The survival of Atlantic salmon (*Salmo salar*) eggs during dewatering in a river subjected to hydropeaking

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ABSTRACT

Hydropeaking in regulated rivers is likely to become more frequent with increasing demands for renewable energy. Sudden fluctuations affect surface and subsurface flow regimes and change hydrological interactions occurring in the hyporheic zone. The hyporheic zone plays an important role for salmon embryonic development, and groundwater influx may create refuges for egg survival during low flow in hydropeaking regulated rivers. The links between salmon embryo survival and hyporheic hydrological processes during hydropeaking have hardly been investigated.

A field experiment was undertaken in a 5 x 20 m side gravel bar subject to dewatering due to hydropeaking. Eleven cylindrical boxes composed of 8 compartments were placed in the permanently wet area and the ramping zone. Sixty eggs were placed in two compartments (at 10 and 30 cm depth) in each box. Surface and interstitial water levels and temperatures were monitored at 2 min resolution. Data was collected for a period of three months, coinciding with early stages of salmonid egg development in this catchment. Egg compartments were checked on 6 occasions for survival after different hydropeaking events. Dead eggs were counted and removed. Survival rates were lower in the top compartments in the ramping zone (78%) compared to the boxes in the permanently wet area and the lowermost compartments in the ramping (survival rates >99%). With no water quality issues in the catchment and very low inputs of fine sediments in the egg compartments, exposure to dry conditions and sub-zero temperatures were the main factors explaining egg mortality in the top compartments of the ramping zone. The rate of survival will thus depend on the surface water and groundwater interactions. Site specific hydrological interactions occurring in the hyporheic zone should be actively considered when managing fish populations in rivers with hydropeaking.

Keywords: hydropeaking, salmon egg survival, hyporheic zone

1 Introduction

The demand for electric energy is growing and suppliers search for efficient and sustainable sources. Storage potential and load balancing have become key issues in the current deregulated energy market with an increasing production of renewable energy from wind and solar sources. Norway, with a 50% of total energy storage potential in Europe through its hydropower system has a great potential for storage and load balancing. Hydropower is a well suited source for load balancing being the only renewable with a feasible storage potential and with high production flexibility. This has led to an increased use of hydropeaking, causing more frequent and rapid changes in flow downstream of power plants, thereby creating unnatural flow changes.

Flow fluctuations are a natural phenomenon in temperate rivers, and flow dynamics play an important role for aquatic organisms. In general, regulated rivers have different instream flows without large short-term variations, but rapid flow changes during hydropeaking operations are gaining increasing interest, as they may alter the riverine habitat dramatically, leading to dewatered riverbeds and affecting riverine organisms through stranding (Cushman, 1985; Hunter, 1992; Hvidsten, 1985; Saltveit *et al.*, 2001). In particular, hydropeaking may also lead to the dewatering of redds containing developing eggs for various periods and lengths of time (Young *et al.*, 2011).

Atlantic salmon (*Salmo salar*) typically spawn in the autumn, by burying their eggs in redds 10 to 30 cm into river gravels (de Gaudemar *et al.*, 2000; Mills, 1989). The high embryo and alevin survival rates in natural conditions, typically about 100% (Elliott, 1984), illustrate that these stages are well protected in the gravel, although they have no capacity to evade malign abiotic factors.

Egg and embryo development occurs during winter and their survival is dependent on the relationship between subsurface and surface water (Schmidt and Hahn, 2012) and on a range of biotic and abiotic factors, including hyporheic water quality, water delivery rate, temperature and gravel composition and the complex interaction between these (Gibbins *et al.*, 2008; Malcolm *et al.*, 2003; Malcolm *et al.*, 2008). The varying patterns of subsurface-surface water interactions may generate a spatial and temporal mosaic and consequently complex conditions for egg development and egg survival (Malcolm *et al.*, 2009). The hyporheic zone may therefore be functionally important, creating heterogeneity in habitat and spawning sites with regards to flow, temperature and oxygen (Power *et al.*, 1999).

The active use of the hyporheic zone by salmonids has been studied with respect to redd site selection, egg deposition and survival, as well as fry development and the use of favourable groundwater inflow sites for spawning and juvenile fish survival (reviewed by Heggenes *et al.* (2011)). The hyporheic zone provides low velocity micro-niches, protection or refuges against extreme temperatures, desiccation and predation, and provides stable substrate during bedload movement. Salmonids often spawn in habitats where groundwater inflows occur, and their spawning success may be dependent on such habitats (Baxter and McPhail, 1999; Garrett *et al.*, 1998; Hansen, 1975). For brook trout, the presence of groundwater in the spawning and incubation habitat appears to be critical for reproductive success (Curry *et al.*, 1991; Fraser, 1985; Gunn, 1986). However, living conditions in the hyporheic can also be negatively affected, such as fish embryo mortality due to domination of hypoxic groundwater (Malcolm *et al.*, 2008). Dissolved oxygen (DO) plays a critical role in the development of the juvenile stages of benthic spawning fish and salmonids in particular (Sear *et al.*, 2012). Upwelling groundwater in some Scottish rivers has been identified as the most likely cause of the major decrease in dissolved oxygen (DO) at redds and the discrepancy found between the numbers of spawning females and the level of juveniles (Soulsby *et al.*, 2005).

The degradation and destruction of valuable spawning and rearing habitats due to anthropogenic changes (e.g. hydropower, flow modification and channelization) is known to have dramatic impacts on fish populations (Enders *et al.*, 2007). The dewatering of salmonid redds (Malcolm *et al.*, 2012) is of great concern for water resource management in regulated rivers. If spawning occurs at high flows, the consequence will be dewatering, especially under hydropeaking operations (McMichael *et al.*, 2005; Vollset *et al.*, submitted), or if spawning is encouraged at flow levels that cannot be maintained (Bauersfeld, 1978; Skoglund *et al.*, 2012).

Physical and chemical conditions in the redds, such as temperature and relative humidity, will be altered when spawning areas are dewatered (Neitzel and Becker, 1985; Young *et al.*, 2011). However, because of unpredictable spatial variability in the intergravel environment and complex interactions between environmental conditions in natural rivers and the varying response of embryonic stages, Eggs with embryos seem most tolerant (Becker *et al.*, 1982), although the consequences of dewatering are not always straightforward (Malcolm *et al.*, 2012). Under natural conditions, eggs of fall-spawners may freeze and die in cold areas during low flow periods in late winter. This may also occur in regulated rivers with large annual variations in discharge or during hydropeaking, if flow is reduced after spawning. This has been documented for Atlantic salmon by Skoglund *et al.* (2012) for regulated rivers in Norway. However, where there are groundwater inputs, egg mortality due to freezing in winter can be reduced as groundwater is typically warmer than surface water, rising survival chances of fry and recruitment (Garrett *et al.*, 1998) and showing an increase in the relative importance of groundwater during low flows in regulated rivers (Casas-Mulet et al., submitted; Colleuille *et al.*, 2005; Saltveit and Brabrand, 2013).

Reviewing five case histories of redd dewatering, Becker and Neitzel (1985) concluded that onsite studies are needed to obtain data for assessment of potential impacts of dewatering situations, and for development of effective mitigation procedures. In many instances, apparent dewatering of rivers does not lead to dewatering of the gravels, especially where groundwater upwelling occurs (Curry *et al.*, 1994). Consequently, the complicated interactions between abiotic controls and biotic response mean that it is hard to predict the impacts of dewatering in the absence of site-specific information (Malcolm *et al.*, 2012). Furthermore, the complexity of stream processes during winter underscores the need for interdisciplinary research to quantify biological changes (Cunjak *et al.*, 1998), and knowledge concerning the interaction between fluctuating flows and hyporheic processes. Of particular interest are the consequences of somewhat regular sudden stops in hydropower production on hyporheic processes at a scale relevant for the response of hyporheic fauna. Findings will be important both for understanding impacts and for mitigation of adverse impacts and management in regulated rivers.

The main objective of this study was to evaluate the effect of dewatering on survival of eggs of Atlantic salmon during several hydropeaking episodes of varying length during different winter conditions in a regulated river, enabling differentiation between impacts from different hydrographical conditions and the surrounding environments, focussing especially on the incubation.

2 Methods

2.1. Study site

The River Lundesokna, located in central Norway, is a 41.2 km long regulated tributary to the River Gaula (Figure 1A). The Lundesokna hydropower system encompasses the Lundesokna and parts of other catchments with a total area of 395 km^2 with an average of 3.8 m^3y^{-1} in annual runoff. The hydropower system consists of three reservoirs, three interbasin transfers and three power plants (Figure 1A) with a total installed capacity of 61MW and an average annual production of 278 GWh. Sokna hydro power plant (Figure 1A) operates according to daily and weekly market price fluctuations *vs* water availability in the three reservoirs. The lower 4km river stretch below Sokna power plant is subject to hydropeaking operations (Figure 2) with a typical flow range from 20 $m^3 s^{-1}$ to 0.45 $m^3 s^{-1}$.

The study site was located in a 30m long and 20m wide lateral gravel bar (Figure 3) with a stable armoured layer present. It is located 700m downstream from Sokna hydropower plant outlet (Figure 1B) with a hydraulic gradient of 0.29% along the river bend.

2.2. Experimental design

The experimental design was based on the main methods developed in Malcolm *et al.* (2010). A total of 11 cylindrical boxes were vertically placed in the gravel at both the permanently wet and at the fluctuating flow areas at the study site (Figure 3). Each box was formed by 8 stacking plastic compartments screwed together. The internal height and diameter of each compartment was 3 and 6.2 cm, respectively, and each compartment was perforated with several 5 mm diameter holes to permit water flow through.

Thirty eggs were inserted into the second and seventh compartments from the top of each box. These two compartments were protected with a 1 mm mesh net on the inside to avoid excess of fine sediments. A 0.5 m long piece of surgical tubing was connected to the two compartments containing the eggs to allow the extraction of water samples. The other 6 box compartments were filled with small stones, pebbles and gravel from the river to resemble the surrounding natural conditions and to exclude light from above. The boxes were then buried, so that the egg compartments were situated at approximately 0.1 and 0.3 m below the ground. They were numbered and marked and located in pairs (1m apart) at 5 sites, except for a single box in the furthermost downstream permanently wet site (W3).

The Atlantic salmon eggs were acquired from a single female from the local hatchery, and fertilized one week ahead of starting the experiments. The experiments were conducted from 2 December 2011 to 11 April 2012, when the first hatching was registered.

A total of six 0.032 m inside diameter Durapipe$^{\mathrm{TM}}$ were used to construct the piezometers next to each pair of egg containers (Figure 3). Eijkelkamp$^{\mathrm{TM}}$ Diver water pressure transducers with integrated temperature loggers were inserted at each of the piezometers and provided 1 to 4 min resolution water pressure (±0.5 cm accuracy) and temperature (±0.1°C accuracy). One Eijkelkamp$^{\mathrm{TM}}$ Baro Diver was located at the left bank of the site to measure air pressure (±0.5 cm accuracy) to compensate the absolute pressure readings in the piezometers, and air temperature (±0.1°C accuracy). Water elevations (both surface and interstitial) were computed for each container by interpolation of the surrounding piezometers.At boxes 1, 4 and 8, ground temperature was monitored at 1 minute resolution at 0.15 and 0.3 m below the ground level using Vemco Minilog II temperature loggers. At box 1, temperature and dissolved oxygen were monitored by means of Campbell Scientific® CR200 Series.

The compartments containing eggs were checked for survival at 6 occasions after periods with several hydropeaking episodes of varying length. Sampling periods occurred at 11, 18, 38, 48, 78, and 100 days after installation. Dead eggs were counted and removed from the container to avoid the development of fungi. Eggs were replaced with a new set of 30 eggs only in the compartments with zero survival. This happened three times during the two first sampling periods. Elevation changes in the container locations due to re-burial were recorded with the aid of a Leica Viva differential GPS. Water samples were collected from the river and extracted from each of the egg compartments using a vacuum pump. Sampling was carried out in 5 occasions comprising *in situ* analysis for dissolved oxygen, conductivity, pH and temperature using a WTW Multi 3410 meter and laboratory analysis for turbidity. Two 30cm depth granulometry samples were collected manually in the river bed of the ramping zone at the downstream and upstream points of the gravel bar where the field experiments took place.

2.3. Data analysis

All water quality values were calculated for the top and bottom compartments located in the permanently wet area and top and bottom compartments located in the ramping zone. These were compared to the values from the surface water in the river.

The granulometry distribution was calculated for each of the two collected samples in the gravel bar.

Survival rates were calculated in each egg compartment at the end of each sampling period as the proportion of surviving eggs in comparison to the initial number of eggs in the compartment.

Survival by periods

A total of 16 variables were identified and calculated after each of the sampling periods (Table 1, top). In order to assess their influence on survival related to each individual period, linear regressions between the proportion of survival and each of the variables were undertaken as a basis for developing a GLM model with the most significant variables.

Survival by locations

The survival in the ramping zone was compared to the survival in the permanently wetted area. In the ramping zone, a total of 9 variables were identified as potentially influencing mortality at the compartment level. Those are listed and described in Table 1(bottom). Durations of exposure to dry conditions were calculated by computing the time steps at which interstitial water elevations were below the bottom of each compartment. Durations of exposures to dry conditions combined with air temperature below or above zero were also calculated. The depth of each compartment below the ground was calculated by comparing the ground elevation with the elevation of the compartment top at its specific location. These data were obtained for every single compartment during each of the surveyed periods. In order to simplify the number of variables, a correlation analysis (>0.7) was undertaken between the 10 variables and only 5 were finally selected for further analysis.

A matrix with 96 observations (6 periods in 16 compartments) of the 5 selected variables was created to assess their relationship with the proportion of survival. A mixed effect model was used to fit all relevant combinations of the variables, considering the 16 compartments as a random effect. The simplest model approach was taken by choosing a significant model built with the least possible amount of variables. Selection was based on significance in variables and the Aikake (AIC) and Bayesian (BIC) information criterion. Similar fitted values to those in a more complex model were also taken in account.

To further understand the differences in survival between the top and bottom compartments, the temperature data obtained from cylinders 1, 4 and 8 was analyzed. Temperature distributions in the top and bottom compartments were analyzed during both exposure to dry conditions and exposure to dry combined with air temperature below zero. Air temperature below zero was potentially considered an indicator of frost in the ground.

Statistical analyses were carried out using the software package R, version 2.14.1 (R Development Core Team, 2012). Significance thresholds were established at 0.05. Sigma Plot version 12.0. was used for graphical presentations.

3 Results

Values of oxygen, temperature, electrical conductivity, pH and turbidity were not significantly different ($p>0.05$) between the river water and the water in any of the egg compartments (permanently wetted area and ramping zone) (Figure 4). Water quality parameters were also non-significant ($p>0.05$) between compartments and therefore not considered to influence the survival of Atlantic salmon eggs in the River Lundesokna.

The substrate in the Lundesokna river gave a D_{95} of 33 to 36 mm and D_{50} between 12 and 17.5 mm (upstream and downstream sampling points respectively), classified as gravel size-class and coinciding with typical spawning sites sediment characteristics according to studies elsewhere (Moir *et al.*, 2002).

The proportion of surviving eggs for each of the periods and locations is summarized in Table 2. The mean survival rate (tops and bottoms) in the ramping zone compared to the survival in the permanently wetted area is shown. By periods, the lowest proportion of surviving (0.75 in average) was found after period 5, with peaking events occurring between 19 January and 18 February, followed by period 1 (events from 2 to 13 December) with a survival rate of 0.84. The highest survival rate (1.00) was found in period 4 (events from 18 February to 11 March).

The data presented here is for egg survival until March, when the first eggs hatched. However, the eggs remained in the experimental site until 16 June, when all the eggs had hatched. Egg survival was >99% during the later periods.

Survival by periods

The values of the 16 physical and chemical environmental variables calculated for each of the periods are summarized in Table 3. The linear regression undertaken between each of these variables and the egg survival concluded that only two variables had a significant ($p<0.04$) relationship with the proportion survival. These were minimum air temperature ($R^2=0.67$) and maximum duration of low flows combined with air temperature below zero ($R^2=0.76$). The applied Generalized Linear Model (GLM) showed a significant intercept ($p<0.0002$), but it showed no significant ($p>0.05$) relationship for either of the two variables. Periods 5 and 1, with events leading to the lowest survival rates, showed amongst the lowest minimum air temperature and had the two longest lasting events of low flows in combination with air temperature below zero. To the contrary, period 4 (highest survival) had the warmer minimum air temperature and the shortest duration of low flow events combined with frost and the highest minimum ground temperature (Table 3).

Survival by locations

Egg mortality occurred only in the top compartments in the ramping zone with a mean survival rate of 0.78. In contrast, survival rate was 1 in the bottom compartments of the ramping zone and >0.99 in the permanent wet areas (Table 2). Out of the initial 10 variables that could potentially influence mortality at the compartment level, only the variables *Max Exp Dry & AT<0*, *N Exp Dry & AT<0, Max Exp Dry & AT>0, N Exp Dry & AT>0 and Depth* (abbreviations defined in Table 1) were considered for further analysis.

The outputs of the mixed effect model combining the 5 selected variables are summarized in Table 4. Model number 5 was chosen to explain the relationship with survival given its significant and that it was the model with the lowest AIC and BIC with values fitted to the more complicated models.

Model 5 indicates that *Max Exp Dry & AT<0* and *Depth* are the variables that significantly ($p<0.0005$ and $p<0.007$ respectively) influence mortality individually. The deeper the egg boxes were buried in the substrate, the higher the survival; and the longer the exposure to dry conditions combined with air temperatures below zero, the higher the mortality. The model, however did not indicate any significant ($p>0.05$) effect of a combination of the two variables in explaining survival.

The duration of individual episodes with combinations of water levels above or below the compartments and air temperatures above or below zero is illustrated for each of the top and bottom compartments and for each of the 6 surveyed periods (Figure 5).

As expected, the boxes located in the permanently wetted area (W1, W2 and W3) were not exposed to dry conditions. For the boxes located in the ramping zone (1 to 8), both the top and bottom compartments, were exposed to dry conditions when air temperatures were below zero (Figure 5).

The bottom compartments had a higher numbers of single exposures to dry and to dry and frost conditions than the tops due to fluctuations in water levels. When exposed, the durations of exposures were also much lower in the bottom compartments (Figure 6, top and bottom left panels). Whilst the top compartments were exposed permanently for a long period, the water level fluctuated in the bottom compartments. The longest duration of exposure to dry conditions was found during period 3 followed by period 6. However, the longest duration of exposure to a combination of dry and air temperature below zero was during periods 1 and 5 respectively. Those two periods had the highest mortality.

Figure 7 illustrates the temperature distribution and the durations of exposure to dry conditions and subzero conditions combined at the compartment scale. The variations in temperatures during both dry and dry and freezing conditions were higher in the bottom compartments than in the top ones. Dry conditions did not always coincide with air temperatures below zero, but on both occasions with subzero temperatures, the duration of exposure were much lower in the bottom compartments than in the top ones.

The top compartments experienced longer durations of exposure to both dry conditions and dry and freezing conditions. During exposure, the top compartments experienced lower temperatures than those at the bottom.

The conditions of exposure to dry and freezing conditions varied between periods showing some mortality in the top compartments. Only in periods with mortality, temperature reached $<-1\ ^{o}$C.

Mortality in the top compartments occurred in periods 1, 2, 5 and 6, showing some variability in durations of exposure to dry conditions and dry and freezing conditions combined. Only in periods 1, 2 and 5, temperature reached $<-1^{o}$C. The highest survival rates in the top compartment (100%) were found in period 3 and 4 with no exposure to combined dry and freezing conditions. This coincides with the results in the bottom compartments, with very low exposure to dry conditions and dry and frost and temperatures above or very close to zero.

4 Discussion

A high percentage of the Atlantic salmon (*Salmo salar*) eggs subjected to dewatering conditions in the Lundesokna River were able to survive despite being desiccated for long periods. Although high, the survival rates in the ramping zone were sub-optimal in comparison to the survival in the permanently wetted area (>99%) and the typically 100% survival reported under natural conditions (*Elliott*, 1984).

There were no significant differences in water quality between the top and bottom compartments of the permanently wetted area and the ones in the ramping zone. Also, no significant differences were found between the compartments and the surface river water quality. Therefore, water quality in the interstitial was similar to the surface water. This emphasizes that water quality, in particular DO did not influence the mortality of embryos in the Lundesokna river.

These findings are in contrast to that found by Youngson *et al.* (2004) and Soulsby *et al.* (2005), where the influence of interstitial water seemed to be the cause of high mortality in Atlantic salmon embryos. Upwelling groundwater in some Scottish rivers has been identified as the most likely cause of the major decrease in DO in redds and the cause for egg mortality. Dissolved oxygen plays a critical role in the development of the juvenile stages of benthic spawning fish and salmonids in particular (Sear *et al.*, 2012). No eggs survived in redds where average oxygen levels were less than 7 $mg.l^{-1}$ (Malcolm *et al.*, 2003). In Lundesokna, with or without groundwater influence, the level of oxygen was never below 10 $mg.l^{-1}$.

During low flows the interface between surface and groundwater changes, with groundwater becoming more important. Subsurface water in Norway generally originates from very shallow aquifers, with short residence times and a high precipitation regime, resulting in partially oxygenated interstitial water (Brabrand *et al.*, 2002). The origin of the subsurface water in the study site was from shallow groundwater, giving it similar characteristics to the surface water (Schmidt and Hahn, 2012). Therefore, water quality of the subsurface water cannot be considered as a mortality factor for salmonid embryos in this situation.

The mortality in the ramping zone of the Lundesokna was mainly due to long exposures to dry and freezing conditions. This finding is supported by the fact that later (March to June), survival in the top compartments was >99%, when air temperature were above zero and there were much shorter periods of low flows as a consequence of stop in production. Findings elsewhere (Bauersfeld, 1978; Casas-Mulet et al., submitted; Chadwick, 1982; Saltveit & Braband, 2013; Skoglund *et al.*, 2012; Young *et al.*, 2011), also describe higher or total mortality due to desiccation of spawning redds as a consequence of low flow after spawning or from stranding for long periods during hydropeaking events in regulated rivers. The main environmental conditions were the same throughout the whole study site, and during each of the periods the egg boxes were exposed to the same hydropeaking flow regime. Therefore, based on the analysis on survival by periods, it can be concluded that the highest mortality is likely to occur in periods with long duration hydropeaking events occurring when air temperatures are below zero.

The analysis of local conditions in each compartment permitted determination of the effect of the hydropeaking regime on survival. Mortality in the ramping zone was only apparent in the top compartments as the bottom compartments showed a 100% survival at all times. This is due to the fact that the bottom compartments were in contact with interstitial subsurface water during low flow events for longer periods than the top compartments.

On some occasions, the bottom compartments showed some degree of exposure to dry conditions coinciding with air temperatures below zero. However, such exposures were much shorter in duration than the eggs in the top compartments experienced. In addition, temperatures in the bottom compartments never reached temperatures as low as those in the top compartments. The degree of exposures to dry conditions coinciding with *in situ* temperatures below zero in the bottom compartments was very short compared to exposures in the top compartments, alleviating the possibility of mortality because of freezing temperatures.

The high survival rate in the bottom compartments also reinforces the assumption that water quality is not a cause for the mortality of salmonid eggs in the river Lundesokna, leaving the exposure to dry and to dry and freezing conditions as the main cause.

Freezing of redds may occur even in a suitable spawning environment (Reiser and Wesche, 1979). The lower temperature limit for freezing of Atlantic salmon eggs is probably close to the freezing point of water, though probably slightly lower due to a small content of salt (DeVries and Cheng, 2005).

The main difference in survival between eggs in the top and bottom compartments was the degree of exposure to dry and freezing conditions and the burial depth in the substrate. The important influence of subsurface water (with no water quality issues) to the bottom compartments aids in keeping the eggs wet or with some degree of moisture at all times and, not least, an incubation environment above zero. Under experimental laboratory conditions, salmonid eggs could survive for weeks in dewatered gravel if they are moist (at least 4% moisture by weight) and not subjected to extreme temperatures, heat or near freezing (about 0.0°C) (Becker and Neitzel, 1985; Becker *et al.*, 1982; Becker *et al.*, 1983; Reiser and White, 1983). High mortality was, however, associated with only small reductions in humidity and increases in exposure time (Neitzel and Becker, 1985). The extent and duration of flow alteration and the stage of embryo development will also influence survival (Becker and Neitzel, 1985). In addition, fine sediments were never observed as a potential issue (Sear *et al.*, 2012), providing good conditions for survival in the bottom compartments.

Although maximum duration of exposure to dry and freezing conditions and burial depth were considered, within periods and specific compartments, some variability in specific survival exist. This illustrates, on a local scale, the highly variable flow in the hyporheic between subsurface and surface water, primarily due to the heterogeneous nature of substrate (Schmidt and Hahn, 2012), and can explain the high influx of interstitial water at a low depth in the boxes located at sites 1 and 2, where survival was 100% at all times.

Both durations of exposures to dry and freezing conditions and the depth of burial are key factors influencing survival in rivers impacted by hydropeaking. Exposures to dry conditions coinciding with air temperatures below zero were more influential to mortality than exposure to dry conditions only. In particular, the maximum duration of an individual exposure event was the most influential factor driving mortality. In terms of burial depth, the deeper, the higher is the chance of survival.

Long duration of low flows during cold periods can be detrimental for survival. However, factors such as the cumulative or total duration of low flows and air temperatures below zero and numbers of single power plant stops did not seem to influence the overall mortality, even if production stopped during the night with lower temperatures. The minimum water elevation reached during each production stops in Lundesokna was very similar, indicating that the production pattern involved simply stopping the power plant.

The population effect of such additional mortality depends on the extent to which the availability and distribution of spawning habitat and reproduction is a bottleneck for the population (Enders *et al.*, 2007). Suitable reproductive habitats are a prime necessity for population sustainability, and river regulation may reduce the abundance and quality of spawning habitat. The dewatering of spawning areas due to hydropeaking might expose intergravel developmental phases to suddenly changed physical and chemical conditions (Becker and Neitzel, 1985), thus directly affecting the potential recruitment of salmonid populations.

From a management point of view, adapting power production to avoid extremely cold air temperatures is strongly recommended. An increase in minimum instream flow during a stop in production is one measure to maintain a higher proportion of the substrate wet or moist by increasing the subsurface water level, and thereby improving the degree of embryo survival. Excavation of the river gravels in armoured surface substrates (occurs in the Lundesokna and commonly observed in other seasonally regulated and hydropeaking rivers), is another potential mitigation measure, creating potentially more suitable and readily available habitat for spawning and increasing the burial depth, thus augmenting survival during dewatering events. From the fact groundwater influx to spawning redds is likely to increase egg survival, groundwater influx in regulated rivers should be actively considered to achieve optimal embryo survival.

5 Conclusions

Dewatering of spawning redds due to hydropeaking regulation does not always mean absolute egg mortality. If redds are influenced by subsurface water typically warmer than surface water during winter and not deficient in oxygen, egg of Atlantic salmon may survive for longer periods even if the air temperatures are below zero. A stable flow covering the redds underlines the importance of subsurface flow between egg hatching and swim-up as an advantage for successful survival during eggs incubation.

With no water quality issues and no major input of fine sediments, the maximum duration of exposure to dry conditions and freezing during dewatering were identified as the main factors influencing Atlantic salmon egg mortality.

These findings suggest that future management of hydropower plants with hydropeaking operations should consider a potential change in their operational strategy during cold periods in winter to the account of subsurface flow influx to achieve optimal survival of salmonid embryos.

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