Efficiency of a fishway on brown trout (*Salmo trutta*) spawning populations

By Morten Kraabøl and Jon Museth

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Summary

Poor efficiency of fishways or other semi-passable hindrances in rivers may impose delays and selection pressure on targeted species. A previous long-term study covering ascending brown trout (*Salmo trutta* L.) through the fishway at Hunderfossen dam concluded that the fishway inflicted stabilizing selection towards medium-sized trout. But the hydropower regulation has created at least three other major obstacles for migration that could influence selection regimes. A three-year mark (n=316) and recapture (n=92) study was thus performed to more specifically address efficiency and selectivity of the fishway. The overall efficiency of the fishway was 29 % and varied between years from 21 to 39 %. The individual delay varied between 6 and 77 days. The experiment did not yield support for stabilizing selection favouring medium-sized trout. However, there was a lower probability of trout with body lengths smaller than 60 cm to enter the fishway compared to larger trout. Gender, origin or degree of secondary sexual characters influenced neither the probability of observing recaptures in the fishway nor the observed delay. Several other factors driving the previously reported stabilizing selection are highlighted by addressing a wider spatial scale covering a range of migratory obstacles where size selection may apply. The effect of ontogenetic body size development and iteroparity on selection patterns is discussed, and it is concluded that stabilizing body size selection caused by a semi-passable and size selective obstacle seems less likely to occur with equal strength among iteroparous compared to semelparous fish species.

Sammendrag

Dårlig funksjonalitet i fiskepassasjer eller andre semi-passerbare hindringer i elver kan medføre forsinkelser og seleksjon på de aktuelle målartene. Et tidligere langtidsstudie på oppvandrende ørret gjennom fisketrappa ved Hunderfossen kraftverk konkluderte med at fisketrappa påførte stabiliserende seleksjon i favør av mellomstor ørret. Imidlertid har denne utbyggingen påført minst tre andre betydelige hindringer som kan virke inn på seleksjonsmekanismene. Et treårig merking (N=316) – gjenfangst (N=92) studie ble gjennomført for å undersøke fisketrappas spesifikke selektivitet. Den gjennomsnittlige effektiviteten til fisketrappa var 29% og varierte mellom 21 og 39 %. Individuell forsinkelse varierte mellom 7 og 77 døgn. Denne studien bekrefter ikke at fisketrappa medfører en stabiliserende seleksjon i favør av mellomstor ørret,

men det ble funnet at de minste ørretene (<60 cm) hadde lavere odds for å komme inn i fiske-trappa sammenlignet med større ørret. Kjønn, opprinnelse og graden av sekundære kjønns-karakterer (gytedrakt) påvirket hverken sann-synligheten for å bli registrert i fisketrappa eller observert forsinkelse. Det rettes et bredere søke-lys på flere andre potensielle vandringshind-ringer som kan fungere som drivere for tidligere dokumentert stabiliserende seleksjon. Effekter av livsløpsbasert kroppsstørrelse på flergangs-gytende bestander diskuteres. Det konkluderes med at stabiliserende seleksjon i favør av en be-stemt kroppsstørrelse som forårsakes av en semi-passerbar fiskepassasje er mindre sannsynlig blant flergangsgytende arter sammenlignet med de som gyter kun en gang i løpet av sitt livsløp.

Introduction

Maintenance and restoration of ecological con-nectivity is a key issue in river conservation biology (e.g. Giller & Malmqvist 1998). Frag-mentation of water bodies have increased exten-sively during the twentieth century (Dynesius & Nilsson 1994), and a significant part of the large river systems in the World are under influence of hydropower dams (Nilsson et al. 2005). Addressing longitudinal connectivity is impera-tive in a conservation perspective, because vital habitats for fish species are often geographically separated (Northcote 1998). Fragmentation of progressively developed river systems has resul-ted in habitat degradations and extinction of anadromous and potamodromous species (Dynesius & Nilsson 1994; Jungwirth,1998). The geographical scale of these problems ranges from local and site-specific migratory problems to global concerns regarding species extinctions (e.g. Sheer & Steel 2006; Slavik et al. 2009). A common mitigation feature to ensure connecti-vity is the establishment of fishways of different design to facilitate upstream fish passage (Clay 1995; Odeh 1999; Travade & Larinier 2002; Schilt 2007). Despite rarely adequately quanti-fied, the efficiency of fishways is important be-cause poor efficiency may impose selection pressure on targeted species (Ovidio et al. 2007).

Sufficient water discharge, the need for pro-per location of fish entrance, fishway design and optimal spillwater attraction schemes are im-portant issues in order to improve fishway effi-ciency (Bunt 2001; Laine et al. 2002; Fernandez et al. 2007; Caudill et al. 2007; Roscoe & Hinch 2010). Fishways constructed in connection to run-of-river hydro power plants are often chara-cterized by a low water discharge compared to the natural water discharge. Typically, fishway discharges in large rivers constitutes 1 % - 1 ‰ of the pre-regulated flow, and raises several im-portant questions regarding selective pressure and delay on migrating fish populations. Sele-ction may occur at the species level by providing suitable passage opportunities only for salmo-nids, and impassable or semi-passable condi-tions for non-salmonid species (Knaepkens et al. 2006; Agostinho et al. 2007; Mallen-Cooper & Brand 2007). Further, intraspecific selectivity may act upon body size, gender and origin of the individual fish (e.g. Jensen & Aass 1995; Laine et al. 1998; Haugen et al. 2008). Such forces may be driven by differences in motivational state, route-seeking behavior and swimming capacity. On a spatial scale selection can be inflicted at various locations affected by hydroelectric interventions, and at a temporal scale selection may act on different life stages. A complex matrix of selection forces can rapidly lead to life history trait evolution, but it is not straightfor-ward to pinpoint the exact causative agent. This problem complex highlight an important chal-lenge for contemporary ecologists and fisheries managers because constructions of dysfunctio-nal or selective fishways might be turned into conflicting conservational issues in relation to the original aims to conserve fish populations.

Scaling up to more heavily modified rivers around the World, evolutionary changes in life history and phenotypes may be a common fea-ture where migrating fish must pass several fish-ways. In order to preserve natural life histories in such ecosystems it is imperative to define causative agents and develop proper counter-measures to prevent demographic as well as evolutionary responses through selection, delay

and disruptions during migrations. A large proportion of studies covering passage efficiency in fishways focus on physical constraints such as attraction flow (Lindmark & Gustavsson, 2009), construction type (Mallen-Cooper & Brand 2007) and gradient (Mallen-Cooper 1994; Barrett & Mallen-Cooper 2006). However, biological aspects in targeted fish species may also be of great importance for the efficiency of fishways. During recent years, the design of fishways has increasingly combined hydraulic engineering with fish biology (Odeh 1999; Castro-Santos et al. 2009). Biological features such as gender, origin (i.e. wild-born or hatchery-reared) and secondary sexual characters may influence the fish's ability to locate and enter the fishway during the spawning migration because these features affect the motivational basis for behavior as the spawning season approaches. The interplay between body size of individual fish and fishway design is complex, and the gross difference between the fishway and the natural river (i.e. Laine et al. 2002) makes it plausible to assume selection pressures on spawning populations as they pass through "an eye of a needle".

The large-sized, piscivorous and migratory brown trout (*Salmo trutta* L.) population in the modified River Gudbrandsdalslågen in SE-Norway represents distinct conservational as well as recreational values (Aass & Kraabøl 1999). Significant effort has been invested into management actions after hydroelectric development, such as a stock rehabilitation program, fishing regulations and establishment of a fixed minimum water discharge on the affected river section and the construction of a fishway (Aass 1993; Jensen & Aass 1995; Arnekleiv & Kraabøl 1996). Today, between 50 and 60 % of the annual spawning populations originate from hatchery-reared F1-generation trout (Kraabøl et al. 2009). A long-term study covering ascending brown trout through the fishway at the Hunderfossen dam during the period from 1966 to 2003 (Haugen et al. 2008) concluded that this fishway inflicted a phenotypic sorting mechanism causing a stabilizing selection towards medium-sized trout.

The main objective of the present study was to assess the efficiency and verify selectivity (Haugen et al. 2008) of the fishway at Hunderfossen dam. Experiments were conducted by attracting trout towards the dam with artificial freshets and the trout were captured, tagged and released into the deep pool below the fishway. The efficiency of the fishway was analyzed by 1) assessing the percentage of trout successfully passing towards upstream locations, 2) assessing the a) overall delay suffered by successful fishway migrants, and b) analyze the influence of body size on delay, 3) testing the effect of body size on fishway passage success and whether the fishway inflicted stabilizing selection favoring medium-sized trout (BL interval: 60-70 cm, optimal BL: 67.7 cm) as proposed by Haugen et al. (2008), and 4) exploring whether gender, origin (wild-born og hatchery-reared) and the degree of secondary sexual characters (a proxy for motivational state in some salmonids) influenced the trout's ability to pass the fishway. The results are discussed by addressing the iteroparous life history as well as spatial and temporal scales of the problem complex.

Material and methods
Study area
River Gudbrandsdalslågen (catchment area of 11.500 km²) is the major spawning and nursery river for the large-sized, piscivorous brown trout in Lake Mjøsa (365 km²). A 78 km river stretch is available for ascending trout, of which 62 km is situated above the Hunderfossen dam (Fig. 1). Out of 17 major and minor spawning areas recorded below and above dam, 7 are located below the dam (Kraabøl & Arnekleiv 1998).

The fish community in Lake Mjøsa (123 m a.s.l) comprise 20 fish species, all of which (brown trout included) colonized the lake by natural immigration from the Baltic region through glacier-fed rivers during the end of the last glaciation (8000-10000 B.P.). Due to isostatic rebound the migratory connection to the sea was gradually disrupted, and the land-locked brown trout has adapted to a potamodromous and iteroparous life history by utilizing more
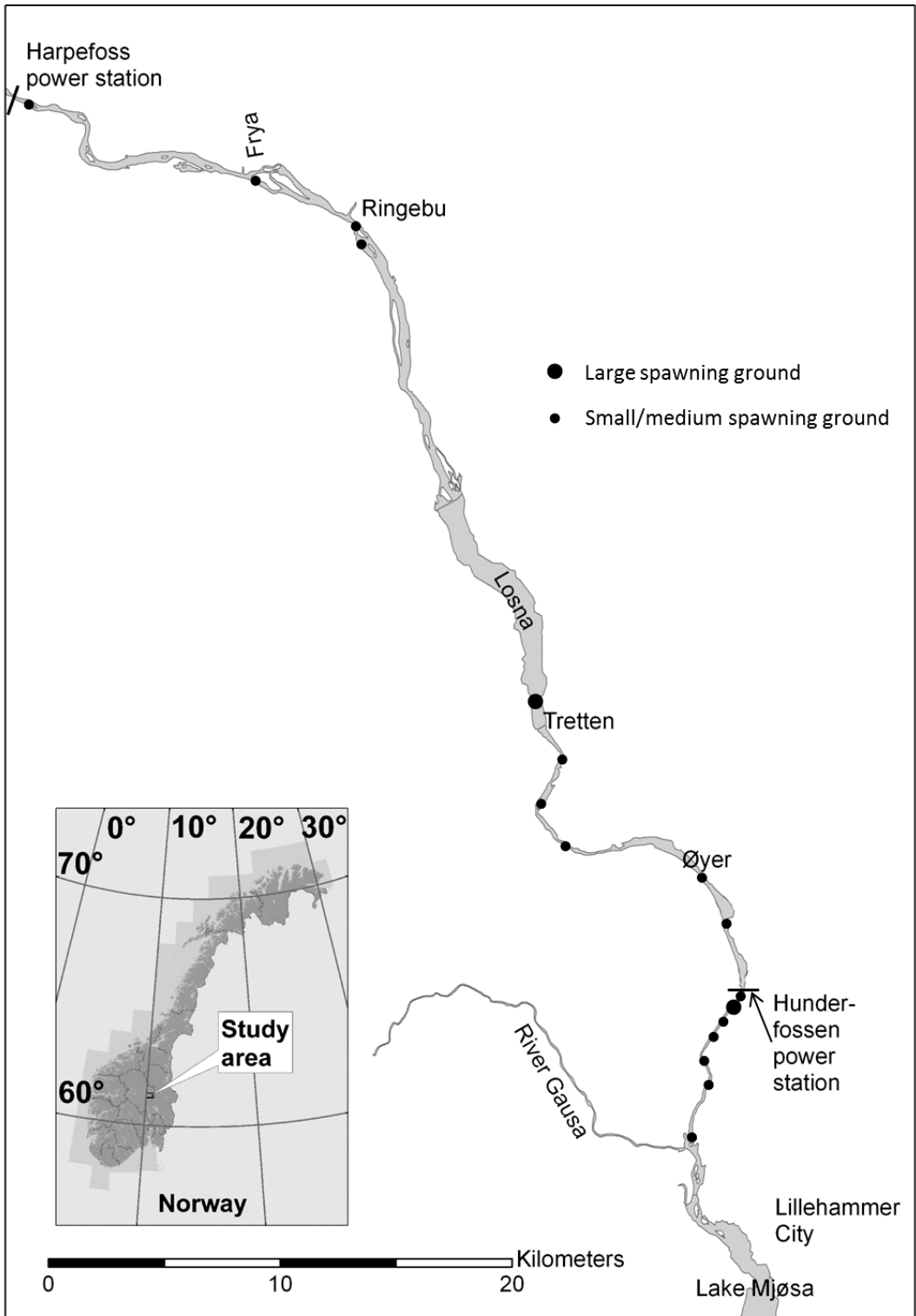
Figure 1. River Gudbrandsdalslågen from the northern part of Lake Mjøsa and up to the migration barrier at Harpefoss power plant. Spawning areas are indicated by relative size.

than 20 spawning tributaries for spawning and rearing (i.e. Rustadbakken et al. 2004). Young trout spend 1-5 years in the rivers before they perform a niche shift to a piscivorous life in Lake Mjøsa where they feed on smelt (*Osmerus eperlanus* L.), vendace (*Coregonus albula* L.) and whitefish (*C. lavaretus* L.) until sexual maturation and subsequent return migration to their natal river for spawning. The Hunder trout spawns in River Gudbrandsdalslågen and is the most abundant trout population in Lake Mjøsa (Aass et al. 1989; Aass 1993; Kraabøl et al. 2009).

Hunderfossen dam was constructed across the river at the head of the falls in 1960-64 and the maximum water capacity of the adjacent Hunderfossen power plant is 300 m³s⁻¹. After power generation, the water is led back to the river 4.4 km downstream the dam. This regulated river section is supplied by law-decreed spillwater in periods when the river discharge above the dam is equal or lower than 300 m³s⁻¹,

based on a fixed minimum water regime spilling 2-5-10-15-20 m³s⁻¹ in time restricted intervals. Spillwater is released through different spillways depending on the flood level and different spillgates adapted for surface and deep-water spill are installed along the dam.

A stock rehabilitation program was initiated when the dam construction started in 1960 to compensate negative impact on natural recruitment (Aass et al. 1989; Aass 1993). Each year 15.000 2-years old F1-generation smolts (BL: 20-25 cm) from wild parents are reared in the Hunderfossen trout hatchery and released in the river and in the northern part of Lake Mjøsa. The adipose fin is cut off from each hatchery-reared smolt to evaluate the effect on trout fisheries and spawning populations and separate them from the wild progeny.

The proportions of hatchery-reared trout in the annual spawning stock ascending the fishway has varied between 40 and 60 % during the
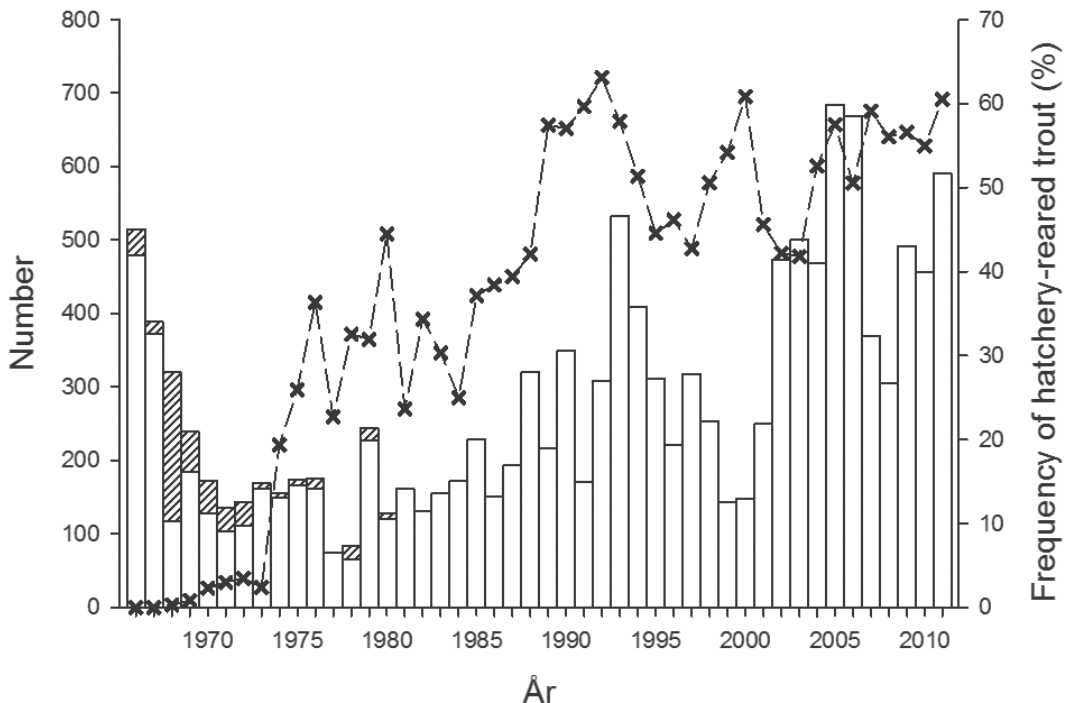

Figure 2. Annual number of trout recorded in the fishway at Hunderfossen Dam in the period 1966 – 2011 (open bars). During the first years of operation a varying number of trout were captured below the dam and manually lifted above the dam (shaded bars). The annual proportion of hatchery-reared trout is indicated with crosses.

last 20 years, and comprise between 30 and 40 % in the trout fisheries in Lake Mjøsa (Kraabøl et al. 2009). Annual spawning populations migrating through the fishway have numbered 70 to 680 individuals (Fig. 2) during the 45 year period 1966 -2011.

The fishway

The fishway at Hunderfossen dam (Fig. 1) is the largest (by means of water discharge and outline dimensions) fishway for inland fish species in Norway (Directorate for Nature Management 2002), and consist of two different but merged sections. The lower part is a pool-overfall type and the upper constitute of five Denil sections of straight rectangular flumes. The lower section of the fishway consists of 26 concrete pools equipped with 80 cm wide notches. The waterfall between the pools is 60 cm, and the gross elevation of the pool-overfall and Denil section is 12 m and 5 m, respectively. The lowermost pools have concrete roofs to prevent deposition of rocks and gravel during floods, and each pool has openings to ensure lighting. The fishway empties directly into the deep pool below the dam through two distinct but closely located 100 cm wide fish entrances at the very end of the fishway. A third fish entrance is located in the lower roofed pool section, and provides an alternative fishway entrance (80 cm wide) for trout approaching the dam. In combination, these three fish entrances can serve ascending trout at a range of water flows and spillway operation schemes. However, the placement of the fish entrances is mainly an adaption to ensure functionality at low spillwater discharge (< 80 m^3s^{-1}) because this is the most common situation during the spawning run from August to October. A previous study on fishway functionality (Jensen & Aass 1995) found that few trout entered the fishway when spillwater release exceeded 180 m^3s^{-1}. In summary, 94 % of the trout entered the fishway at spill discharges less than 150 m^3s^{-1}, and 66 % entered between 2 and 50 m^3s^{-1}. Furthermore, wild-born trout entered the fishway earlier than hatchery-reared, and females arrived earlier than males.

The fishway has been unchanged since it came into operation during summer 1966 and re-opened the access to the spawning areas above the dam after a few years with blocked passage routes caused by the construction and operation of the power station from 1961-1965. The water discharge through the fishway is 1.8 m^3s^{-1} during all seasons. All passing trout are captured and manually registered and Carlin-tagged before release into the upper Denil section of the fishway.

Capture, tagging and categorizing

A total of 316 brown trout were attracted towards spillway 1 at the eastern side of Hunderfossen dam by artificial freshets, captured, tagged and released into the deep pool below the fishway during the migration seasons in 1998, 2008 and 2011 (Table 1). When significant amounts (>10 m^3s^{-1}) of spillwater is released through the eastern spillway (spillway 1), the ascending trout gathered in the deep pool below the dam, responded immediately to artificial freshets by negotiating the semi-natural falls and rapids towards backwaters below spillway 1. During floods, this spillway normally releases 50-200 m^3s^{-1}, and trout quickly aggregate in backwaters where they are hindered from further upstream passage. Trout trapped in pots or stranded on the gully after spillway closure, were netted and secured as quickly as possible in a 1 m deep pool. Trout were slightly anaesthetized with 2-fenoxyetanol and tagged with Floy tags in a water-filled cylindrical tank and gender, origin, body coloration (a proxy for degree of secondary sexual characters) and total fish length (L_T) were determined. Sex determination was done based on typical morphological features for sexually mature trout. The origin of each trout was determined by inspection of the adipose fin, which is removed from hatchery-reared trout. Hatchery-reared trout were exclusively F1-generation from wild-born trout captured in the fishway, whilst the ancestry of wild-born trout is a medley between natural recruitment resulting from an unknown mixture of wild-born and hatchery-reared trout spawning above and below Hunderfossen dam.

Table 1. Number of trout tagged at different dates below the Hunderfossen dam and subsequently recaptured in the fishway (dates not shown) in 1998, 2008 and 2011.

Year	Number tagged (M)	Number recaptured (R)	R (%)
1998			
July 21	18	6	33,3
August 4	84	26	33,0
August 22	22	4	18,2
Total 1998	**124**	**36**	**29,0**
2008			
July 21	37	9	24,3
August 20	71	14	19,7
Total 2008	**108**	**23**	**21,3**
2011			
August 4	62	25	40,3
August 25	22	8	36,4
Total 2011	**84**	**33**	**39,3**
Total	**316**	**92**	**29,1**

The degree of secondary sexual characters was determined by assessing the overall body coloration into four categories; 1=silvery, 2=grey, 3=light brown and 4=brown/yellow/orange. Different scales of coloration were applied between the sexes, as males generally develop stronger colors than females. Trout entering the river are always silvery, and the body coloration gets increasingly colorful with residence time. The Floy tags were inserted in front of the dorsal fin by a Floy-pistol. After tagging and measurements all tagged trout were carried in concealed and dark plastic bags filled with water and released in the deep pool below the dam and fishway. Data from recaptures of tagged trout in the fishway trap was provided by daily control by the staff at Hunderfossen trout hatchery.

Various discharges of spillwater were released through different spillways in the period between tagging and recapture of trout. The influence of spillwater on fishway efficiency was not investigated in this study. Artificial freshets were only released through spillway 1 during two-three short bursts each year to attract trout for tagging (Table 1).

Study design, data analysis and sources of errors

A basic assumption of the present study was that capture and tagging of trout having negotiated the semi-natural rapids towards this spillway represents a sample of trout motivated to pass Hunderfossen dam, as confirmed by previous telemetry studies (Arnekleiv & Kraabøl 1996). This design enabled studies of delay and selection caused by the fishway by comparing the successful fishway entrance of Floy-tagged group by the un-successful group that were forced to spawn below the dam and fishway.

According to Haugen et al. (2008), the fishway at the Hunderfossen dam caused stabilizing selection by favouring medium-sized trout in length-class 60-69.9 cm and at an optimal L_T of 67.9 cm. In the present study, the migratory fate of tagged trout was considered a binary response variable with trout recaptured in the fishway trap classified as "successes" (n = 92) and trout not recaptured in the fishway as "failures" (n = 224). Three different logistic regression models describing the relationship between logit $[\pi(x)]$ were carried out in PASW Statistics 18.0.2,

where $\pi(x)$ denotes the probability of recapture in the fishway. Three alternative explanatory variables were investigated: 1) linear effect of L_T (quantitative variable) 2) deviation from the optimal L_T of 67.9 cm estimated by Haugen et al. (2008) (absolute value, quantitative predictor) and 3) Length class (L_T) 60-69.9 cm (termed medium sized fish by Haugen et al. 2008) vs. L_T-classes $\leq$ 59.9 cm and $\geq$ 70 cm (qualitative predictors). The two latter approaches test for stabilizing selection. In all alternative models, "year" was included as a qualitative predictor, because the length-distribution and number of tagged trout varied between years. Due to relatively low number of recaptures (n = 92), additional parameters than the three approaches to "fish length" and "year" were not included in the main model. However, the effects of "sex", "origin", and "colour" on the probability of recapture in the fishway were tested separately in three different logistic regression models.

The study design also involved factors which could inflict physiological stress responses, such as anaesthesia, sudden crowding and stranding after water withdrawal, tagging procedures and transportation in bags before release into the river again. Rapid dewatering and sudden confinement of trout are shown to increase plasma cortisol concentrations (Arnekleiv et al. 2004). Elevated blood glucose levels may also persist for many hours after handling, and can affect behaviour of released fish for considerable time (Pickering et al. 1982). However, trout were kept submerged during tagging and measurements, and carried in water filled bags to the release site. The beat rate of the operculums was also monitored during tagging, and no changes were observed. The beat rate of the operculum reflects perturbations in the handled fish, and increased ventilation occurs when oxygen demands rise or blood carbon dioxide levels increase (Laitinen & Valtonen, 1994). All tagged trout had intact righting reflexes and performed neophobic responses during all handling procedures. The low degree of anaesthesia is also believed to have reduced post-handling effects in this study. However, behavioural effects cannot be ruled out, and may therefore have contributed to the delays between tagging and recapture in the fishway.

Results
Assessment of fishway effectiveness
The recapture rate and thus the observed functionality of the fishway varied between years from 21 % in 2008 (23 out of 108) to 39 % in 2011 (33 out of 84). In 1998, the recapture rate was 29 % (36 out of 124) (Table 1). It was 0.22 – 0.81 times less likely (95 % CI for the odds ratio) to observe successful migrants in the fishway in 2008 than in 2011 (Table 2), but no significant differences between other years.

Factors affecting overall delay
The median number of days between releases of tagged fish downstream the dam and recapture in the fishway (i.e. delay) were 20 (range: 6 – 72) in 1998, 34 (range: 7 – 77) in 2008 and 49 days (range: 20 – 67) in 2011, respectively, and differed significantly between years (Kruskal-Wallis One Way Analysis of Variance on Ranks, H = 25.26; $P < 0.001$). Pairwise multiple comparisons showed that the observed delay was higher in 2011 than in 1998 and 2008 (Dunn's method, $P < 0.05$). Delay was neither influenced by sex (multiple linear regression: t = 0.31, P = 0.757), origin (multiple linear regression: t = 1.15, P = 0.252) nor body colouration (multiple linear regression: t = 1.39, P = 0.123).

Effect of L_T on observed delay between time of tagging and recapture in the fishway
It was a significant positive correlation between L_T and delay (Linear regression, r = 0.386; $F_{1,58}$ = 9.98; $P = 0.003$), but no significant correlation between deviation between L_T and 67.9 cm and observed delay between time of tagging and recapture in the fish way (Linear regression, r = 0.073; $F_{1,58}$ = 0.316; $P = 0.576$). The median values of delay between the three L_T-class $\leq$ 59.9 cm (small), 60-69.9 cm (medium) and $\geq$ 70 cm (large) did differ significantly (Kruskal-Wallis One Way Analysis of Variance on Ranks, H = 8.19; $P = 0.017$), and multiple pairwise compa-

Table 2. Logistic regression models exploring the relationship between the probability (P) of observing recaptures in the fish ladder at the Hunderfossen dam, and the coefficients of the explanatory variables "L_T" (model 1), "deviation (absolute value) between "L_T" and 67.9 cm" (model 2) and "length-class 60-69.0 cm vs smaller ($\leq$ 59.9 cm) and larger individuals ($\geq$ 70 cm) (model 3). "Year" is included as a categorical predictor in all models. The results of the Wald – statistic and the odds ratios with 95 % C.I. are given.

Model	Predictor	Coefficients	Z	P	Odds	95% C.I.
		Wald statistic				
1	Constant	-1.27	2.02	0.16	0.28	0.48-1.62
	L_T	0.01	0.94	0.33	1.01	0.99-1.04
	Year					
	1998	-0.41	1.82	0.18	0.66	0.37-1.20
	2008	-0.85	6.75	0.01	0.43	0.23-0.81
	2011				1	
2	Constant	-0.33	1.43	0.23	0.72	0.42-1.23
	L_T - 67.9 cm (absolute value)	-0.14	0.45	0.50	0.99	0.95-1.03
	Year					
	1998	-0.44	2.20	0.14	0.64	0.36-1.15
	2008	-0.87	7.13	0.01	0.42	0.22-0.79
	2011				1	
3	Constant	-0.55	4.86	0.03	0.58	0.36-0.94
	L_T-class $\leq$ 59.9 cm	-0.91	5.82	0.02	0.40	0.19-0.84
	L_T-class $\geq$ 70 cm	-0.37	1.72	0.19	0.69	0.40-1.20
	L_T-class 60-69.9 cm				1	
	Year					
	1998	-0.41	1.75	0.19	0.67	0.37-1.22
	2008	-0.86	6.82	0.01	0.42	0.22-0.81
	2011				1	

risons revealed that the median delay of L_T – class $\geq$ 70 cm was significantly higher than L_T -class 60-69.9 cm (Dunn's method, P < 0.05).

Effect of L_T on recapture rate

The average total length (L_T) of tagged trout (N = 316) was 67.6 cm (SD = 10.3) and the average lengths of recaptured (R = 92) and not recaptured (NR = 224) trout were 68.7 cm (SD = 9.95; C_v = 14.5%) and 67.1 cm (SD = 10.44; C_v = 15.5%), respectively. There were no significant differences in the likelihood of fishway recaptures and L_T , suggesting no linear effect of L_T on the recapture rate in the fishway (Table 2, Model 1). There were no significant differences (P = 0.33) in the likelihood of recaptures in the fish-

way and the deviation (absolute value) between observed L_T at tagging and the estimated length of 67.9 cm (max probability of fishway passage, estimated by Haugen et al. (2008)) ($Z = 0,027$; $P = 870$; Table 2: Model 2).

However, there were significant differences (P = 0.02) in the likelihood of being recaptured in the fishway between fish in L_T-class 60-69.9 cm (termed medium sized fish by Haugen et al. 2008) and smaller individuals (L_T-class $\leq$ 59.9 cm). The estimated odds of observing recaptures of trout $\leq$ 59 cm in the fish way was 0.42 (95% C.I.: 0.19-0,94) compared to medium sized fish (L_T-class 60-69 cm). The estimated odds of observing recaptures of trout $\geq$ 70 cm compared to the medium sized fish was 0.69

(95% C.I.: 0.40-1,20), but did not differ significantly (*P* = 0.190; Table 2 Model 3, Fig. 3). These results do not provide evidence for stabilizing selection favouring medium-sized trout inflicted by the fishway, but the probability of trout ≤ 59.9 cm to enter the fishway was significantly lower compared to larger trout.
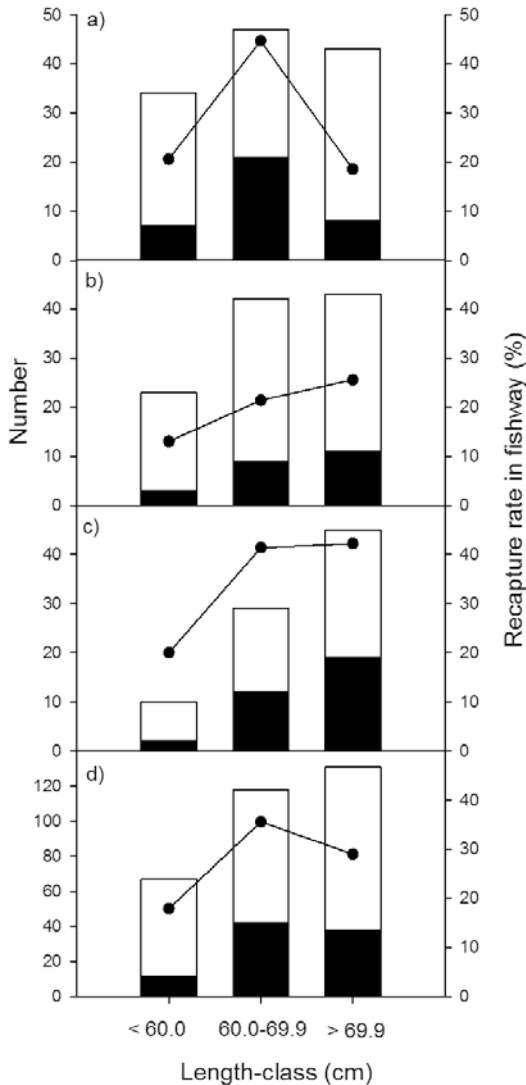

Figure 3. Number of Floy-tagged brown trout below spillway 1 at Hunderfossen dam subsequently recaptured in the fishway (solid bars) and not recaptured (open bars) during the study years a) 1998, b) 2008, c) 2011 and d) all years. The line shows recapture rates in the fishway (%) for each length-class.

Effect of origin, sex and degree of secondary sexual characters

No significant relationship was detected between the probability of observing recaptures in fishway and the parameters "sex" (Z = 2.47; P = 0.12; 95% C.I. for odds ratio of recaptures of males vs. females = 0,91-2,48), "colour" (Z = 0.03; P = 0.86; 95% C.I. for odds ratio of recaptures by increased colour index by one unit = 0.72-1.49 and origin (Z = 0.04; P = 0.84, 95% C.I. for odds ratio of recaptures of wild-born vs. hatchery-reared trout = 0.58-1.55) were found (Table 3, models 4-6).

Discussion

The overall fishway efficiency was 29 % for all three study years combined. The successful fishway migrants were delayed from 6 to 77 days, and the duration of delay varied between years. Fishway efficiency and delay did not correlate, and the year with highest functionality was also associated with longest delay. The observed efficiency of the fishway and duration of delay was influenced neither by the degree of secondary sexual characters, gender nor origin. Finally no evidence for stabilizing selection for medium sized trout were found, but the probability of smaller trout (≤ 59.9 cm) to enter the fishway was lower compared to larger trout.

The overall efficiency varied between 21 and 39 % (factor 1.86) during the three study years. This is partially consistent with other studies covering fishway efficiency for Atlantic salmon (*Salmo salar* L.), representing a similar iteroparous life history (Haltunen 2011). For example, passage efficiency varied between 21 and 23 % in Scandinavian rivers (Karppinen 2002; Lundquist et al. 2008) and up to 63 % in a Scottish river (Gowans et al. 2003). Anadromous trout in Emån, Sweden, performed as high as 95 and 97 % upstream passage efficiency at two consecutive fishways, and successful passage occurred within 2 days after arrival to the tailrace (Calles & Greenberg 2009). The reported efficiency differences between localities illustrate the need for site-specific approaches when assessing passage efficiency. With an overall passage efficiency

Table 3. Logistic regression models exploring the relationship between the probability (P) of observing recaptures in the fish ladder at the Hunderfossen dam, and the coefficients of the explanatory variables "sex" (model 4), "colour" (model 5), and "origin" (wild-born vs. hatchery-reared (model 6). "Year" is included as a categorical predictor in all models. The results of the Wald – statistic (Z) and the odds ratios with 95 % C.I. are given.

Model	Predictor	Coefficients	Z	P	Odds	95% C.I.
		Wald statistic				
4	Constant	-0.63	5.97	0.02	0.53	0.32-0.88
	Sex					
	Male	0.41	2.47	0.12	1.5	0.91-2.49
	Female				1	
	Year					
	1998	-0.39	1.70	0.19	0.67	0.37-1.22
	2008	-0.88	7.34	0.01	0.51	0.22-0.78
	2011				1	
5	Constant	-0.49	1.56	0.21	0.61	0.28-1.32
	Colour	0.03	0.03	0.86	1.03	0.72-1.49
	Year					
	1998	-0.46	2.39	0.14	0.63	0.35-1.13
	2008	-0.87	7.22	0.01	0.42	0.22-0.79
	2011				1	
6	Constant	-0.41	2.67	0.10	0.66	0.41-1.09
	Origin					
	Wild-born	-0.52	0.04	0.84	0.95	0.58-1.55
	Hatchery-reared				1	
	Year					
	1998	-0.46	2.34	0.13	0.63	0.35-1.14
	2008	-0.87	7.20	0.01	0.42	0.22-0.79
	2011				1	

of less than 40%, the migrant trout population in River Gudbrandsdalslågen is believed to experience considerable negative demographic impact due to delay, crowding, superimpositions of redds and increased intraspecific competition due to the restricted spawning and nursery areas below the dam (i.e. Ligon et al. 1995).

The distribution of suitable spawning areas within the river system may also affect the motivational basis driving upstream migration. A total of 17 distinct spawning grounds are mapped in the distribution range of the trout in River Gudbrandsdalslågen (Fig. 1), of which 7

are located below Hunderfossen dam (Kraabøl & Arnekleiv 1998). Two spawning grounds are situated approximately 100 and 500 m below the dam, and are easily accessible for trout during their attempts to locate the fishway entrance. The presence of suitable spawning areas and sexually mature conspecifics may trigger spawning or provide stop signals of increased strength after several weeks of unsuccessful attempts to enter the fishway. A likely consequence is that delayed or late runners are more prone to spawn below the dam compared to early runners. Unsuccessful migrants may therefore aggregate on the spawning grounds below the

dam, suffering reduced survival due to super-impositions and environmentally unfriendly regulation scheme compared to early runners homing to their ancestral and natural spawning grounds above the dam.

The annual median delay ranged between 20 and 49 days, and represents a major interruption of the upstream spawning migration. If the delay allows engagement in spawning at normal timing, fitness consequences are uncertain (Thorstad et al. 2008). Delay is an important criterion when evaluating efficiency of fishways, because it involves an array of biologically important consequences, such as energy costs (Pon et al. 2009), stress (Young et al. 2006), overripening of eggs (de Gaudemar & Beall 1998), disease and injuries (Cooke et al. 2006), all of which are linked to the time spent on route seeking behaviour. However, the magnitude of delays does not always mirror passage efficiency, and long delays are sometimes recorded at easily passable obstacles (Thorstad et al. 2008). Studies linking these biological aspects to physical and behavioural constraints are difficult to design because they must involve spillway manipulations and flow levels (Caudill et al. 2006), specific hydraulics at the fish entrance(s) and fallback behaviour caused by overshooting the natal sites (Boggs et al. 2004).

The results did not provide significant support for stabilizing selection inflicted by the fishway, but the probability for the smallest body size group of migrating trout (≤ 59.9 cm) to enter the fishway was lower compared to larger trout. The overall results from this three years mark-recapture study indicated a consistent directional selection pressure in disfavour of small trout. The results from the first trials in 1998 revealed that the probability for recapture of medium-sized trout was higher compared to smaller and larger trout this year. However, the data this year may be biased due to a severe outbreak of fungus infections (possibly Ulcerative Dermal Necrosis, UDN, and *Saprolegnia spp*. ulcers as secondary infections) on the spawning stock from 1996 to 2004 (Kraabøl 2006). The duration of the disease period (1996-2004) may have biased the results of the present study and the data analysed by Haugen et al. (2008) as well. In addition, a significant proportion of trout officially recorded as fishway migrants between 1966 and 1980 (Fig. 2) were actually captured in pools below the spillways and manually lifted above the dam (Kraabøl et al. 2009), and inevitably recorded as fishway migrants by Haugen et al. (2008).

Low passage efficiency for smaller trout (≤ 59.9 cm) may depend on a variety of explanatory variables. Smaller trout are almost exclusively novel spawners, without experience from previous spawning runs. Precise homing to natal sites may involve sequential learning as an important factor, and the role of olfaction seems to influence the degree of philopatry in Atlantic salmon (Hansen et al. 1987). Several theories have been launched as driving forces for philopatry, including optimized access to suitable breeding habitats, mates and parental resources (Hendry et al. 2004). Maiden spawners should be expected to have lower degree of philopatry compared to veteran spawners in iteroparous fish species, because they are driven by heritage alone, whilst veteran spawners can add previous experience to the ability and motivation for precise philopatry. Other and more feasible explanations are body size dependent differences in the capability to negotiate challenging rapids and falls, and maximum swimming speed correlate well with body length (e.g. Beamish1978; Videler & Wardle 1991). Body size dependent intraspecific competition to hold attractive positions within the rapids in the tailrace below the dam (Höjesjö et al. 2007) may as well have disfavoured maiden spawners. Thus, it seems possible that smaller trout are less able and less present in the strategic staging areas necessary to locate the fish entrances compared to larger trout.

The lack of gender distinctions contrasts the results obtained from a longitudinal data set from Hunderfossen fishway, where females were found to ascend the fishway earlier than males (Jensen & Aass 1995). This inconsistency reveals the significance of methodical approaches.

Recordings of temporal trends in abundance and first arrival date (Jensen & Aass 1995) make it impossible to distinguish between timing of river entry and actual gender related ability to locate the fishway, whereas the mark-recapture design in the present study warrants separation of gender distinctions from arrival time. An important detail in order to correct for different seasonal timing of river entry in this study was the categorization of body coloration among tagged trout as a proxy for river residency prior to capture and tagging, which turned out to be insignificant as an explanatory parameter.

The lack of difference between wild-born and hatchery-reared trout was expected because all hatchery-reared trout are F1-generations from successful fishway migrants, and both hatchery-reared and wild trout tagged in this study should from a heritage perspective perform strong homing towards ancestral sites located above Hunderfossen dam. Both groups performed equally during homing migration through the fishway. However, Jensen & Aass (1995) found a consistent pattern of hatchery-reared trout arriving later in the fishway compared to wild-born trout, but it is suggested that this temporal difference may mirror different timing of river entry rather than unequal abilities to pass the fishway.

The degree of body coloration had no influence on fishway passage success. However, it is recommended that endogenous mechanisms such as motivational state should be integrated in studies covering passage effectiveness for other species (Roscoe & Hinch 2010). Body coloration in salmon and trout typically develops from a silvery towards colourful appearances as the spawning season draws nearer (e.g. Quinn 2005), and may represent a suitable proxy for determination of the fish's motivation to migrate. As spawning time approaches the relationship between reproductive hormones and behaviour becomes increasingly determinate for the individual behaviour. Males and females become mutually influenced by each other's cumulative interactions (Colgan 1993) as body coloration develops, which in turn may affect time allocated to route seeking behaviour.

Another consideration that may counteract BL selection in the fishway is the temporal scale in the iteroparous life-history. As many as five spawning runs (typically every second year) are documented during a life cycle (Aass et al. 1989, Aass, P. pers.comm.). A possible scenario for a proportion of trout with natal origin above the dam might be that they can reproduce both below and above the dam during their lifetime. Following Haugen et al. (2008), small-bodied trout (< 60 cm) will have reduced probability to pass the fishway compared to medium sized trout (60-69 cm), and may be forced to spawn below the dam. Two years later, the same trout has attained a medium-sized BL, and may successfully pass the fishway and succeed to spawn at the natal site upstream the dam. When the very same individual later returns as a large-bodied veteran spawner, it may reproduce successfully below the dam as it did during the first spawning season. Therefore, body length selection is difficult to predict with such a scenario for iteroparous fishes. Notably, stabilizing body size selection caused by a semi-passable and size selective obstacle seems less likely to occur with equal strength among iteroparous compared to semelparous fish species, especially when the degree of iteroparity is high and spawning areas below the dam are available.

Another intriguing question regarding the observation of stabilizing selection by the fishway (Haugen et al. 2008) is that other passage locations in the river are also likely to inflict selective forces. The first passage problem for upstream migrants occurs at the confluence of the bypass section (regulated river stretch) and the tailrace from the power station (tunnel opening), situated 4.4 km downstream the dam. Telemetry studies have documented a discharge dependent passage problem at the tunnel outlet and the regulated river stretch. Passage is unhindered when water discharges >20 m³s⁻¹ is released on the regulated river section. At lower discharges, the upstream migrating trout was disrupted at this point (Arnekleiv & Kraabøl 1996), inflicting a major disadvantage among late runners from Lake Mjøsa. The regulated

water flow is gradually reduced from 20 to 2 m^3s^{-1} during September, which is known as an active period for late migrants in this river (Jensen & Aass 1995; Arnekleiv & Kraabøl 1996; Aass & Kraabøl 1999). Under normal situations, this flow-dependent migration hindrance will reduce access to both the fishway and natal spawning grounds for late runners in September, and may certainly have the capacity to inflict selective forces on annual spawning stocks.

Ascending trout that have successfully passed the tunnel outlet in July and August must pass a 4.4 km river section with heavily reduced water discharge. During September, the discharge is stepwise reduced (15-10-5-2 m^3s^{-1}). The steep gradient and coarse river bed containing boulders and large rocks may have the capacity to create discharge-dependent obstacles and prevent fractions of the trout population from migrating all the way up to the fishway and upstream located spawning areas.

Selection on body size may also be inflicted during return migration of spent adult trout from spawning sites above the Hunderfossen dam. Telemetry studies have revealed a bimodal temporal pattern in downstream migration. The first group of kelts is dominated by females and large individuals from both sexes, and constitutes 44 - 62% of the annual spawning stock passing the fishway. The descent takes place during and after spawning season in October and November (Arnekleiv et al. 2007). This group has historically been partly prevented from passing the dam during autumn unless spates occurs (Kraabøl et al. 2008). Forced overwintering in the basin may inflict size-selective and gender-dependent mortality among kelts due to different energetic and other health-related body conditions (Jonsson et al. 1997). During spring floods, surviving kelts and smolts pass through a variety of spillways, but mainly during release of surface flow (Kraabøl et al. 2008).

In summary, this site-specific examination of passage efficiency of a specific fishway and other problem areas within the same river clearly illuminates the complexity involved in the revelation of the interplay of possible selective forces occurring within a relatively simple migratory system. If selective forces are inflicted at all locations, the combined direction and strength of the selection may vary considerably between years, leaving stabilizing or directional selection difficult to retrace to a single origin. The fishway clearly represents a potential problem area, but should not be regarded as the only bottleneck that may inflict selective forces on spawning stocks. A noteworthy perspective is the recognition of both temporal and spatial scales, and especially the problem of different selective forces acting during ontogeny in iteroparous species. The present study highlight the need for a broader perspective when exploring and tracing evolutionary changes in life history traits as responses to anthropogenic influence (Haugen et al. 2008) where semelparous and iteroparous species represent different evolutionary trajectories (Kraabøl et al. 2009; Crespi & Teo 2002).

Acknowledgements

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