**Effect of competition and hydropeaking on growth of juvenile Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*)**

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**Short title:** Competition and hydropeaking affecting salmonids

**Key words:** Dewatering; stranding; hydropower production; stream channels; interspecific; intraspecific

**ABSTRACT**

The effects of hydropeaking and intra- and interspecific competition on performance (growth in length, mass and lipid content) of juvenile Atlantic salmon *Salmo salar* and brown trout *Salmo trutta* were studied in six experimental channels (three experiencing hydropeaking; three with stable discharge) during autumn. To prevent stranding, changes in water-covered area in the hydropeaking channels was small. Each channel was divided into three similar sized sections and stocked with either a low or high density of Atlantic salmon or a mix of Atlantic salmon and brown trout equalling the high density Atlantic salmon treatment. Hydropeaking had only minor and insignificant effects on performance: Growth in Atlantic salmon experiencing hydropeaking was reduced by 9% (length) and 7%(mass), respectively. Trout experiencing hydropeaking grew on average 4% less in length, but had on average 2% more mass than control fish. Both salmon and trout from the hydropeaking treatment had more body lipids at the end of the experiment than fish from the control channels (salmon: 2%; trout: 3%). A marked effect of competition was visible as salmon in the low density treatment were significantly larger (27 – 33%) and had more mass (30 – 38%) than salmon in either the high density salmon treatment or the high density salmon and trout treatment. Increasing both intra- and interspecific competition for juvenile salmon had a larger effect on growth than the effect of hydropeaking. The effects of hydropeaking were small, but even small changes in growth may translate into increased smolt age.

**INTRODUCTION**

Discharge in natural rivers is mainly influenced by precipitation, groundwater influx, and the geography of the catchment area. Discharge therefore varies on timescales of hours, days, seasons, years, and even longer time periods (Poff *et al.*, 1997; Allan and Castillo, 2007). Especially in the temperate and polar regions, rivers display a seasonal pattern in discharge with low flows during winter, peaking floods in spring when the snow is melting, low flows during summer, and spates during autumn. These are natural fluctuations which trigger natural processes like hatching of fish larvae (Sloat *et al.,* 2014) or fish migration (McCormick *et al.,* 1998). They also maintain the aquatic and riparian habitat (Poff *et al.,* 1997) by for example washing out fine sediments that would otherwise block interstitial spaces.

 Hydropower plants with dams and reservoirs may change these seasonal patterns because water is stored and released on demand (Poff *et al.*, 1997; Casas-Mulet *et al.,* 2015; Dodrill *et al.,* 2015). An advantage of hydropower over other renewable energy sources is the flexibility in energy-production, where turbines may be run and stopped according to temporal fluctuations in electricity demand. Human-induced rapid and frequent fluctuations in water discharge are termed hydropeaking. Hydropeaking is unpredictable for riverine organisms and the fluctuations exceed those observed naturally (Poff *et al.,* 1997; Taylor *et al.,* 2014; Puffer *et al.,* 2015). There has been a lack of controlled experiments to investigate long-term, cumulative effects of rapid and frequent discharge changes (Young *et al.,* 2011). Negative effects of hydropeaking may mainly be associated with the exposure of substrate and desiccation or to the rapid changes in hydraulic conditions. If fish are displaced they may have high energetic costs to return to suitable habitats which in turn might reduce their overwinter survival (Scruton *et al.,* 2005; Taylor *et al.,* 2014). It has been argued that these peaking flows are acute stressors in fish (Flodmark *et al.*, 2002). To study the effects of changing discharge with a stable water-covered area, Puffer *et al.* (2015) performed experiments with Atlantic salmon parr *Salmo salar* in experimental flumes. Growth rate of experimentally hydropeaked salmon were reduced with only 10% in summer, and with no statistical valid difference in winter experiments.

 Here, we present a study designed to test both the effects of fluctuations in water discharge and the effects of density and species composition on growth of juvenile Atlantic salmon and brown trout *Salmo trutta* during autumn. Hydropeaking experiments without the loss of water covered area (i.e. no stranding) were set up and designed similar to Puffer *et al.* (2015), to verify the published growth results obtained from the very same semi-natural, controllable environment. Variation in intra- and interspecific competition are known to affect the growth of salmonid fishes (e.g. Nislow *et al.,* 2011). The results of the hydropeaking experiments were therefore compared with the effect of increased competition by changing (i.e. doubling) density of Atlantic salmon and brown trout parr.

**MATERIAL AND METHODS**

Methods were similar to those of previously conducted experiments (Puffer *et al.,* 2015). In addition to the effect of hydropeaking flow, the present study set-up was designed to test the effect of competition (both interspecific and intraspecific) on performance of Atlantic salmon (Fig.1 A).The interspecific competition effect was studied using both the additive and the substitutive design (Weber and Fausch, 2003) (Fig. 1 B). The additive design compared replicates (3 replicates per flow condition) where brown trout parr were introduced into study arenas containing Atlantic salmon parr with controls without brown trout. This set-up is confounded with the increased density that it causes, and it doesn’t measure the relative competitive ability of salmon parr against brown trout parr (Fausch, 1998; Weber and Fausch, 2003). A substitutive set-up comparison was therefore also used, in which density was held equal among treatments (with 3 replicates each for the two different flow conditions). Experiments with 10 and 20 Atlantic salmon parr allowed an analysis on intraspecific competition effects on growth and body lipids (Fig.1). The growth effects determined at the termination of the experiment included length and mass change and body lipid content (nonpolar lipid stores).

The autumn experiment was conducted from the 29th of August until the 6th of October 2011 (duration: 38 days). Water temperature (mean temperature 13.2 °C) decreased steadily during the experiment from 16.6 °C (29. August) to 9.1 °C (6. October). The experimental facility consisted of six parallel, semi-natural outdoor stream channels (each 25.5 m long x 1.5 m wide) at the Finnish Game and Fisheries Research Institute’s research station in Paltamo, northern Finland (64°30’ N; 27°10’ E). Each channel was further divided (wire mesh panel 6 mm mesh size) into three 8.5 m long sections, which were stocked with different densities (0.8-1.6 fish m-2) or species composition (Atlantic salmon and brown trout combined group) (Fig. 1 A). These fish densities were well within the range of densities of juvenile Atlantic salmon in streams of Scandinavia (Bremset and Berg, 1999; Niemelä *et al.,* 2001; Korsu *et al.*, 2009).

 The stream bed in each channel consisted of a 10–15 cm layer of coarse gravel/pebble (20–35 mm in diameter), and shared the same water source (a nearby lake), thus also having the same temperature regime. Temperature was recorded by temperature loggers (Hobo H8; www.onsetcomp.com and Tinytags TG4100; www.geminidataloggers.com) every 2nd hour. In each channel, a meandering flow pattern was created gravel deflectors protruding the water surface, with three deflector in each of the channel sections. Three of the channels (control, Fig.1), were kept under stable water flow conditions (stable discharge 35 l s-1). The other three channels experienced hydropeaking on a diurnal basis, with high discharge (65 l s-1) during day time for 9 hours (0700 – 1600 hours; UTC+2), and low discharge (18 l s-1) during the remaining 15 hours. Control and experimental channels thus had the same total discharge (3060 m3) during 24 hours. The water-covered area remained nearly constant in the different treatments (control channels 35 m2, hydropeaking channels during low flow 35 m2, and during high flow 36 m2). The abiotic characteristics of the channels (depth, current etc.) were similar at a common discharge (see Puffer *et al.,* 2015).

Both salmon and trout (fork length ranging between 60–80 mm) originated from captive reared broodstock of the River Oulujoki (Finland) strain, hatched in spring 2010 and reared under standard rearing conditions in circular tanks. They were starved for one week, anaesthetized (clove oil), had their fork lengths (± 1 mm) and body mass (± 0.1 g) measured, and were tagged with individually coded passive integrated transponder (PIT) tags (tag model HDX Oregon RFID, tag size 12 mm X 2.15 mm, mass 0.1 g; www.oregonrfid.biz).

After tagging, fish were divided into groups of near identical length distribution (Tukey Honest Significant Differences, p ≥ 0.86) and stocked into the channel sections so that each of the treatments was located once in the upper, middle and lower section of both control and hydropeaking channels (Fig. 1). All channels had the same stable flow conditions (discharge 35 l s-1) for one week, after which hydropeaking was initiated. It has earlier been ensured that the channels supported benthic invertebrates providing a natural food supply (Korsu *et al.,* 2009; Puffer *et al.,* 2015).

At the end of the experiment, salmon parr were re-captured from the stream channels by electrofishing, identified by PIT code, killed, and their fork length (± 1 mm) and body mass (± 0.1 g) was measured. Further, the fish body cavity was opened, the PIT tag removed, and the stomach was emptied. Thereafter the fish were weighed and frozen for body lipid content analyses by standard proximate analyses (e.g. Dobush *et al.,*1985; Berg *et al.,* 2011).

Data analyses

The statistical analyses were performed with R, v. 3.1.3 (R Core Team, 2015). To test for possible channel and section effects, linear mixed-effects models with section nested within channel as random factors were fitted using the function lme from the package nlme (Pinheiro *et al.,* 2013) and compared to generalized least square (gls) models without random factors using log likelihood ratio tests (Zuur *et al.,* 2009). When no significant differences between the two models were found, the simpler gls-model was used, and *vice versa*.

 All following models are the full models before model selection. Model selection procedures followed Zuur *et al.* (2009) using log likelihood ratio tests, final models were re-fitted using restricted maximum likelihood (REML) and model residuals were checked for normal distribution. Both final body length and final body mass were modelled as a function of the density treatment, the hydropeaking treatment, the interaction between these two, and with their initial values as covariates. Body lipids were modelled as a function of the density treatment, the hydropeaking treatment, the interaction between these two, and with final body mass as a covariate.

**RESULTS**

Out of 120 salmon in each the control and hydropeaking treatment 106 and 112 fish survived, respectively. Out of 30 trout in each the control and hydropeaking treatment 29 and 28 fish survived, respectively. There was no effect of hydropeaking, density or species composition on survival.

 Fish grew well during the experiments, i.e. Atlantic salmon grew from (mean ± SD) 3.3 ± 0.6 g to a final body mass of 4.5 ± 1.2 g, and from 67 ± 4 mm to 76 ± 6 mm in length. Trout body mass increased from 4.2 ± 0.9 g to 7.3 ± 1.8 g, and body length increased from 71 ± 5 mm to 87 ± 8 mm.

Growth in length

In the model comparison for the final body length, channel and section had a significant effect (log likelihood ratio test: *L* = 6.04, *df* = 2, *p* = 0.0488), thus we chose the linear mixed-effects model. From the full model of final body length, both the interaction between the density and the hydropeaking treatment(*L* = 1.10, *df* = 2, *p* = 0.58), as well as the main effect of the hydropeaking treatment (*L* = 1.40, *df* = 1, *p* = 0.24) could be removed during model selection. Both the density treatment (*L* = 20.10, *df* = 2, *p* < 0.0001) and initial body length (*L* = 226.2, *df* = 1, *p* < 0.0001) remained in the model. Final length increased significantly with initial length (1.39 ± 0.07; t = 20.13; p < 0.0001) (Fig. 2 A). Both the high density salmon treatment and the high density salmon and trout treatment had a significant negative effect on final length of salmon (High density salmon treatment: slope-value ± SE: -3.2 ± 0.6, *t* = -5.15, *p* = 0.0004; high density salmon and trout treatment: -3.6 ± 0.7, *t* = -5.23, *p* = 0.0004). Growth in length for salmon was reduced from 11.4 ± 4 mm in the 10 salmon treatment to 8.1 + 4 mm in the 10 salmon and 10 trout treatment (= 29%), and to 7.8 ± 4 mm in the 20 salmon treatment (= 31%) (Fig. 2 A).

 Hydropeaking *per se* had no significant effect on growth in length: Salmon experiencing hydropeaking had on average a 9% lower growth rate in length than salmon experiencing stable water flow (control: 9.2 ± 4 mm; hydropeaking: 8.4 ± 4 mm). Trout experiencing hydropeaking had on average a 4% lower growth rate in length than trout experiencing stable water flow (control: 17.2 ± 4 mm; hydropeaking: 16.5 ± 5 mm).

Growth in mass

In the model comparison for the final body mass, channel and section had a significant effect (*L* = 15.27, *df* = 2, *p* < 0.0001), thus we chose the linear mixed-effects model. From the full model of final body mass, both the interaction between the density and the hydropeaking treatment(*L* = 0.61, *df* = 2, *p* = 0.74), as well as the main effect of the hydropeaking treatment (*L* = 0.64, *df* = 1, *p* = 0.43) could be removed during model selection. Both the density treatment (*L* = 14.70, *df* = 2, *p* < 0.0001) and initial body mass (*L* = 243.08, *df* = 1, *p* < 0.0001) remained in the model. Final mass increased significantly with initial mass (1.58 ± 0.07; t = 21.31; p < 0.0001) (Fig. 2 B). Both the high density salmon treatment and the high density salmon and trout treatment had a significant negative effect on final mass of salmon (High density salmon treatment: -0.45 ± 0.12, *t* = -3.73, *p* = 0.004; high density salmon and trout treatment: -0.60 ± 0.13, *t* = -4.53, *p* = 0.001). Growth in mass for salmon was reduced from 1.59 ± 0.84 g in the 10 salmon treatment to 1.05 ± 0.68 g in the 10 salmon and 10 trout treatment (= 34%), and to 1.04 ± 0.79 g in the 20 salmon treatment (= 35%) (Fig. 2 B).

 Hydropeaking *per se* had no significant effect on growth in mass: Salmon experiencing hydropeaking had on average a 7% lower growth rate in mass than salmon experiencing stable water flow (control: 1.2 ± 0.8 g; hydropeaking: 1.1 ± 0.8 g). Trout experiencing hydropeaking had on average a 2% higher growth rate in mass than trout experiencing stable water flow (control: 3.06 ± 1.1 g; hydropeaking: 3.11 ± 1.2 g).

Body lipids

In the model comparison for the body lipids, channel and section had no significant effect (*L* = 4.99, *df* = 2, *p* = 0.08), thus we chose the simpler generalized least square model. From the full model of body lipids, both the interaction between the density and the hydropeaking treatment(*L* = 1.12, *df* = 2, *p* = 0.57), as well as the main effect of the hydropeaking treatment (*L* = 0.04, *df* = 1, *p* = 0.85) and the main effect of the density treatment (*L* = 2.83, *df* = 2, *p* = 0.24) could be removed during model selection. Final body mass (*L* = 201.37, *df* = 1, *p* < 0.0001) remained in the model. Body lipids increased significantly with final mass (0.035 ± 0.002; t = 18.11; p < 0.0001). Thus, inter- and intraspecific competition had no significant effect on body lipids: Body lipids increased from 4.3 ± 0.7% in the 10 salmon treatment to 4.5 ± 0.9% in the 10 salmon and 10 trout treatment (= 4%), and to 4.7 ± 0.7% in the 20 salmon treatment (= 8%).

 Hydropeaking *per se* had no significant effect on body lipids: Salmon experiencing hydropeaking had on average 2% more body lipids at the end of the experiment than salmon experiencing stable water flow (control 4.5 ± 0.7%; hydropeaking: 4.6 ± 0.8%). Trout experiencing hydropeaking had on average 3% more body lipids at the end of the experiment than salmon experiencing stable water flow (control: 2.5 ± 06.%; hydropeaking: 2.6 ± 0.5%).

**DISCUSSION**

There are a limited supply of reports on the effects of hydropeaking on survival and growth of salmonid fishes. This is alarming considering the frequent use of hydropeaking in regulated rivers. The result of the present experiments of hydropeaking with stable water covered area confirms that effects on growth performance were limited and hardly visible. The differences in growth performance (body length, body mass, and body lipids) were not statistically significant, but there was a trend towards a reduction in growth (length: 9%, mass: 7%) among experimentally hydropeaked salmon. This result corresponds well with the results of earlier summer experiments, where a growth reduction of 10% was reported (Puffer *et al.,* 2015). These earlier experiments were based at the same facility (without sectioning of each channel) and based on the same procedures. The results of the two experiments with stable water covered area correspond and support a conclusion that there is a limited effect of hydropeaking on growth performance of salmon and trout in the absence of stranding. The results are also in accordance to results of earlier brown trout growth determination under fluctuating flow experiments, where only a small effect of hydropeaking was seen (Flodmark *et al.,* 2006). The authors concluded that if stranding were avoided, hydropeaking has relatively small direct effects on stream salmonids, a conclusion also underpinned by the results from the present series of experiments. The main growing season for salmonids in the northern hemisphere expands from spring to autumn and Atlantic salmon populations have a freshwater stage lasting 1–8 years (Thorstad *et al.,* 2011). In northerly rivers with low summer water temperatures, the seemingly small reduction in growth rate of juvenile salmonids in hydropeaked rivers can accumulate over long periods, which **c**ould result in delayed smoltification (Thorstad *et al.,* 2011). Even a small effect size can have an important role on salmonids living in northern areas.

 The density dependent growth differences were in correspondence to what could be expected based on competition theory and previous observations (e.g. Nislow *et al.,* 2011). The experiments did not reveal any difference between intraspecific and interspecific competition: increased fish density reduced growth equally. The intraspecific competition effect may be increased by the similarity in initial size of salmon parr. The intraspecific competition between fish of same size can be especially severe (e.g. Nislow *et al.,* 2011). The trout growth in mass was, however, more than double that of salmon parr in the experimental channels, but in spite of this rapid growth of trout, no difference between inter- and intraspecific competition was detected. Brown trout is traditionally held as more aggressive and social dominant to Atlantic salmon (e.g. Stradmeyer *et al.,* 2008; Nislow *et al.,* 2011), but there are also indications of selective segregation between the species (Berg *et al.,* 2014). The rapid growth of trout is in accordance to other investigators (Nislow *et al.,* 2011).

 The experiments were performed to investigate the effects of changes in water discharge and water level *per se*, omitting the stress and possible lethal effects on both fish and other organisms (Weber *et al.,* 2014). The energetic cost of fishes living under hydropeaking conditions may be compensated by fish maintaining position without actively swimming. Previous studies of behavioural changes in mountain whitefish (*Prosopium williamsoni*) concluded that fluctuating flows were no more energetically costly than stable flows (Taylor *et al.,* 2012). Also for bull trout (*Salvelinus confluentus*) living in a large hydropeaking river, only minor amounts of variance in energetic expenditure were explained by the discharge pattern in spite of a hydropeaking ratio in flow of 0: 1045 m3 s-1 (Taylor *et al.,* 2014). There are examples of increased growth rate of fish species affected by hydropeaking conditions (Finch *et al.,* 2015). Atlantic salmon are geographically widely distributed and can be found in a variety of habitats, i.e. streams, rivers, lakes, and ocean (Thorstad *et al.,* 2011). As generalists, they are well adapted to varying environmental conditions and are capable of dealing with seasonal variations. Human induced alterations in e.g. water discharge and temperature due to hydropower plants usually do not exceed the boundaries Atlantic salmon are adapted to, but the magnitude, frequency, duration, timing, and the rate of change cause problems for the fish (Poff and Zimmerman, 2010).

 The effects of hydropeaking in the present experiment were overall small and it indicates that juvenile Atlantic salmon and brown trout can handle variable water discharges well, at least with the magnitude and frequency examined here. Under poor growth conditions (e.g. reduced water temperatures during summer in northerly areas), it should be noted that even small changes in growth may sum up to potential significant effects on smolt production, particularly through changes in smolt age distribution.

**ACKNOWLEDGEMENTS**

Teija Haataja and Anna Harjunpää assisted in fish tagging and sampling and took care of the hydropeaking conditions. The staff of Kainuu Fisheries Research, the Finnish Game and Fisheries Research Institute, offered logistical help during the experiment. Anne Lohrmann is acknowledged for the body composition analysis in the laboratory. The experiment was approved by the Finnish ethics committee on animal experiments (licence for AHu). The work has been financed by Centre of Environmental Design of Renewable Energy (CEDREN), one of the Norwegian Research Council’s Research Centres for Environmental Friendly Energy (FME) (FME contract-number: 193818).

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 **Figure captions**

Fig. 1 A. Study design used to test the strength of intra- and interspecific competition on the performance on juvenile Atlantic salmon and brown trout under both stable and hydropeaking flows.

B: The experimental channels with the three different treatments. White channels experienced control flow (stable flow conditions) and shaded ones experienced hydropeaking flow (see text for details). Treatments: 10S = ten juvenile Atlantic salmon, 20S = twenty juvenile Atlantic salmon, 10S + 10T = ten juvenile Atlantic salmon and ten juvenile brown trout.

Fig. 2. Growth performance in length (A) and mass (B) for the three different density treatments: 10 salmon = black solid line and dots; 20 salmon= light grey dashed-dotted line and diamonds; 10 salmon and 10 trout = dark grey dashed line and triangles. Individual data points and common regression lines for different densities and species composition are indicated and include both the control and hydropeaking channels (since there was no significant effect of hydropeaking on growth). The high variation in response variables should be noted.

**Figures**



Fig. 1



Fig. 2