1–6 June, 9–25 June) and every second day in the interstitial and later periods towards 5 August 1998.

Trials of spillwater release

In 1994, trials were carried out on releases of surface water (water temperature increasing from 8.5 to 10.5 °C) through a fully elevated spillgate measuring 16 m width at the eastern side of the Hunderfossen dam (Fig. 2), releasing 267 m^3s^{-1} during three periods; 8–9 June (34 h), 15–16 June (21 h) and from 28 June onwards. The total spillwater discharge through several spillgates in these periods varied between 350 and 463 m^3s^{-1} during the first, 94 and 337 m^3s^{-1} during the second, and 4 and 273 m^3s^{-1} during the last trial. Tracking was done twice a week between these periods. During each tracking, all fish were positioned and no fish could pass the dam undetected. In 1998, trials of surface water releases (water temperatures increasing from 7 to 13 °C) were performed by using a smaller spillgate (8 m wide) situated on the western side of the dam close to the turbine intakes. The surface water release varied between 1 and 40 m^3s^{-1} by lowering the gate during the trials (Fig. 2). The total spillwater discharge varied between 0 and approximately 700 m^3s^{-1} during the trials.

Data analysis

Two separate binary logistic regression models were used (Minitab 14.0) to analyse the relationship between the probabilities of observation: test 1 – autumn return emigration from the spawning grounds and downwards to the Hunderfossen dam (success) vs river residency during winter (failure); and test 2 – early spring descend through the spillways (success) vs later descend (failure). The use of only two options in the tests was based on the study design, which detected and corrected for mortality and passage through the dam between spawning and spring floods. The explanatory variables *study year* (1993/94 and 1997/98) and *sex* were considered as qualitative predictors whereas BL was considered as a quantitative predictor. Among kelts, there was no difference in BL between the sexes ($t = 0.547$, d.f. = 39, $P = 0.587$). The Akaike Information Criterion (AIC_c) adjusted for small sample sizes (sample size, *n*/number of parameters, K < 40) was used to select the model (Burnham & Andersson 2002). Delta AIC (Δ_i) and

Table 1. Logistic regression model describing the relationship between the probability of observing autumn return migration (21 of 41) vs river residency during winter (20 of 41), and the coefficients of the explanatory variable *sex*. With references to AIC, the explanatory variables BL and *study year* were removed from the model. The results of the Wald-statistic and the odds ratios with 95% CI are given

		Wald-statistic			
Predictor	Coefficients	*Z*	*P*	Odds ratio	95% CI
Constant	−2.66	−2.15	0.032		
Sex					
Male	0	−1.92	0.054		
Female	1.65	2.31	0.021	5.19	1.3–21.1

Akaike weights suggested that three-way interactions and all possible combinations of two-way interactions of the explanatory variables should be eliminated in both test 1 (Delta AIC range: 6.3–14.8; Akaike weights range: < 0.01–0.02) and test 2 (Delta AIC range: 4.0–11.2; Akaike weights range: < 0.01–0.07). In test 1, the model with the explanatory variable *sex* had the lowest AIC_c (model weight: 0.42). However, Delta AIC of the model *sex* + *study year* was 1.29 (< 2) (model weight: 0.22) and both models were kept for further interpretation (Table 1). Delta AIC of other models with all possible combinations of main predictors was in the range 2.2–6.8 (Akaike weights range: 0.01–0.14). In test 2, the model *sex* + BL had the lowest AIC_c (model weight: 0.50) and was kept for further interpretation. Delta AICs of other models with all possible combinations of main predictors were in the range 2.5–11.9 (Akaike weights range: < 0.01–0.14). A linear regression analysis was used to test whether the time of smolt descend through the spillways was dependent on the length of the smolt (Fig. 3). Time of smolt descend was expressed as Julian day.

Results

Radio-tracking of brown trout kelts ($n = 41$) revealed that 21 individuals (51.2%) initiated emigrations from the spawning grounds located at Øyer, Tretten, Ringebu, Frya and Harpefoss, 6–78 km upstream Hunderfossen dam (Fig. 1), 1–3 days after the cessation of individual spawning. These brown trouts were forced to spend the winter in Hunderfossen dam, whereas 20 individuals (48.8%) undertook small-scale movements (10–500 m) to deeper river sections adjacent to the spawning grounds where they spent the winter (Fig. 1). According to the logistic regression model (Table 1), it was 5.2 times (95% CI: 1.3–21.1) more likely to observe autumn return migration among female kelts

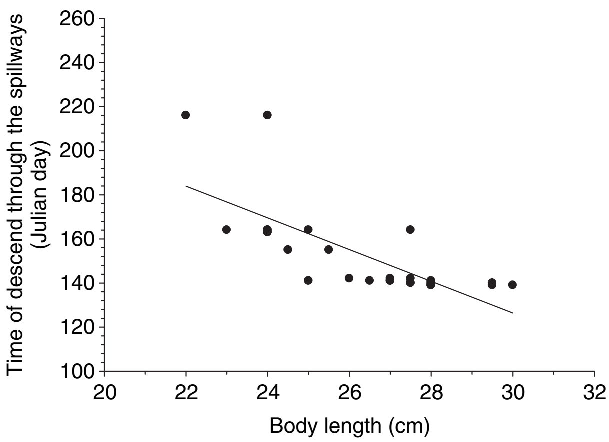

Figure 3. Relationship between time of descend (Julian day) of smolts through the spillway at Hunderfossen power plant (y) and body length (BL) (n = 27), May to August 1998 [linear regression: (y) = 342–7.19 BL; $P < 0.001$; $r^2 = 0.51$].

than male kelts. Downstream migration was observed in 25.0% (four of 16) of the male kelts and 68.0% (17 of 25) of the female kelts. Both the likelihood-ratio statistic and AIC suggested there were no effects of BL and differences between the years (*study year*) in the probability of observing autumn emigration vs over-wintering adjacent to the spawning grounds.

Radio-tracking of kelts descending through spillways in the following spring (n = 35) revealed that 18 (51.4%) descended through the spillway during the first release of surface spillwater in early spring and 17 (48.6%) descended during later floods in the early summer. There was an eightfold (95% CI: 1.2–54.3) greater chance of observing early descending female kelts than male kelts (Table 2); early descent was observed in 20.8 (four of 13) and 65.6% (14 of 24) male and female kelts, respectively. In addition, early

Table 2. Logistic regression model describing the relationship between the probability of observing early spring descend through the spillways (18 of 35) vs later descend (17 of 35), and the coefficients of the explanatory variable *sex* and BL. With reference to AIC, the explanatory variable *study year* was removed from the model. The results of the Wald-statistic and the odds ratios with 95% CI are given

Predictor	Coefficients	Wald-statistic		Odds ratio	95% CI
		Z	P		
Constant	−18.06	−2.93	0.003		
Sex					
Male	0	−1.92	0.054		
Female	2.08	2.14	0.032	8.04	1.2–54.3
BL	0.20	2.73	0.006	1.22	1.1–1.4

descent was 1.22 times (95% CI: 1.1–1.4) more likely when the BL increased by one unit (10 mm; Table 2). Both the likelihood-ratio statistic and AIC suggested that there were no differences between the study years in the observed pattern of descend.

Descent of radio-tagged smolts (n = 27) through the spillways was monitored over 77 days. Smolt *BL* explained 51.4% of the observed variation in timing of the descent through the spillways. There was a strong negative correlation between the time of descend and BL (y = 342–7.19 BL; $F_{1, 26} = 28.45$; $P < 0.001$; $r^2 = 0.51$; Fig. 3), i.e. large smolts passed the spillway earlier than smaller smolts.

Discussion

The attachment of external radio transmitters may influence the behaviour and performance of the fish (Lewis & Muntz 1984; Peake, McKinley, Scruton & Moccia 1997). However, the BL interval among brown trout adults and smolts in this study was considerably larger than studies on physiological and behavioural responses on other adult and smolt salmonids (Peake *et al.* 1997; Thorstad *et al.* 2000). It was thus concluded that negative effects caused by the external attachment of the different radio transmitters used in this study were negligible.

Female kelts were five times more likely to initiate downward emigration from the spawning grounds after spawning in October to November than male kelts, which were more probably to delay return migration until the following spring flood. However, autumn migrators failed to reach the Lake Mjøsa because of emigration problems caused by the dam. These autumn migrators were forced to over-winter in the reservoir after approaching the dam several times because of lack of spillwater releases between the end of spawning season and spring (see Arnekleiv *et al.* 2007 for descriptions of behaviour the radio-tagged brown trout in the reservoir). Of the over-wintering fish, female kelts were eight times more likely to pass the spillway than male kelts during surface spillwater release in spring floods. Further, large hatchery-reared smolts passed the spillgates earlier than small smolts during spring floods. These results suggest that the timing of downstream migration of brown trout kelts and smolts is affected by sex (kelts) and BL (smolts).

Salmonid kelts are energy deficient after spawning (Jonsson, Jonsson & Hansen 1991) and rapidly return to the sea or lake to recover their condition (Northcote 1978; Gross, Coleman & McDowall 1988; Jonsson & Jonsson 1993). The overall energetic cost associated with migration towards the breeding areas, nest preparation, courtship, competition and loss of gonads (Wootton 1990) affects both sexes evenly (Lien 1978; Jonsson *et al*. 1991). However, loss of somatic energy reserves during spawning may be more severe among males than females, because males act far more vigorously than females during spawning (Rubin, Glimsäter & Jarvis 2005). Additionally, males enter the river earlier and are active on the spawning grounds for a longer period than females (Rubin *et al*. 2005). The combination of low somatic energy content (Jonsson *et al*. 1991) and prolonged spawning activity among males (Rubin *et al*. 2005) may explain the sex difference in emigration frequencies during autumn. Low somatic energy content in males may reduce both the capacity and motivation to perform migrations. Furthermore, the protracted duration of spawning among males may lead to unfavourable temperature conditions for return migrations in late autumn combined with skin lesions from fighting and subsequent secondary infections. In a management context, the timing differences between the sexes illuminates the importance of surface spillwater release both during autumn and spring to avoid emigration problems and sexual selectivity imposed by the hydroelectric scheme.

Descending salmonid smolts use different passage routes at hydroelectric dams. Submerged waterways, such as Kaplan turbines are commonly used by smolts (Wilson, Giorgi & Stuehrenber 1991) with mortality rates ranging between 5 and 30% (Cada 2001). However, surface flow outlets seem to be the best option with respect to survival (Rivinoja 2005; Arnekleiv *et al*. 2007). Further, several studies found that the smolt run is favoured by elevated water discharge because it reduces predation mortality (Hvidsten & Hansen 1989; Abrahams & Kattenfield 1997) and accelerates downstream displacement (Jonsson 1991). Release of surface water should therefore occur at an early phase of floods to reduce mortality from turbine passage and predators. The release of surface water flow is advantageous for migrant juvenile salmonids because they are surface-oriented and averse to sound during their downstream migration (Andrew & Geen 1960). The negative correlation between the date of sluiceway passage and BL may perhaps be explained by size-dependent individual motivational state of hatchery-reared smolts. The results provide limited relevance to wild brown trout smolts because they attain smoltification length (25 cm) at an average age of 4.1 years compared with 2 years among hatchery-reared smolts (Aass *et al*. 1989; Aass 1993). Major differences in overall life experience may also limit the relevance to wild smolts.

Management strategies regarding iteroparous salmonid species have paid little attention to the problems encountered by downstream-migrating kelts at hydroelectric facilities or their different environmental and individual conditions compared with upstream-migrating mature adults. The results from this study indicate that female kelts and large smolts pass spillways earlier than male kelts and smaller smolts. Therefore, any setting of narrow time windows for release of spillwater through hydroelectric dams during spring floods may select for large smolts and thereby prevent smaller smolts from descending. Thus, to safeguard the annual emigration of kelts and smolts, surface water should be released over spillways for several weeks both during the autumn and spring and actions that impact on emigrating kelts and smolts should be avoided.

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