

1 **Hydropower operations in groundwater-influenced rivers: implications for Atlantic**
2 **salmon (*Salmo salar*) early-life stages development and survival**

3 **Abstract**

4 During their early-life stages (egg maturation, hatching, alevin development), between late autumn and
5 early spring, young Atlantic salmon are exposed to surface-groundwater interactions in the hyporheic
6 zone and may depend on influx of sub-surface water during periods of regulated low discharge for
7 survival. Two recent studies, one in a seasonally regulated river and one in a river exposed to
8 hydropeaking, displayed unexpectedly high survival of eggs in surface de-watered areas because of the
9 influx of oxygen-rich sub-surface water. Field observations of newly-hatched alevins in these two
10 rivers showed them to be more sensitive (i.e. suffered higher mortality from) to surface de-watering
11 than were eggs. Exposure to dry conditions in drawdown areas was highlighted as the main cause for
12 alevin mortality. Therefore, shorter periods of surface de-watering in the river with hydropeaking
13 resulted in higher alevin survival compared to the seasonally-regulated river when still permanently
14 drained after egg hatching. Greater consideration should be given to all early life-history stages when
15 implementing discharge release strategies, and the extent of groundwater influence and the potential
16 for flexible hydropower operations should be taken into account.

17

18 **Keywords:** hydropower regulation, hydropeaking, sub-surface water influx, egg survival, hatching
19 success, alevin survival

20

21 **Introduction**

22 Atlantic salmon (*Salmo salar*) spawn in the autumn by burying their eggs in river gravels, with egg
23 development during winter and hatching in spring. After hatching, alevins remain in the gravel until

24 they have absorbed their yolk sac and then emerge from the substratum, ready for external feeding
25 (Mills 1989; de Gaudemar *et al.* 2000). In regulated rivers, changes in discharge regime, which may
26 leave salmon redds exposed to dry and even freezing conditions during winter, can affect egg and
27 embryo survival (Skoglund *et al.* 2012; Harnish *et al.* 2014). Even if the embryo and alevin stages of
28 Atlantic salmon are well protected in the gravel, then they have no opportunity to evade malign abiotic
29 factors such as reduced discharge induced by river regulation. For optimal survival in regulated rivers,
30 discharge release operations should take into account not only man-made changes in the hydrological
31 regime, but also the influence of sub-surface water on spawning areas (Casas-Mulet *et al.* 2014,
32 2015a, 2015b).

33 Desiccation of salmonid redds is of great concern in water resource management (Malcolm *et al.*
34 2012). If spawning occurs at high flows, then these areas may be de-watered as a result of hydropower
35 operations (McMichael *et al.* 2005; Harnish *et al.* 2014), and physical and chemical conditions in the
36 redds may then be altered (Neitzel & Becker 1985; Young *et al.* 2011). However, because of complex
37 interactions between surface and groundwater and intra-gravel physical and chemical processes, the
38 consequences of de-watering for eggs and alevins are not easily predicted (Malcolm *et al.* 2012).
39 When moist salmonid eggs can survive de-watering for weeks (Saltveit & Brabrand 2013; Casas-
40 Mulet *et al.* 2015a, b), but newly-hatched alevins are more vulnerable and may die 4–10 hours after
41 de-watering (Becker & Neitzel 1985; Becker *et al.* 1982, 1983; Neitzel & Becker 1985; Reiser and
42 White 1983).

43 The influence of hydropower regulation type and the importance of groundwater and interstitial
44 water for the survival of eggs have been discussed previously regarding two Norwegian rivers: the
45 Lundesokna, which is subjected to hydropeaking (Casas-Mulet *et al.* 2015a), and the Suldalslågen,
46 which is subjected to permanent winter drawdown (Casas-Mulet *et al.* 2015b). In both rivers, egg
47 survival has been unexpectedly higher in the zone subject to discharge fluctuations compared with the
48 permanently wet area, with a mean survival of 89% and >99% in the River Lundesokna, and 72% and
49 95% in the River Suldalslågen. Sub-surface water influxes have the potential to reduce egg mortality

50 during de-watering events. However, little is still known regarding the consequences of discharge
51 regulation on egg hatching and the alevin stage. Based on field observations of hatching success and
52 alevin survival in the two above mentioned rivers, the aim of the present study was to assess the
53 importance of adapting hydropower operations and taking into account the effect of sub-surface water
54 on salmon populations during their early life stages within the substratum. For this, research that
55 integrates knowledge of ecology and environmental processes is required, so the present study
56 considers key factors for evaluating different discharge scenarios to develop a technically feasible
57 operation strategy that could support hatching success and alevin survival.

58

59 **Methods**

60 *Study sites*

61 The two rivers used in the experimental field studies, the Lundesokna and the Suldalslågen, support
62 natural salmon populations and are located in central and south-west Norway, respectively. The River
63 Lundesokna is a tributary to the River Gaula, the largest river in central Norway, and listed among the
64 top five Norwegian Atlantic salmon angling rivers. Its lowermost power plant, the Sokna, operates on
65 a regime that varies according daily and weekly market price *vs.* available water in the reservoirs.
66 Hydropeaking in the Lundesokna, therefore, results in periodically abrupt discharge fluctuations that
67 can change from ≈ 20 to $0.45 \text{ m}^3\text{s}^{-1}$ in < 20 min, with a drop in water level of > 0.6 m. The River
68 Suldalslågen, known for its large-sized salmon, is a seasonally regulated water course. Because of
69 water transfers, its instream discharge is reduced throughout the year, ranging between $\approx 12\text{--}65 \text{ m}^3\text{s}^{-1}$,
70 depending on the time of the year and purpose (smolt migration, angling or flushing). A stable
71 minimum discharge of $12 \text{ m}^3\text{s}^{-1}$ is released between 15 December and 1 May from the dam at
72 Suldalsvatn. The areas affected by discharge reductions (hydropeaking in the Lundesokna and
73 permanent discharge reduction during winter in the Suldalslågen) are termed the drawdown zone in
74 both rivers.

75 The experimental sites in both the Lundesokna (Fig. 1a) and the Suldalslågen (Fig. 1b) were the
76 same as selected in previous studies on egg survival (Casas-Mulet *et al.* 2015a, 2015b) and each was a
77 large gravel bar located 500–700 m below a dam. The study sites were selected because of their
78 suitability for addressing the objectives of the present and previous studies (within a broader research
79 programme), and in terms of their substratum and water quality for the construction of redds by
80 indigenous salmon populations, rather than as locations known to support high salmon spawning
81 activity.

82 *Experimental design*

83 The experimental set-up and procedure for data collection were also similar to those described in
84 Casas-Mulet *et al.* (2015a, 2015b). Cylindrical boxes (24 cm high and 6.2cm diameter) comprising
85 eight stacked, perforated compartments (Malcolm *et al.* 2004, 2009) were placed in the riverbed in two
86 types of location in both rivers: permanently-wetted areas (used as a reference), and drawdown zones.
87 Eleven boxes were used in the River Lundesokna and eight in the Suldalslågen (Fig. 1). Atlantic
88 salmon eggs were acquired from local hatcheries at the same time as those used in the studies by
89 Casas-Mulet *et al.* (2015a, 2015b). The eggs, fertilised one week earlier, were introduced into the
90 second and seventh compartments from the top of the cylindrical boxes, 30 eggs per compartment in
91 the River Lundesokna and 50 in the River Suldalslågen. The boxes were then buried so that the egg
92 compartments were situated at ≈ 0.1 and 0.3 m below ground level. Six VEMCO® (Lundesokna) and
93 five HOBO® (Suldalslågen) temperature loggers were attached to the top and bottom compartments of
94 representative boxes in each river. Water pressure transducers were installed in piezometers in the bed
95 to measure water levels in each pair of cylindrical boxes (Fig. 1). In addition, air pressure and
96 temperature loggers were installed at both field locations.

97 The total number of eggs used in the study was 518 and 641 in the rivers Suldalslågen and
98 Lundesokna, respectively, with 178 and 179 of these being in the reference wetted areas, respectively.
99 Based on field observations, egg hatching started 11 March 2012 in Lundesokna. In the Suldalslågen,

100 hatching started on 18 April 2012 according to field observations and estimates based on temperatures
101 in 2008, 2009 and 2011 (Crisp 1981; Saltveit & Brabrand 2013). Boxes were inspected on day 22 in
102 the Lundesokna and on day 36 in the Suldalslågen after the onset of hatching, which was in agreement
103 with the timing and duration of natural egg development and hatching in the study areas. After
104 removing the cylindrical boxes from the substratum, the total number of hatched vs. non-hatched eggs
105 and live vs. dead alevins were visually identified and counted for each of the egg compartments.

106

107 **Results**

108 During the study period, the discharge in the River Lundesokna was severely reduced in twelve
109 occasions due to breaks in hydropeaking production (Fig. 2a) – these were irregular and resulted in
110 different combinations of reduced water level and duration: at the start of the observation period, the
111 breaks were more frequent, and were lower and longer; towards the end, they were less frequent,
112 shorter and more intensive. Starting in late March 2012, the spring flood coincided with higher air
113 temperatures and almost no production stops (Fig. 2a). In the River Suldalslågen, a stable winter low
114 discharge of $\approx 12 \text{ m}^3\text{s}^{-1}$ was maintained. Two temporary peaks in discharge were released for smolt
115 migration on 1 and 15 May. After the latter peak, high discharges were continuously released until the
116 end of the study period (Fig. 2b). Statistically significant differences in water temperatures were found
117 between both rivers (Fig. 3) in surface ($P < 0.001$, 4.2 and 1 °C, respectively) and in sub-surface
118 waters ($P < 0.001$, 0.8 and 3.9 °C and 2 and 3.9 °C, respectively). In the River Lundesokna, water
119 temperatures were lower (mean = 1 °C) and less variable in comparison to sub-surface water
120 temperatures (mean = 2°C in the bottom compartments). Between the compartments located in the
121 substratum, the top ones showed higher variability and were colder than the bottom ones (Fig. 3).
122 Water temperatures in the River Suldalslågen were the highest (mean = 4.9 °C), compared to
123 temperatures found in the top and bottom egg compartments located in the substratum (means = 4.2
124 and 3.9 °C, respectively).

125 Differences in hatching rates between the drawdown zones of the Suldalslågen and the Lundesokna
126 (54 and 38%, respectively, Fig. 4a) were non-significant ($P = 0.7$). In the Lundesokna, differences in
127 hatching success (Fig. 4a) between the permanently-wetted area and the drawdown zone were also
128 non-significant ($P > 0.05$, Table 1) and showed similar variability and mean values (40 and 38%,
129 respectively). In the Suldalslågen, significant differences in hatching rates were found between the
130 permanently-wetted area (97%) and the drawdown zone (54%) with greater variability in the latter
131 (Fig. 4a, Table 1). In both rivers, the top and bottom compartments located in the drawdown zone
132 showed differences in hatching success (20 and 49% in the Lundesokna and 63 and 44% in the
133 Suldalslågen, Fig. 4b). However, these differences were only significant (Table 1) in the River
134 Lundesokna, where hatching success in the bottom compartments was higher (49%, Fig. 4b). No
135 significant differences in hatching success were found between top and bottom compartments in the
136 River Suldalslågen (Table 1).

137 Alevin survival (Fig. 5) was high in the permanently-wetted areas, however there were no
138 significant ($P = 0.2$) differences between both rivers. Alevin survival rates in the drawdown zone were
139 significantly higher in the Lundesokna ($P = 0.03$) than in the Suldalslågen. In the Lundesokna, the
140 survival of alevins was not significantly different in the drawdown zone compared to the permanently-
141 wetted area. In the Suldalslågen, rates were significantly ($P = 0.009$) lower in the drawdown zone than
142 in the permanently-wetted area (Table 2, Fig. 5a). The top compartments showed significantly higher
143 alevin survival than the bottom ones in the River Lundesokna ($P = 0.004$, Table 2), but no significant
144 differences in the vertical distribution of alevin survival were found in the Suldalslågen ($P = 0.4$, Table
145 2, Fig. 5b).

146

147 **Discussion**

148 The regulated rivers Lundesokna and Suldalslågen illustrate distinct regimes in terms of hydropower
149 operations and discharge regimes that affect surface-groundwater interactions. This has clear

150 consequences for egg survival (Casas-Mulet *et al.* 2015a, 2015b), hatching success and alevin survival
151 in Atlantic salmon. Hatching success in the Suldalslågen was higher than in the Lundesokna, despite
152 the shorter duration between the start of hatching and the end of the study period. These differences
153 may be explained by the overall higher substratum water temperatures in the Suldalslågen compared
154 with the Lundesokna. Assuming a wet or moist environment around the egg boxes, different
155 temperature regimes could explain the differences in hatching success between the top and bottom
156 compartments in both rivers. Indeed, the significant differences in hatching success between the
157 bottom and the top compartments in the Lundesokna could be explained by differences in sub-surface
158 water temperature – with lower mean and more variable temperatures in the top compartments
159 compared to the bottom. This is presumably due to the fluctuations in river water levels, resulting in
160 periods of air exposure. In the Suldalslågen, higher hatching success in the top compared to the bottom
161 compartment could be related to small difference in temperatures, with a greater influence on egg
162 incubation after 1 May due to inundation of the cylinders.

163 Inter-gravel stage mortality in both rivers was found to be higher for the alevin stage than for the
164 eggs, with time of exposure to dry conditions being a key factor for alevin survival. This agrees with
165 the findings in the literature, which state that newly-hatched alevins are less tolerant to de-watering
166 than are eggs (Becker *et al.* 1982, 1983; Reiser & White 1983; Becker & Neitzel 1985; Neitzel &
167 Becker 1985). For a reach with hydropeaking in the Columbia River, U.S.A., high mortality of the
168 inter-gravel life stages of fall Chinook salmon (*Oncorhynchus tshawytscha*) was attributed to de-
169 watering of redds, resulting in a pronounced effect on the productivity of the salmon population
170 (Harnish *et al.* 2014). In particular, de-watering events that occurred after hatching but prior to swim-
171 up resulted in low egg-to-presmolt survival, whereas de-watering events that occurred prior to egg
172 hatching had little effect on pre-smolt survival (Harnish *et al.* 2014).

173 Differences in alevin survival rates between the drawdown areas of both rivers clearly reflected
174 differences in hydropower operation strategies. Alevin mortality was significantly lower in the
175 drawdown zone of the Lundesokna than in the Suldalslågen. In the Lundesokna, shorter and more

176 infrequent de-watering episodes due to lower hydropeaking activity resulted in a high survival as a
177 consequence of almost permanent high discharges inundating the egg boxes during the hatching
178 period. The high variability in survival rates in the drawdown zone of the Suldalslågen may be linked
179 to the vertical and horizontal placement of the eggs, which could induce variable surface and sub-
180 surface water levels. However, it can also be hypothesised that very high alevin mortality was found
181 amongst alevins hatching before 1 May due to desiccation of the substratum before the peak release,
182 which inundated the egg compartments. High mortality could also have occurred amongst alevins
183 hatching between 1 and 15 May. The drop in water level between the two peaks in discharge could
184 have desiccated the boxes. Only late-hatching salmon, i.e. after 15 May, could have survived given the
185 stable, higher discharge that inundated the boxes.

186 Results shown in the present paper highlight the importance of developing customised stream
187 discharge releases in regulated salmonid rivers. In addition to the moist environment required by the
188 eggs (Casas-Mulet *et al.* 2015a, 2015b), alevins need to be continuously inundated in order to survive.
189 Given a lack of groundwater availability, the recommended mitigation measure for hydroelectric dam
190 operation should focus on lowering discharge rates during spawning (Harnish *et al.* 2014, Skoglund *et*
191 *al.* 2012). In contrast, the presence of sub-surface influx in regulated rivers may alleviate the effects of
192 hydropower production and allow more flexible operations during the embryo stages. However, a
193 strong focus on maintaining higher and constant discharge rates may be required in the alevin stages to
194 ensure their survival.

195 Rigid regulation regimes designed to fulfil pre-established environmental regulations may not
196 always result in the best conditions for the survival of early salmonid life stages, as demonstrated in
197 the case of the seasonally-regulated River Suldalslågen. In the River Lundesokna, the 2012 flow
198 conditions were particularly favourable for alevin survival given the continuous hydropower
199 production in spring. However, this production regime may be the exception in other years with
200 greater power demands and/or little water availability. Moreover, rapid winter water level fluctuations
201 due to hydropeaking may increase stranding mortality in older recruits (Saltveit *et al.* 2001).

202 In order to maintain a sustainable salmon population in regulated rivers, all life history stages must
203 be taken into account when designing and implementing discharge regulation regimes. This requires
204 evidence that integrates information on salmon biology and on environmental processes. Customised
205 discharge regimes that resemble natural hydrological conditions have the potential to increase egg and
206 alevin survival in salmon rivers. Such discharge regimes should be flexible and may also prove to be
207 more cost-effective than non-flexible permanent minimum discharge releases designed to comply with
208 rigid legislative requirements (Casas-Mulet *et al.* 2014).

209 The outcomes of the present study are particularly relevant to current environmental hydropower
210 operations in Norway, as the design of stream discharge regulation does not take into account the
211 alevin stage. In addition, hydropower facilities do not always possess the infrastructure for flexible
212 electricity production that permits compliance with environmental needs. It is therefore relevant to
213 consider three main factors when assessing the potential for flexible operations for stream discharge
214 regime implementation. They include all early life-history stages, the type of hydropower regulation in
215 place, and the extent to which groundwater influx could potentially alleviate the hydro-production
216 effects. This knowledge needs to be integrated and used actively in the future management of
217 regulated rivers.

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286 **Figures**

287 Fig. 1. Illustration of the site topography and specific position of the egg boxes in relation to
288 groundwater and surface-water levels during low and high discharge periods in the Norwegian rivers
289 (a.) Lundesokna and (b.) Suldalslågen.

290

291 Fig. 2. Water level fluctuations and air temperature changes during the study periods in two
292 Norwegian rivers: (a.) the Lundesokna, which is subject to hydropeaking; and (b.) the Suldalslågen,
293 which is seasonally-regulated.

294

295 Fig. 3. Surface river and sub-surface water temperatures distribution in the rivers Lundesokna and
296 Suldalslågen (Norway) during the study period. Sub-surface water temperatures were measured at the
297 top and bottom compartments of a representative box in each of the study sites (Box 1 in the River
298 Lundesokna (see Casas-Mulet *et al.* 2015a) and Box 2D in the River Suldalslågen (see Casas-Mulet *et*
299 *al.* 2015b)). Note: temperature values at the bottom of the graph are sample means.

300

301 Fig. 4. Distribution of hatching success rates (including alive and dead alevins) for: (a.) all boxes in
302 the permanently-wetted or reference areas and in the drawdown zone (DZ); (b.) top and bottom
303 compartments of the DZ of the rivers Lundesokna and Suldalslågen (Norway). Note: percentages
304 shown at the top of the graphs are sample means.

305

306 Fig. 5. Distribution of alevin survival rates for: (a.) all boxes in the permanently wetted areas and in
307 the drawdown zone (DZ); (b.) top and bottom compartments of the DZ of the rivers Lundesokna and
308 Suldalslågen (Norway). Note: percentages shown at the top of the graphs are sample means.

309

310 **Tables**

311 Table 1. Number of hatched eggs sample size (n), mean, maximum and minimum and *P* values
312 between same-river samples for: (a.) all boxes in the permanently-wetted or reference areas *vs.* the
313 drawdown zone (DZ); (b.) top *vs.* bottom compartments of the DZ of the rivers Lundesokna and
314 Suldalslågen (Norway).

315

316 Table 2. Number of surviving alevins sample size (n), mean, maximum and minimum and *P* values
317 between same-river samples for: (a.) all boxes in the permanently wetted or reference areas vs. the
318 drawdown zone (DZ); (b.) top vs. bottom compartments of the DZ of the rivers Lundesokna and
319 Suldalslågen (Norway).