Introduction

Groundwater may constitute 40-100 % of the total discharge in inland Norwegian rivers during low flow periods in late summer and winter (Colleuille *et al*., 2005). The total groundwater inflow is usually lower, or shows higher variation in western coastal rivers, due to steeper topography and glacial-alluvial valley deposits of coarser sand and gravels of high permeability (Koestler & Brabrand, 2001). Geological heterogeneity will produce a potential for local underwater sites of groundwater flux, with heterogeneous hyporheic substrates (Hayashi & Rosenberry, 2002; Schmidt & Hahn 2012) that will determine microspatial influx sites (Heggenes *et al*., 2010), thus creating spatial variability in habitat and spawning sites with regard to flow, temperature and oxygen (Power *et al.*, 1999). The hyporheic zone is an important component of the lotic ecosystem (Ward, 1989) with variable flux of groundwater and surface water, creating high vertical heterogeneity with associated ecological implications. Both spatial and temporal fine scale variability of hyporheic hydrochemistry, in particular dissolved oxygen, appears to be common and may affect eggs revival in gravel spawning salmonids (Greig *et al*., 2007; Soulsby *et al*., 2009; Malcolm *et al*., 2009).

Salmonids often spawn in habitats where groundwater inflows occur, and their spawning success may be dependent on the limited availability of such habitats (Hansen, 1975; Garrett *et al*., 1998; Baxter & McPhail, 1999; Barlaup *et al.,* 2008). Eggs have the most restrictive winter niche of all life stages of Atlantic salmon (Cunjack *et al*., 1998), due to the specific hydraulic condition and substrate chosen for spawning (Peterson, 1978; Fleming, 1996). This, and a reproduction strategy with one or few spawnings per female fish, renders Atlantic salmon vulnerable to human interventions, such as river regulation (Enders *et al*., 2007). Suitability of spawning sites varies with flow, and in many cases their accessibility will increase with artificial high discharge providing access to areas that are not wetted during low flows (Bauersfeld, 1978; Chadwick, 1982).

In regulated rivers groundwater influx may therefore create refuges for juveniles during low flows or hydropeaking episodes (Saltveit *et al*., 2001). Eggs of fall-spawners may freeze during low flow periods in late winter. This may also occur in regulated rivers when instream flow is reduced after spawning. Such egg mortality has been documented for Atlantic salmon by Skoglund *et al*. (2012). However, where there is groundwater influx, freezing of eggs and egg mortality in winter might be minimized since groundwater during winter is usually warmer than river surface water. It has been documented that eggs of Atlantic salmon may survive in groundwater fed substrates for months during winter drawdown in the river Suldalslågen or when exposed to hydropeaking (Saltveit & Brabrand, 2013; Casas-Mulet *et al*., in review). The prerequisite for this property of groundwater is that there is no oxygen deficiency (Soulsby *et al*., 2005). Moreover, a significantly higher survival rate for kokanee (*Oncorhynchus nerka*) and bull trout (*Salvelinus confluentus*) embryos was documented in habitats influenced by discharging groundwater with a clear selection of those sites for spawning (Garrett *et al*., 1998; Baxter & McPhail, 1999).

Juvenile salmonids may take advantage of groundwater upwellings and actively seek out such patches as thermal refugia both in winter and summer, migrating deep into substrates with groundwater upwelling (Douglas, 2006). Small streams in alpine environments may freeze to the bottom in winter, causing juvenile fish mortality and ensuing recruitment failure (Borgstrøm & Museth, 2005), while groundwater inflows may provide more stable (temperatures and flow) and ice-free habitats for overwintering fish and eggs (Cunjak *et al.,* 1998; Heggenes *et al*., 2010; Saltveit & Brabrand, 2013). Physical and chemical conditions in redds will be altered when spawning areas are dewatered (Young *et al*., 2011). The extent and duration of flow alteration and the stage of development will influence the survival, and newly hatched alevins are less tolerant (Becker & Neitzel, 1985; Neitzel & Becker, 1985). If not subjected to extreme temperatures (in this case warm water) or predation, laboratory studies have confirmed that salmonid eggs may survive for weeks in dewatered gravel if they are kept moisty (Becker *et al*., 1982; 1983; Becker & Neitzel, 1985; Reiser & White, 1983). The aim of our study was to investigate the survival of Atlantic salmon eggs in a large area of potential spawning grounds that is permanently dewatered during most of the egg incubation period due to regulation. Specifically, selected environmental variables were assessed and related to such survival.

Material and methods

Study site

The river, Suldalslågen, Western Norway, runs 22 km from Lake Suldalsvatnet to the inner part of the Ryfylke fjord. Due to regulation, the flow in Suldalslågen is reduced, with an instream flow ranging between c. 12 and 65 m^3s^{-1}, depending on the time of year, but with a stable minimum flow in winter (15 December to 1 May) of 12 m^3s^{-1} released from the dam in the outlet of Lake Suldalsvatnet, but with higher flows and artificial floods during the rest of the year, to take account of smolt migration, angling and flushing.

In the Suldalslågen, Atlantic salmon spawn relatively late compared to other Norwegian rivers, with a peak in early January (Heggberget, 1988). Based on models for egg and alevin development (Crisp, 1981; 1988; Jensen *et al*., 1989; 1991), spawning in the beginning of January leads to "swim up" between 17 June and 4 July, i.e. one month later than can be observed *in situ* in this river (Saltveit *et al*., 1995), and which is indicated to be a consequence of egg development in redds influenced by groundwater (Saltveit & Brabrand, 2013). It is reasonable to assume that groundwater seepage gives a higher temperature with less variation. In historic times local people have linked the early hatching of juvenile Atlantic salmon in Suldalslågen to groundwater influx areas within the river (Slagstad, pers. com.). Prior to its regulation, Suldalslågen had very large seasonal variations in discharge. The mean spring flood was c. 400 m^3s^{-1}, while winter flows as low as 3 m^3s^{-1}, indicate that redds could be dewatered and desiccated also under natural conditions during cold periods.

The *in situ* incubation experiments were carried out in the uppermost part of the river, 1 km below the Suldalsvatn dam. The study site was a 100 m long and 50 m wide gravel area on the southern side of the river (Figure 1). The studies were undertaken from January to June 2012. The river discharge was stable during the study period, except for the two smolt migration floods in May, as illustrated in Figure 2.

In Situ experimental set-up

Egg boxes and water quality

The experiments were conducted using eight cylindrical boxes, height 24 cm and 6.2 cm in diameter, divided into eight compartments. Fertilized eggs were placed in two of the compartments in each of the cylinders, i.e. in the second compartment from the top and in the second lowermost compartment. The compartments above and below those with the eggs were filled with small stones, pebbles and gravel from the river. All compartments were perforated with 10 holes (diam. 5 mm) to allow water flux. The boxes with corresponding compartments were numbered and marked.

The boxes were planted within the river bed on 18 January 2012 at three sites (sites 2-4) in the drawdown zone with desiccated river bed, but with influx of groundwater indicated by temperature. Two boxes were introduced at each site, c. 1m apart. In addition, two other boxes were placed within the river substrate as reference for survival under permanent flow conditions, site 1 (Figure 1). Fifty eggs from Atlantic salmon were placed in each of the compartments, and these also had a 0.5m long piece of surgical tubing connected to allow the extraction of water samples. The egg compartments were protected with a 1 mm mesh net to avoid excess fine sediments. The boxes were placed in the river substrate, so that the uppermost compartment of each box was situated at the upper edge of the bed. When introduced, the dry river bed was covered by a 10 cm layer of snow and the air temperature was -5 ºC.

The eggs were acquired from the local hatchery, fertilized one week ahead of the start of the experiments.

Egg compartments were controlled for survival and water samples were collected on three occasions during the egg incubation period; on 23 March (after period 1), 19 April (after period 2) and when terminating the experiments 24 May (after period 3). Dead eggs were removed to prevent fungal development. All eggs that hatched between April and May, including dead alevins, were considered as surviving the incubation period. Elevation changes due to re-burial were recorded with a differential GPS for each of the boxes and each of the control periods. When assessing survival, egg boxes were taken out of the river bed and reburied immediately to avoid disturbances. Water quality samples were obtained pumping water from the egg compartments through the surgical tubing on four occasions (February, March, April and May). Oxygen, temperature, pH and conductivity were measured *in situ* with means of a WTW Multi 3410 meter and water samples were taken to the laboratory for turbidity analysis.

Water elevations, temperature and oxygen

Five Eijkelkamp® Diver water pressure transducers with integrated temperature loggers were inserted in pipes constructed of 32 mm inside diameter Durapipe®. They were located next to each pair of egg boxes and provided 10 minute resolution data on surface and subsurface water levels and temperatures in the ground (Figure 1). One Eijkelkamp® Baro Diver was installed in the site to measure air temperature and air pressure to compensate the absolute readings in the pressure transducers.

Single point water elevations were measure at the lowest and highest flows with a differential GPS and used as a reference to convert the continuous water levels data to elevations. Those were also linked to discharge data provided by the Norwegian Water Resources and Energy Directorate, NVE.

Substrate temperature was monitored in boxes 2, 3 and 4 at 1 hour time resolution from 7 February at 0.15 and 0.3 m below the ground (the level of the top and bottom compartments, respectively) by means of HOBO®

temperature loggers installed next to each compartment. In box 2D, logging devices included an AADI® Datalogger 3634 with two optopodes measuring temperature and dissolved oxygen.

Geometry and grain size distribution

A high resolution (10 cm of maximum separation between individual xyz points) geometrical characterization of the study area was obtained by means of Laser scanning (dry areas) combined with differential GPS point data (wet areas) in order to have a reliable reference on the egg boxes location in relation to the ground level. Two subsurface and subsurface samples were collected at the upstream (around Sites 2 and 3) and downstream (Site 4) areas of the drawdown zone in April during low flows. A 0.5 by 0.5 m wooden frame and coloured spray was used to separate the surface substrate and by collecting only the painted gravels. Subsurface substrate was collected manually by shoveling out material at 30 cm depth inside the wooden frame. Samples were taken to the lab for particle size distribution analysis. It was obtained through a standard method of analysis by sieving and weighing, with sieve sizes of 0.075, 0.15, 0.3, 0.6, 1.18, 1.7, 2.36, 3.35, 4, 4.75, 6.3, 9.3, 12.5, 19, 25 and 37.5 mm. Cumulative granulometry curves were drawn to derive representative particle size ranges or D values.

Data analysis

Subsurface water elevation data at sites 2, 3 and 4 were used to calculate Vertical Hydraulic Gradients (VHG) in relation to the surface water elevation. Water elevations were compared to the elevation of each compartment and durations of exposure to dry and dry and freezing conditions (maximum, total and number of occasions) were computed for each of the sampling periods.

The percentage of survival was calculated in each compartment as for each of the sampling periods. The cumulative percentage of survival was also computed.

A total of 10 field-collected environmental variables (Table 3) were considered for statistical analysis. A correlation analysis was carried out to select non-correlated variables only and they were individually compared with survival rates through linear regressions. Several combinations of GLM models were tested with selected

Data analyses were carried out in Microsoft Excel and the software package R, version 2.14.1 (R Core Team, 2013). Sigma Plot version 12.0 was used for graphical presentations.

Results

Flow variations

The discharge released from the dam was very stable throughout the study period (Figure 2). From 1 January until 30 April the average flow was 13.6 m^3s^{-1} with very little variation, meaning that the eggs were never inundated with river surface water during that period (Figure 1). On 1 May, when the discharge from the dam was increased from the first artificial spring flow of 40 m^3s^{-1}, the water elevation increased by c. 40 cm, inundating the eggs placed in the dry river bed until the experiment was terminated on 24 May.

Environmental conditions

River water temperatures were fairly stable during the experimental period, increasing only slightly from 2 to 5.5 ºC. The air temperature during the study period varied from -7.7 ºC on 1 February to 17 ºC when terminating the experiments in May, with several periods below 0 ºC in January and February (Figure 2).

Granulometry characteristics in Suldalslågen are summarized in Table 1. Aggregates ranged from coarse gravel (D_{90}), fine and medium gravel (D_{50}) to coarse sand (D_{10}), generally with coarser surface materials in Sites 2-3. Fine sediments (<1 mm) represented a low percentage of the surface samples and were 17% and 11% in the subsurface samples of Sites 2-3 and 4 respectively.

Survival

The percentage of surviving eggs and the cumulative survival in each compartment and for each surveyed period is illustrated in Figure 3. Total average survival and average survival by periods is summarized in Table 2, for both the reference site 1 and sites 2-4 and for each of the compartments and the overall box.

High variability in survival between individual compartments and periods was observed. However, as expected, the reference site 1 showed very high average survival rates with a total average of 95.5% and up to 100% in period 1. The top compartments showed a slightly lower survival than the bottom compartments, but with less than 4% difference.

Sites 2 to 4 also gave high average survival rates of an overall 72.2%, with differences between the top and bottom compartments of 5%.

Water quality

The distribution of the data collected for each of the compartments is illustrated in Figure 4. Dissolved oxygen varied from 6 to 14 mg l^{-1} and 60-110% between sites. Temperature variation (1 to 14 ºC) reflected the seasonal differences. Electrical conductivity values were between 6 and 90 μScm^{-1} and pH between 6 and 8, both parameters with higher variability in the top compartments. The large spatial variation in conductivity and pH in some of the compartments had no relevance for mortality comparing with those having less variation. Turbidity was higher in the bottom compartments with values up to 400 NTU.

Substrate temperatures in the boxes 1U and 1D, 2D, 3D and 4B were at all times above 0 ºC (Figure 5). In the drained area, a vertical and lateral gradient in temperature changes was observed. Vertically, temperatures in the bottom compartments showed as expected less variation. The larger fluctuations in temperature in the top compartments reflected a greater influence of air temperature. Within substrate temperature in the wetted site (1U and 1D) showed minimal fluctuations in temperatures, while the dewatered sites show an increased influence of air temperature as they became further away from the river thalveg (4B).

Figure 6 shows the continuous levels in dissolved oxygen around the top and bottom compartments of box 2D, and several point measurements in the river. Dissolved oxygen levels in the subsurface water in the drained substrate were at all times lower than in the river. Changes in dissolved oxygen were directly linked to changes in groundwater level. However, the bottom compartments had higher dissolved oxygen concentrations than the top compartments during the majority of the low flow periods (except for very cold periods with temperatures below 0 ºC). In contrast, during the high flows in May, this is reversed with the top compartments having higher levels of dissolved oxygen indicating a greater influence of highly oxygenated surface water in the upper compartment areas. The dipping oxygen concentrations when the two flow peaks occur (Figure 6), suggests that a different type of water, possibly older less rich in oxygen groundwater that was accumulated in the gravel, is mobilised during the peak, leading to a decreased oxygen concentration in the bottom compartments.

VHG and exposure to dewatering

A positive vertical hydraulic gradient (VHG) at Sites 2 and 3 during the low flow periods indicate an upwelling potential in these areas during the drained period (Figure 7). Further downstream, at site 4, the negative VHG values indicated a downwelling potential. At high flows, VHG values were closer to zero, translating to a decrease of both upwelling and downwelling potentials.

The reference boxes at Site 1 (1U and 1D) were permanently covered by river surface water. The rest of the boxes, although located in an apparently dry area, had quite stable groundwater influx that prevented them from total desiccation. However, slight fluctuations in the groundwater influx and the relative position of the compartments in the study site, exposed some of them to desiccation, as shown in Figure 8. Further, these events were sometimes combined with air temperatures below zero, potentially leading to freezing, also illustrated in Figure 9, where all the top compartments and the bottom compartments of 3D and 3U were exposed to water levels below the compartment and were also combined with air temperatures below zero, especially in period 1.

Relationship between variables and survival

A correlation analysis was made between all the environmental variables considered on each compartment (Table 3). Total durations of exposure (to dry and dry and freezing conditions) and dissolved oxygen saturation levels were discarded in further analysis due to their high correlation (>95%) to maximum durations of exposure to desiccation and frost and dissolved oxygen concentration respectively.

The outputs (R^2 values and significance) of the individual linear regressions carried out are summarized in Table 4. Data is shown for the total dataset and for each of the periods. All regressions showed a normal distribution of the residuals.

For period 1, a significant relationship between survival rates and temperature, dissolved oxygen and duration of exposure to dry and to dry and freezing conditions was found, however, only temperature showed a high R^2

value. In period 2, only dissolved oxygen and conductivity showed a significant relationship with survival, but R^2 values were low. In period 3, no relationship between survival and the measured variables exist.

The overall period analysis show very low R^2 values, but significance between survival and the variables, turbidity, dissolved oxygen and maximum duration of exposure to dry conditions, was found. Several GLM models were tested with the combination of these three variables (Table 5), all models showing a normal distribution of the residuals. The best-fitted model was the combination of the three variables: duration of exposure to dry conditions, dissolved oxygen concentration and turbidity. The model showed significance for all combinations and interactions and the lowest AIC.

Discussion

We selected the river Suldalslågen as site for this experimental study because of the low winter discharge both prior to and due to regulation. The minimum unregulated discharge in winter during the egg incubation period of Atlantic salmon was 3 m^3s^{-1}, but with spawning occurring at far higher flows, spawning redds could be dewatered, with egg mortality as a possible consequence. However, local informants linked the early egg hatching, in spite of very late spawning of Atlantic salmon in this river, to groundwater influx areas, which also could minimize egg mortality in spawning redds during low flows (Saltveit & Brabrand, 2013).

Numerous spawning locations in regulated rivers are only found to become accessible during limited high flow periods and an obvious possible consequence are a subsequently dewatering of redds when the flow declines after spawning, leading to high egg mortality due to desiccation or frost (Barlaup *et al*., 1994; Young *et al*., 2011; Skoglund *et al.*, 2012; Vollset *et al*., Submitted). In the regulated river Bjoreio, Western Norway, the number of dewatered redds and egg survival was a direct function of flow regime from spawning to "swim up" the following spring (Skoglund *et al*., 2012). In this river the mortality was 100% in those redds that became stranded during the egg incubation period, but freezing was considered as the limiting factor.

In spite of dewatering, eggs may survive in dewatered areas (Brabrand & Saltveit, 2013; Casas-Mulet *et al*., in review). In the present study, both survival rates for each of the three periods and also for the whole study period were relatively high. Despite the high survival rates (72%), eggs in the drawdown compartments showed lower survival than those in the compartments permanently covered with surface river water (95.5%). Factors critical for egg survival in dewatered redds were duration of dewatering, time of year, weather conditions, substrate conditions, the stage of egg development and not least the presence of subsurface or groundwater. Given that groundwater inflow provided wetness, freezing was not a serious mortality factor in Suldalslågen. The two main variables having a significant effect on egg mortality was exposure to desiccation and to desiccation and frost simultaneously, but there was a difference between the periods with regards to the controlling parameters. During the final period, no main factor could be identified, but during the first periods, survival rates were significantly linked to temperature, dissolved oxygen and duration of exposure to desiccation with and without freezing. A highly significant vertical and horizontal difference in survival rates was also observed between the egg boxes and different periods in the drawdown area. Such variability cannot be explained by a single variable. The combination of survival variables can vary both spatially and temporally, as shown in the regression analysis between different periods and for the overall period. These differences could be explained by local streambed heterogeneity (e.g. Malard *et al.,* 2002; Boulton, 2007), creating a horizontal and vertical mosaic of interstitial flow, humidity, temperatures and dissolved oxygen in the river bed.

Subsurface water in Norway generally originates from very shallow aquifers in coarse river deposits, resulting in usually well oxygenated groundwater (Brabrand *et al*., 2002), and during low flows the groundwater become more important for river water quality, including levels of dissolved oxygen. Except for the compartment 3Ub and 4Bb, the level of oxygen was never below 7 mg l^{-1} close to the egg boxes. Similarly, in the River Lundesokna, with or without groundwater influence, the level of oxygen in the river bed was never below 10 mg l^{-1} resulting in high egg survival, dependent on periods, varying between 75 and 100% during hydropeaking events (Casas-Mulet *et al*., in review). Also, Garrett *et al*. (1998) and Baxter & McPhail (1999) found that groundwater influx to spawning redds seemed likely to increase survival for kokanee (*Oncorhynchus nerka*) and bull trout (*Salvelinus confluentus*) embryos. However, in contrast, no eggs survived in redds where average oxygen levels were less than 7 mg l^{-1} in Scottish rivers (Malcolm *et al*., 2003). Differences in reported critical values in dissolved oxygen probably reflect differences in methods (including sampling frequency), salmonid species and water temperature between studies (Malcolm *et al*., 2002). Dissolved oxygen in bottom substrate plays a critical role in the development of the juvenile stages of benthic spawning fish and salmonids in particular. Factors influencing the dissolved oxygen regime within spawning gravels include the accumulation of fine sediment, penetration of groundwater or surface water into the gravels, the thermal regime and the consumption of oxygen by organic fractions in sediments (Jones *et al*., 2012).

Differences in local substrate composition and distribution might affect survival and this is illustrated from the high rates of survival in box 3D (top and bottom) during periods 1 and 2, in comparison to the high mortality in box 3U, only 1 m apart. However, substrate composition at such small spatial scale was not measured in this study, and only differences between upstream and downstream (through a representative sample) areas is shown. There are no indications that the effect of substrate manipulation during sampling had effects on survival, as great care was taken and the lapse of time between sampling periods was long enough to allow recovery between periods. In addition, no effects were detected in the river Lundesokna (see Casas-Mulet *et al.*, in review), where the same methods were applied. The relative position of some of the compartments to the slightly fluctuating groundwater elevation and then the duration of exposure to desiccation and freezing might explain the high mortality in period 1 in some of the compartments such as the tops of 3U, 2U and 2D, which were exposed to long lasting desiccation and frost periods and showed low survival. However, other compartments were equally exposed during this period and showed high survival, such as 3D and 4T tops (100 and 95% survival, respectively, in period 1). Therefore, micro-scale local conditions of groundwater influence, clogging and dynamic processes occurring in the compartments, including possible variability in the eggs biology, not analyzed in this study, could have affected the survival.

Despite never exposed to dry or frost, the final survival in the bottom compartments of 4B, 3U and 3D was 0%, 0% and 18%, respectively. Turbidity levels were relatively high and in addition large amounts of fine organic sediments were noticed inside these compartments during sampling, potentially leading to critically low dissolved oxygen levels in the micro environment close to the eggs that was not detected from the water sample pumped from the compartment or the loggers. As such, high level of turbidity is probably not a mortality factor if not settling on egg surface preventing oxygen supply. Similar high turbidity level were found in the top compartments 2U and 4B, with low survival rates of 36% and 29% respectively, but also in the bottom compartments 2D and 2U with high survival rates (74% and 82% respectively). This variability in results illustrates that the local conditions around the boxes and the complex groundwater dynamics affecting each compartment may have affected the final results. Fine sediments were not the primary factor determining within-redd mortality rates in the Newmills Burn (Soulsby *et al.*, 2001). However, variations of only a few percent of silt content can strongly decrease survival to emergence (Lapointe *et al*., 2005). Increasing hydraulic gradients has a positive effect on median survival, but the effect depends both on sediment composition and the height gradient. There is no single threshold interstitial flow velocity that ensures survival to emergence. Even when maintaining a constant interstitial velocity, survival tended to be reduced in substrate with a higher fine-content (Olsson & Persson, 1986; 1988; Lapointe *et al.,* 2005).

Suitable reproductive habitats are a prime necessity for population sustainability, and river regulation may reduce the abundance and quality of spawning habitat, thus directly affecting recruitment of salmonid populations. Even though the importance of groundwater for salmon redd site selection and egg survival appears obvious (Soulsby *et al*., 2005), and that the use of groundwater upwelling sites for spawning has been reported for several salmonid species (e.g. Garett *et al*., 1998), there is little data to substantiate the idea that groundwater outflows directly affect spawning site selection (Baxter & McPhail, 1999). Varying patterns of interactions between groundwater and river surface water may generate a spatial and temporal mosaic and consequently complex conditions for egg survival (Malcolm *et al*., 2009), egg development and spawning time. During low flow periods in regulated rivers, there may therefore be an increase in the relative importance of groundwater for salmonid survival.

Conclusions

A certain proportion of Atlantic salmon eggs located in dewatered redds can survive during winter even when covered with ice and snow. However, this survival was lower in comparison to survival in permanently wetted locations.

Survival rate of eggs in the dewatered redds can vary with both the relative horizontal position along the gravel bar. The main drivers for survival were found to be linked to groundwater influx with regard to water level and water quality characteristics such as oxygen and turbidity as a potential indicator of fine sediments.

Such findings are important for the management of regulated rivers by emphasizing the importance of considering groundwater influx when assessing the management needs for the conservation of Atlantic salmon populations.

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Table captions

Table 1. Particle size characteristics at the upstream (Sites 2-3) and downstream (Site 4) sections in the study area.

Table 2. Percentages of average survival for each of the sampling periods and for the total duration of the experiment. Survival is calculated as an average of the reference boxes at site 1 and the boxes at sites 2, 3 and 4. Results are presented for the whole box and for the top and bottom compartments respectively.

Table 3. List of considered variables for statistical analysis.

Table 4. Outputs of the linear regressions between each of the selected variables and the survival rates at all boxes. Number of samples n=16 for each of the periods and n=48 for the total duration of the experiment.

Table 5. Outputs of the four combinations of GLM models. Consideration of model selection was based on the AIC values. Note on abbreviations: WL= maximum duration of water levels below compartment (min.); O_2= dissolved oxygen (mg l^{-1}); Turb= turbidity (NTU).

Figure captions

Fig1. Illustration of the location of the sites in Suldalslågen and the experimental set-up.

Fig2.Water elevation and air temperature changes in the river Suldal, during the whole study period.

Fig3. Percentage of survival for the top and bottom compartments in each of the boxes for each of the three sampling periods. Note: n.d. refers to periods with no data after a period of zero survival.

Fig4. Distribution of the water quality variables values measured for each of the boxes (t: top compartment, b: bottom compartment) for all periods.

Fig5. Differences in temperatures between sites and between top and bottom compartments.

Fig6. Continuous oxygen data from the top and bottom compartments of box 2D in comparison to point measurements in the river and the same compartments on 4 occasions.

Fig7. Vertical Hydraulic Gradient (VHG) between the river and the subsurface water elevations at Sites 2, 3 and 4. VHG values presented are an average of the whole low flow and high flow period respectively. Upwelling potential is indicated by positive VHG values and downwelling potential by negative ones.

Fig8. Egg compartment elevations in comparison to water elevations for each of the sites. Note1: ground temperatures are taken at the depth at which the piezometers were buried (see Figure 1). Note 2: vertical lines denote the date at which sampling was undertaken; therefore egg compartment elevation might change slightly from sampling period to sampling period. Note 3: Filling of the boxes was done in January and February, in February no degree of survival was measured.

Fig9. Duration of episodes with water levels above or below the egg compartment combined with air temperature above or below 0 ºC.