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RESEARCH ARTICLE

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Assessing the occurrence of egg stranding for trout and salmon in a regulated river

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Abstract

A key challenge in many regulated rivers is to define adequate flow levels to protect aquatic organisms. Provisioning of suitable flow can be pivotal bottlenecks for fishes such as salmon and trout that use the riverbed as an incubation habitat. Additionally, the locations where females spawn will define the probability that embryos will be dewatered during the incubation period in a regulated flow regime. We investigated the water flow, dewatering, and incubation mortality in Atlantic salmon and brown trout in natural nests over 19 years in the regulated Bjoreio River in western Norway. During the study period, different flow strategies were applied to mitigate the dewatering of incubating salmon and trout embryos. Average survival in nests sampled in late winter ranged from 54% to 92% among years and was significantly correlated with the minimum water flow occurring during the incubation period. Mortality was significantly higher in nests in shallow areas, reflecting nests exposed to dewatering. The results demonstrate a strong link between incubation mortality and managed flow regimes for river spawning salmonids. Using detailed information on the nest location and incubation mortality, we estimate minimum flow requirements for this river and demonstrate an approach to effectively mitigate the impact of river regulations on embryo survival in Atlantic salmon and brown trout.

KEYWORDS
dewatering, environmental flows, *Salmo salar*, *Salmo trutta*, spawning

1 | INTRODUCTION

Alterations of river flows due to hydropower remain a pressing topic for freshwater conservation worldwide (Acreman & Dunbar, 2004; Bunn & Arthington, 2002). For fluvial substrate spawning fishes, flow during spawning and incubation is a concern because the nests may be dewatering (Becker & Neitzel, 1985; Harnish, Sharma, McMichael, Langshaw, & Pearsons, 2014; Malcolm, Gibbins, Soulsby, Tetzlaff, & Moir, 2012). Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) typically spawn in the fall by burying their eggs in a series of nests (called a redd) excavated by the females, often on shallow gravel bars containing the suitable combination of substrate, water depth, and surface water velocity (Armstrong, Kemp, Kennedy, Ladle, & Milner, 2003; Fleming, 1996). The embryos incubate in the nests during winter until the alevins emerge as free-swimming juveniles/fry during spring or early summer. Natural mortality is typically low during the gravel incubation stages (Elliott, 1984; Malcolm, Youngson, & Soulsby, 2003), but the embryos have limited mobility and thus few possibilities to evade unfavorable conditions such as dewatering events.

Embryos of salmonid fishes depend on flowing water for their survival, such that fluctuations in the water level can threaten their survival and potentially the viability of the population. Salmonids prefer spawning in shallow areas (Crisp & Carling, 1989; Heggberget, Haukebø, Mork, & Ståhl, 1988) and often during periods of relatively high flow (Gibbins, Moir, Webb, & Soulsby, 2002; Vollset, Skoglund, Wiers, & Barlaup, 2016; Webb, Gibbins, Moir, & Soulsby, 2001). Dewatering is documented to be lethal for embryos (Becker & Neitzel, 1985, McMichael et al. 2005, Casas-Mulet, Saltveit, & Alfredsen, 2015), but embryos are sometimes found to survive for extended periods of dewatering ranging for several weeks (Becker, Neitzel, & Abernethy, 1983; Casas-Mulet, Saltveit, & Alfredsen, 2015; Reiser & White, 1983). The moisture content and temperature conditions in the nest environment appear to be crucial for embryo survival, and mortality may occur even during brief exposure to desiccation or freezing (Becker & Neitzel, 1985). The interstitial conditions during dewatering are likely impacted and affected by several factors, including moisture retention in the gravel, temperature, oxygen supply, gravel composition and groundwater influx (Becker & Neitzel, 1985; Casas-Mulet, Saltveit, & Alfredsen, 2015). While several studies have tested embryo survival in response to dewatering under experimental conditions or on single field sites, and in particular in response to short-term water fluctuations (i.e., hydropeaking, McMichael, Rakowski, James, & Lukas, 2005, Casas-Mulet, Alfredsen, Brabrand, & Saltveit, 2015, Casas-Mulet, Saltveit, & Alfredsen, 2015), little data exists testing the effects of dewatering in situ on larger spatial (i.e., river) or temporal (among years) scales in rivers prone to seasonal dewatering.

We investigated flow, nest stranding, and embryo survival for Atlantic salmon (*Salmo salar*) and anadromous brown trout (*Salmo trutta*) over a period of 19 years in the regulated Bjoreio River in western Norway. The aims were to examine the effect of a regulated discharge regime on natural redd site selection followed by incubation success. We tested various discharge regimes with a goal to generate a managed, environmental flow regime that best protects the incubation success of these two species.

2 | MATERIALS AND METHODS

2.1 | Study area

The study was performed in the Bjoreio River, which is one of two main tributaries of the Eidfjordvassdraget River system draining into the inner parts of Hardangerfjord in western Norway

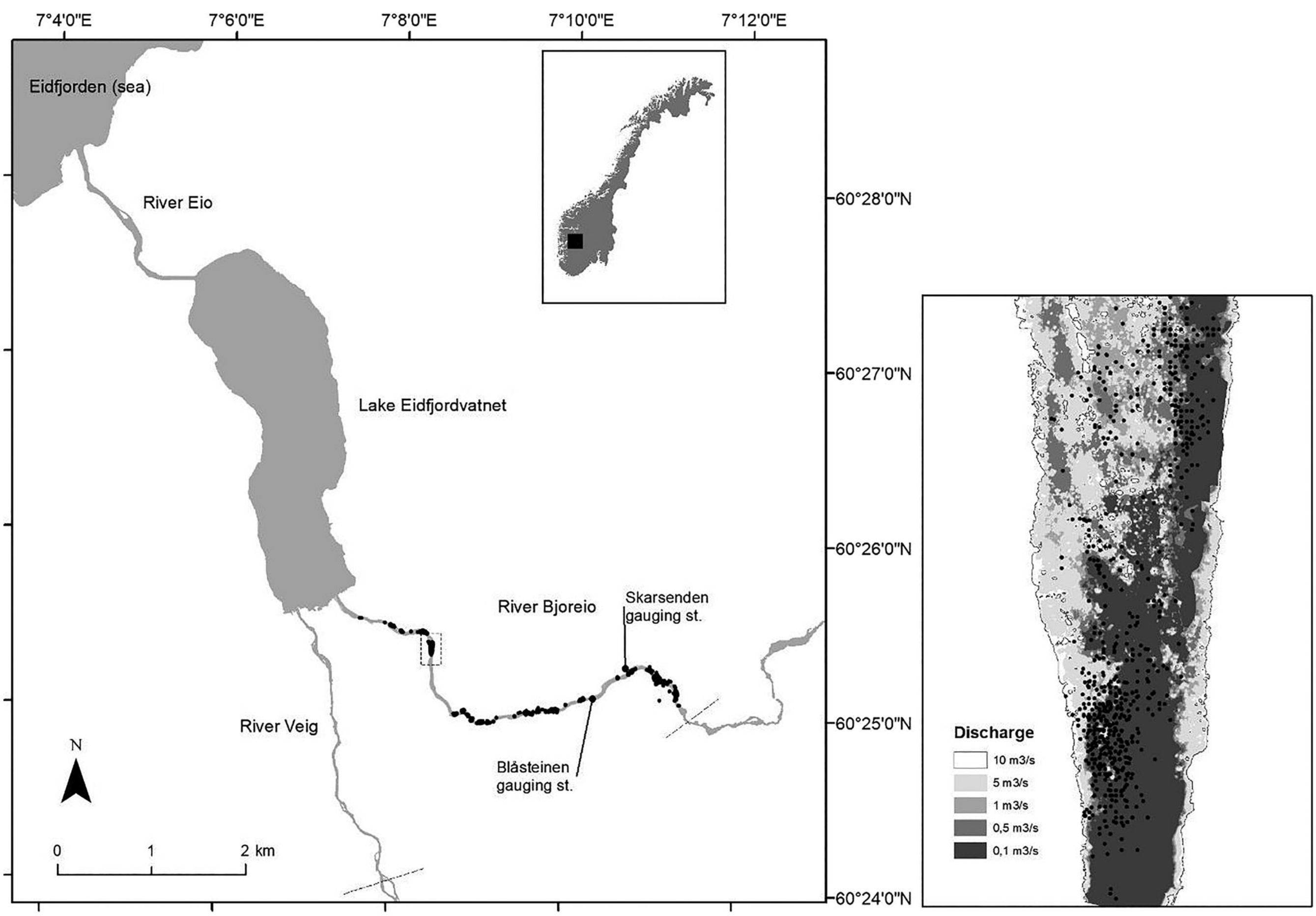

FIGURE 1 Map of the Bjoreio River and the Eidfjord River system. The dots indicate the locations of recorded nests in river Bjoreio over multiple years, and the dotted lines indicate the migration barriers for anadromous fish. The right frame displays the location of nests on one location (square) in relation to wetted area at different discharges

(Figure 1). The Bjoreio River sustains populations of anadromous brown trout (also called sea trout) and Atlantic salmon, and the passable river length for anadromous fish (from Lake Eidfjordvatnet) is 5 km. The river has a relatively steep gradient (2.7%), and large sections of the river is dominated by rapids and a riverbed consisting of boulders and cobbles.

2.2 | Flow regime

The flow of Bjoreio River is regulated for hydropower purposes with 74% of the original drainage area transferred to the Sy-Sima power station, a high-head power station with outflow directly to the sea. The regulation results in flow reductions downstream on the river reach used by salmon and sea trout. A minimum flow requirement of 12 $m^3{\cdot}s^{-1}$ was initially regulated during the period of 1 June–15 September. This flow was set mainly for the aesthetics during the summer season of the Vøringsfossen waterfall. The absence of flow requirements in the period between 15 September and 1 June frequently resulted in extremely low discharge levels (<0.1 $m^3{\cdot}s^{-1}$) during dry fall and winter periods which raised concern about dewatering of salmon and trout nests. To mitigate the effect of low water levels in various periods, water has been released from the main upstream reservoir Sysendammen (874–940 m above sea level). From 2003, the power company released up to 0.3 $m^3{\cdot}s^{-1}$ during dry winter periods. From 2007 and onwards, winter flow releases from the reservoir were managed by reducing flow requirements during summer, and then release the equivalent water volume through periods of the winter. Through the years, a series of different flow regimes with varying volumes and periods of flow releases have been implemented (Table 1). The current study was undertaken to document effects of the winter release and to provide a scientific basis for flow requirements that avoid dewatering of nests.

2.3 | Sampling of nests

Nests of brown trout and Atlantic salmon were sampled during late winter (March–April) from 2004 to 2022. Sampling was performed by systematically surveying by snorkeling and/or wading the majority of the riverbed that contained suitable spawning substrate (Figure 1). The riverbed is dominated by coarse substrate (boulders and cobbles), and potential spawning areas for salmonid fish in the river are typically located on smaller deposits of gravel and small stones near river margins and at the tail of the pools. To locate nests, patches of gravel with suitable spawning substrate were carefully excavated with a small, pointed spade. When eggs were located in the gravel, the water depth (cm) above the nest was recorded as the distance from the water surface to the riverbed with a meter stick. This distance is hereafter called nest depth. If the nest was located on dewatered riverbed, the distance above water surface level in the river the time of sampling was measured and recorded as negative depth values. In dewatered nests, the groundwater table could in many cases be observed and usually corresponded to the surface water level in the river.

Incubation survival was estimated by counting living and dead eggs exposed in the nest, or by lifting the gravel and catching eggs floating downstream in a dipnet. Dead eggs were typically white or opaque, but otherwise intact and therefore easy to distinguish from live eggs. To minimize disturbance to the nests, excavation was ceased as soon as approximately 10–20 live eggs had been found; the remaining eggs were left undisturbed. While this may be considered a small sample, it is expected to give a representative estimate as survival typically has a bimodal distribution (either high or low; see Results). From each nest, one egg was frozen for species identification in the laboratory. After sampling, the original redd structure was restored by carefully closing the nest and covering the eggs with gravel. Sampling was almost always performed just prior to hatching and at low flow, and just before the typical snowmelt-related seasonal discharge increase (Figure 2). During surveying, effort was taken to sample nests as representatively as possible with respect to distribution of spawning areas in the stream (shallow to deep). Eggs taken from each of the nests were analyzed using isoelectric focusing (Mork & Heggberget, 1984; Vuorinen & Piironen, 1984). Species identification was in most cases not possible for dead eggs, therefore no taxonomic assignment could be made for nests that had only dead eggs.

TABLE 1 Overview of flow requirements in the Bjoreio River throughout the study period

	Flow requirements				
Year	Summer 1 June–15 sept:	Autumn 15 Sept–15 Nov	Winter 15 Nov–14 Apr	Spring 14 Apr–1 June	Comments
2004–2006	12.0 $m^3{\cdot}s^{-1}$	-	(0.3 $m^3{\cdot}s^{-1}$)	-	Voluntary release of 0.3 $m^3{\cdot}s^{-1}$ from reservoir during dry periods during winter
2007–2011	11.5 $m^3{\cdot}s^{-1}$	-	0.5 $m^3{\cdot}s^{-1}$	-	Winter release only during 15 Dec–31 Mar
2011–2013	11.5 $m^3{\cdot}s^{-1}$	-	0.4 $m^3{\cdot}s^{-1}$	-	Winter release only during 1 Dec–13 Apr
2014–2018	11.0 $m^3{\cdot}s^{-1}$	-	0.7 $m^3{\cdot}s^{-1}$	-	
2018–2021	11.0 $m^3{\cdot}s^{-1}$	1.5 $m^3{\cdot}s^{-1}$	0.7 $m^3{\cdot}s^{-1}$	1.5 $m^3{\cdot}s^{-1}$	

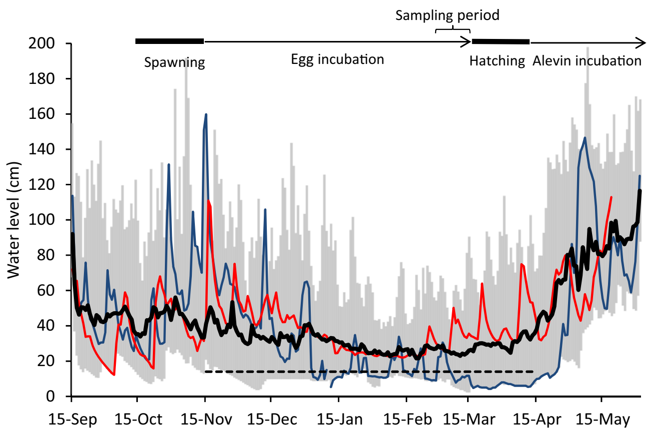

FIGURE 2 Water level in the Bjoreio River during winter period in the years 2004–2022. A water level of 0 corresponds to a discharge of 0 $m^3 \cdot s^{-1}$, and also corresponds to a standard nest level of 0. The black line indicates the median daily average water level through the period whereas the grey area indicates the range. Daily average discharge levels for two years with contrasting flow patterns during spawning and incubation is indicated in blue (2005–2006) and red (2013–2014) lines. The periods of peak spawning, incubation, hatching and sampling period is indicated at the top, while the dashed line indicated the water level that corresponds to a discharge of 0.7 m3/s that constitutes the present winter release flow [Color figure can be viewed at wileyonlinelibrary.com]

2.4 | Relationship between water level and dewatering of nests

Since the water level, and hence nest depths, is directly related to discharge, we used the water level/stage measured at a gauging station at the time of sampling as a benchmark for assessing exposure to dewatering, comparing nest depth levels between years and for comparing nest depths in relation to flow. During the study period, the water stage was recorded on an hourly basis at either of two gauging stations that were operated during different periods (Skarsenden station, 2004–2011; Blåsteinen station, 2011–2022, data provided from Statkraft Energy AS) located in the upper part of the study reach (Figure 1). To assess the extent of nests being exposed to dewatering, the nest depth that would occur during the lowest flow during the incubation period was estimated for each nest using the recorded nest depth and the difference in water stage between sampling and the lowest daily average water stage recorded at the gauging station during each season. A nest was considered dewatered if the estimated nest depth during the lowest flow <0 cm. Furthermore, to compare the distribution in nest depths between years, nest depth was standardized based on the water stage measured at the gauging stations during sampling. To set a common scale, the standard nest depth level was set to zero at the water stage level where discharge was estimated to approach zero in the established water level-discharge function at the Skarsenden gauging station (data from Statkraft Energy AS). This approach rest on the assumption that the water stage on the gauging site will change proportionately with water level on the different spawning sites. While this may cause some uncertainties with regards to estimating exposure to dewatering, we regard this to be a reasonable approximation given the relatively narrow flow/water level range of interest in this case.

Further, to quantify the relationship between dewatering and discharge was calculated using standard nest depth level distributions together with the water level discharge function developed for the Skarsenden gauging station. One year (2018) was omitted from the relationship due to uncertainties in representability of nest depth distribution this year.

2.5 | Statistical analysis

The relationship of embryo mortality with nest location and incubation flow was modelled by fitting a binomial generalized linear mixed model using the lme4 library (Bates, Machler, Bolker, & Walker, 2015). Initially, a fit was attempted using the number of live and dead eggs in each of the nests as a response variable for mortality. However, because of overdispersion and problems with convergence, the model was refitted and defined nests with mortality above/below 50% as failure or success, then using this criterion as a binary response variable. This simplification is reasonable because mortality data suggest that, in most nests, mortality was either high or low (see Results). Our main hypothesis is that incubation success was negatively impacted by dewatering, and therefore predict that mortality would be highest in nests located in shallow areas and higher in years when incubation flows were low. Consequently, our full model included the standardized nest depth and minimum daily average water level prior to sampling as fixed effects, and year as a random intercept. In addition, the relationship between the minimum daily average discharge and average egg survival between years was fitted using a simple linear regression model.

To explore the effects of flow during the spawning period on the nest depth distribution, a linear mixed model was first fitted with standard nest depth as the response variable, the median water level in the period during 18 October–7 November (assumed to be the peak spawning period) as the explanatory variable, and year as a random intercept. This model would reveal if variation in flow during spawning across years affects the average depth location of nests. To test specifically whether spawning flow affected the proportion of nests in shallow areas, a linear regression model was fitted with the proportion of nests in the potential dewatering zone (i.e., nest with std. nest depth levels <0) as a response variable, and the median water level in the spawning period as an explanatory variable. All statistical modeling were performed using R (R Core Team, 2021).

3 | RESULTS

From 2004 to 2022, a total of 2,360 nests were sampled (Table 2). Species identification of eggs was possible in 1832 of the nests: 1406 (76.7%) were spawned by trout, 402 (21.9%) by Atlantic salmon, while 24 (1.3%) classified as salmon/trout hybrids.

Year	N	% mean survival (SD)	% nests with total mortality	% nests dewatered
2004	130	66.8 (37.4)	20.0	16.2
2005	84	68.9 (38.6)	19.0	14.3
2006	68	54.2 (46.0)	38.2	36.8
2007	55	66.7 (41.3)	21.8	12.7
2008	156	77.3 (32.8)	9.0	9.6
2009	149	80.4 (32.4)	11.4	17.4
2010	174	87.8 (24.3)	5.2	7.5
2011	148	76.5 (35.4)	14.9	20.3
2012	105	76.7 (36.9)	15.2	17.1
2013	124	59.4 (42.5)	29.0	29.0
2014	144	81.1 (31.8)	9.0	9.0
2015	176	85.4 (27.7)	6.8	9.1
2016	111	83.7 (26.4)	6.3	11.7
2017	71	91.5 (18.5)	2.8	21.1
2018	139	81.5 (29.2)	9.4	18.7
2019	130	90.2 (24.3)	4.6	10.8
2020	148	89.0 (21.3)	2.0	11.5
2021	111	81.2 (32.9)	9.0	9.0
2022	137	85.9 (22.6)	3.6	8.8

TABLE 2 Number of nests of Atlantic salmon and brown trout investigated (N), mean egg survival and standard deviation, percent of nests with total mortality and estimated percentage of nests dewatered at the lowest water level.

Note: The percentage of nests dewatered was estimated from the nest depth and the difference in water level between the sampling date and the lowest occurring water level (daily mean) throughout the incubation period.

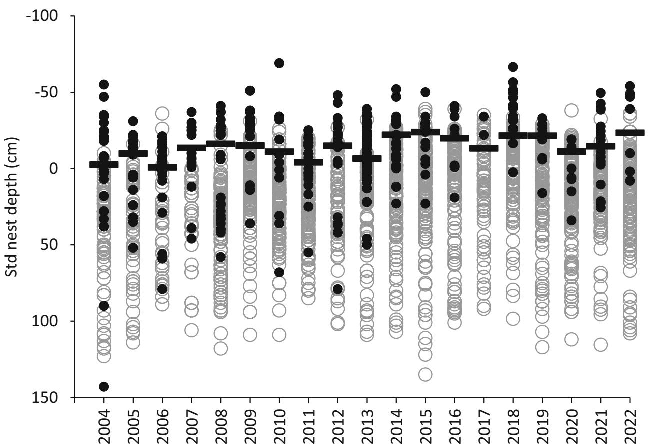

FIGURE 3 Standardized nest depth level for nests in the Bjoreio River during 2004–2022. The filled black markers represent nests with high mortality (>50%), whereas open grey markers represent nests with low mortality (<50%). The nests levels are standardized so that a nest level of 0 represents the water levels at a discharge equaling 0. The horizontal markers indicate the lowest daily average water level recorded during the incubation period in each of the years, and nests located above these markers have thus been exposed to dewatering

Nests were located at depth levels ranging more than 2 m, with 50% of the nests being concentrated within a depth range of 40 cm (Figure 3). Based on depth at the time of sampling and recorded water level during the incubation period, 13.8% of the nests were estimated to be exposed to dewatering during the 19 years (Figure 3; Table 2). However, the lowest water level during incubation, as well as the number of nests potentially dewatered, varied among the years.

Overall, mean embryo survival in the nests was 79%. The pattern of mortality was bimodal, and typically either low (<20% mortality in 70% of the nests) or high (> 95% mortality in 11% of the nests). Highest mortality occurred in 2006, when total mortality was recorded in over 38% of the nests (Table 2).

Mortality was significantly higher in shallow nests exposed to dewatering, and higher in years when incubation flows were low (Figure 4, GLMM: nest depth: $z = 16.6$, $p < 0.001$; minimum water levels: $z = -4.7$, $p < 0.001$; random effects: var $= 0.58$). The average survival in nests exposed to dewatering was 36%, whereas survival in continuously submerged nests was on average 87%.

The relationship between mortality and minimum water level also yielded a significant relationship between the lowest flow level during incubation and average egg survival among years (linear regression model: $F = 26.0$, df $= 18$, $p < 0.001$; Figure 5). The level of minimum flow occurring during the winter varies among years because of natural variations in weather conditions and runoff and because of different strategies for mitigation (i.e., for flow release from the reservoir) in all these years. From autumn 2013 and until spring 2022, the flow release strategy involved an increased flow release of 0.7 $m^3 \cdot s^{-1}$ from the upstream reservoir. This is higher than in the previous years in the

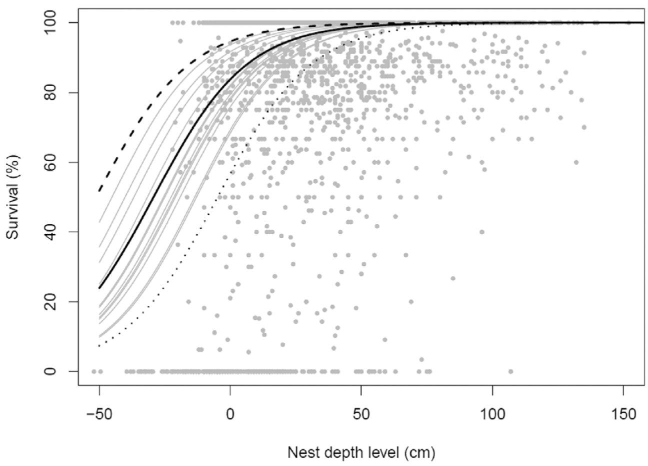

FIGURE 4 Survival in nests along the nest depth gradient. The grey dots indicate observations from individual nests ($N = 2{,}360$). Overlaid is the estimated relationship between likelihood of survival and nest depth (GLMM). The results are plotted for an average (solid line), low (dashed line) and high (dotted line) minimum winter flow level. The thin grey lines indicate random effects for the different years

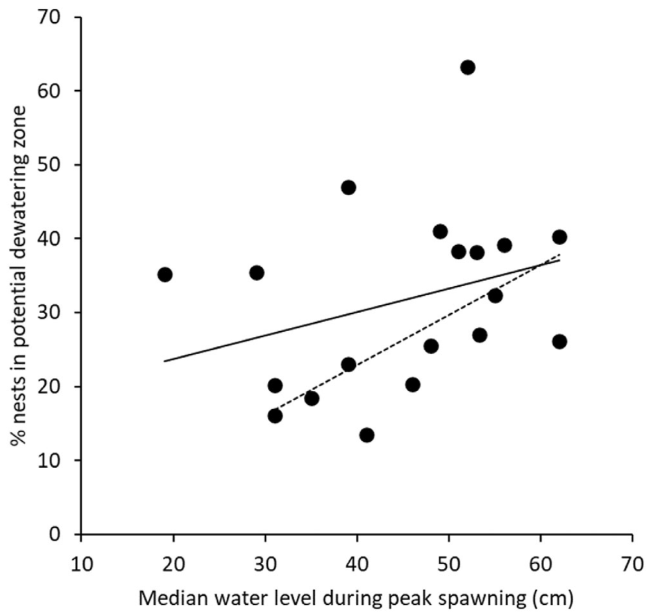

FIGURE 6 The relationship between median water level during the 3-week period of peak spawning and the proportion of nests located in the potential dewatering zone. The dashed line indicates the significant relationship when the four outlier years are excluded

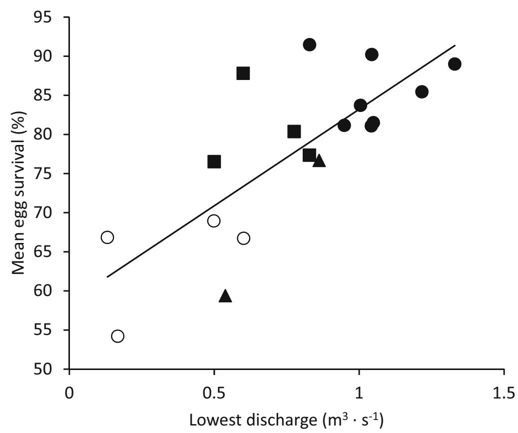

FIGURE 5 Relationship between mean egg survival and the lowest weekly average discharge recorded during the incubation period (from 1 November until sampling) in the different years of the study period. The symbols indicate the years with different mitigation flow releases during the winter; (◦) 2004–2007:0.3 $m^3{\cdot}s^{-1}$, (■) 2008–2011:0.5 $m^3{\cdot}s^{-1}$, (▲) 2012–2013:0.4 $m^3{\cdot}s^{-1}$, (●) 2014–2022:0.7 $m^3{\cdot}s^{-1}$

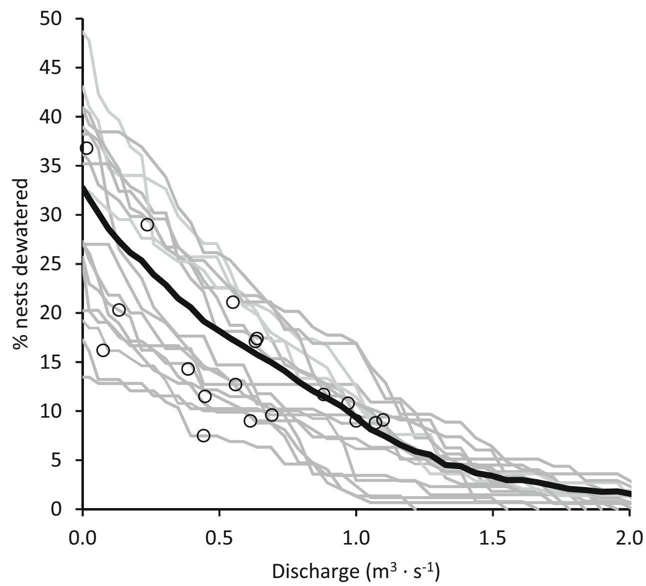

FIGURE 7 The relationship between discharge and nest dewatering in the Bjoreio River, based on nest depth level gradients and the water level-discharge function. The grey lines indicate each year during 2004–2022, whereas the black solid line indicates the average for the period. The open circles indicate the lowest discharge level recorded during the incubation periods in each of the years

study period when the flow release has been from 0.3 to 0.5 $m^3{\cdot}s^{-1}$ for various periods (Table 1). The increased flow release corresponds with higher egg survival through the winter seasons 2014–2022 (Figure 5).

Analyses of linear mixed models did not reveal any effect of spawning discharge on the std. nest depth ($\chi^2 = 0.70$, df $= 1.00$, $p = 0.40$), therefore the variation in spawning discharge did not affect the depth level of nests between years. Likewise, no significant effect of spawning water level on the proportion of nests in the shallow areas was observed ($R^2 = 0.31$, $F = 1.78$, df $= 18$. $p = 0.20$; Figure 6). Four years (2013, 2016, 2017 and 2018) had a strong influence on the outcome of the model. If these were omitted, a significant relationship between water level during spawning and proportion of nests in shallow areas is observed ($R^2 = 0.72$, $F = 13.9$, df $= 14$, $p = 0.003$; Figure 6).

The estimated relationship between nest dewatering and discharge is shown in Figure 7. On average, 32% of the nests were positioned at levels exposed to dewatering when the discharge approaches zero. However, a discharge of about 2 $m^3 \cdot s^{-1}$ would be sufficient to keep >98% of nests submerged in all years.

4 | DISCUSSION

By monitoring embryo mortality in relation to depth position of nests over a period of 19 years, we demonstrate a strong relationship between incubation mortality and water flow regime for brown trout and Atlantic salmon in the regulated river Bjoreio. In all years, higher embryo mortality occurred in nests that had been spawned in the shallow zone of the riverbed and thereafter episodically exposed to dewatering during periods of low flow during winter. In concordance, mortality was significantly correlated to the depth locations of nests; nests located in shallow areas and exposed to dewatering had over fourteen times higher probability of experiencing total mortality than did nests located at levels that were continuously submerged throughout the incubation period. Mortality associated with dewatering of nests also varied significantly with water flow between years. Mortality was higher in years when minimum water levels/flow were low, that is, when a higher proportion of nests was exposed to dewatering. The highest mortality in Bjoreio River occurred after a dry period of low runoff in late winter 2006, when 38% of the nests incurred total mortality. Furthermore, the extent of dewatering, as well as egg mortality, was lower in years when the baseflow levels was increased through mitigation releases of water. Thus, incubation mortality can be effectively mitigated by sustaining sufficient flow during the incubation period.

High mortality in nests located in shallow areas appeared to be caused mainly by desiccation and/or freezing of eggs during periods of dewatering. Although our sampling design did not allow for testing exposure time to dewatering or for freezing in individual nests explicitly, the nest depth level at which increased mortality occurred corresponded closely with the lowest water level during incubation, thereby suggesting that even brief exposure to dewatering may result in extensive mortality. However, the specific critical level at which mortality occurred was not an absolute, some nests were found to maintain high survival despite being located at high levels in the dewatering zone (i.e., 10–30 cm above the lowest water level and also above the groundwater table) and consequently being exposed to long periods (i.e., several weeks) of dewatering. Several other studies, under laboratory studies and in the field (Becker et al., 1983; Casas-Mulet, Saltveit, & Alfredsen, 2015; Reiser & White, 1983), have likewise found that eggs can withstand extended periods of dewatering. The tolerance of eggs and alevins for dewatering is likely related to whether the moisture content, temperature conditions, and other interstitial conditions are sufficient for survival, and it is also likely to vary from site to site according to the duration of the dewatering period (Becker & Neitzel, 1985). In Bjoreio River, the lowest water levels typically coincided with low runoff during cold and dry periods, which likely caused an exposure to frost in the dewatering zone as well as in shallow areas. Moisture content and temperature conditions may be more favorable for survival in areas subject to influx of groundwater (Casas-Mulet, Alfredsen, et al., 2015; Garrett, Bennett, Frost, & Thurow, 1998; Saltveit & Brabrand, 2013). This may also be the case in Bjoreio as nests in some areas with apparently residual influx of groundwater also appeared to experience lower mortality, and in nests with deep burial depths, but we were not able to explicitly test these relationships in this study. The tolerance for dewatering also depends on the developmental stage because embryos are more tolerant than the post-hatched alevins (Becker et al., 1983; Becker, Neitzel, & Fickeisen, 1982). In the river Bjoreio, the embryos will usually hatch from the eggs after the onset of snowmelt season in the spring, and thus after the period when lowest water levels typically occur during late winter. However, this is likely to vary among species and populations depending on the timing of spawning, the temperature, and the discharge levels during incubation. Increased mortality may also occur in submerged nests exposed to bottom freezing (Reiser & Wesche, 1979) or to hypoxia induced by low intra-gravel water flux during low discharge (Becker & Neitzel, 1985). Consequently, egg survival is likely to depend on a wide range of interacting factors that are likely to vary among locations and among years. Thus, measurement of the effect of low flow periods during incubation in situ is critical. Even though some eggs can survive extensive periods of dewatering, the majority of nests suffered heavy mortality in the present study.

To what extent nests are likely to be subject to dewatering will depend on the level where nests are spawned. Many salmonid species prefer shallow areas for spawning (Crisp & Carling, 1989; Heggberget et al., 1988), and several studies also indicate that salmonids often prefer to spawn in periods of high flows (Gibbins et al., 2002; Vollset et al., 2016; Webb et al., 2001). It also appears that more nests are spawned in the potential dewatering zone during years with high discharge during the spawning period in the Bjoreio River, although the relationship between spawning discharge and depth distribution of nests was not significant. However, our analysis may be constrained by difficulties in modeling the appropriate response of spawning flow rates, as the flow may vary considerably on short time scales, and because the exact spawning period is unknown.

Spawning at shallow areas and high flow levels may at first appear to be maladaptive in terms of increasing the risk of embryo mortality caused by dewatering, but the risk of dewatering may be offset by the benefits of spawning at shallow locations. Firstly, because a larger amount of the riverbed is wetted and water levels increase with increasing flows, the availability of suitable spawning sites at shallow gravel bars and bank margins is also likely to increase with increasing flow (Webb et al., 2001). Thus, if access to favorable spawning habitat is limited in the deeper parts of the riverbed, utilization of shallower sites during periods of higher discharge may be favorable by avoiding crowding and superimposition of nests. Avoidance of crowded spawning sites by spreading of nests at larger parts of the riverbed is also likely to reduce local density-dependent mortality among juveniles during the critical period immediately after emergence from the nests (Einum & Nislow, 2005). Further, spawning at deeper locations near the middle of the channel may result in a higher probability of egg loss due to scouring (Lapointe, Eaton, Driscoll, & Latulippe, 2000). Lastly, offspring will be better positioned to colonize the shallow areas near the margins that constitute the most favorable rearing habitat for young juveniles after emergence (Armstrong et al., 2003; Armstrong & Nislow, 2006). Consequently, spawning at shallow areas may be beneficial for reproductive success if dewatering and freezing are avoided during the incubation period.

While nest dewatering also may occur due to natural flow variations (Barlaup, Lura, Sægrov, & Sundt, 1994), flow fluctuations imposed by river regulations often exceed by far the natural flow variations, thereby increasing mortality related to stranding of nests and of juveniles (Young, Cech, & Thompson, 2011). Dewatering of nests may be reduced by managing flow patterns, either by increasing minimum flows during the incubation period, as in the case of the Bjoreio River, or by decreasing flow during spawning. For example, flow restriction to avoid dewatering of nests and juveniles has been successfully implemented to increase fish productivity of pacific salmonids below the Priest Rapids Dam in Colombia River (Harnish et al., 2014), as well as in the upper Skagit River in Washington (Connor & Pflug, 2004). Flow management has also been implemented to limit reproduction of unwanted species, such as below Canyon Dam in Colorado River where the flow difference between spawning and incubation was increased to limit reproduction of nonnative rainbow trout and thereby enhance reproduction of native endangered fishes (Korman, Kaplinski, & Melis, 2011). However, the biological responses of implemented flow management projects are often difficult to validate because appropriately designed monitoring programs are lacking, or because monitoring objectives are insufficiently defined (Souchon et al., 2008). In the Bjoreio River, water was released from an upstream mountainous reservoir to increase water levels during the incubation period so that embryo mortality of Atlantic salmon and brown trout on the downstream anadromous reach was reduced. The initial management target was set by local stakeholders to secure incubation discharge such that less than 10% of the nests were exposed to dewatering. However, in several years the magnitude of the flow releases was found to be too low to reach the 10% target. By quantifying the vertical distribution of nests and then relating this to the relationship between water level and flow, we were able to estimate the flow requirement for specific management targets with respect to dewatering. For example, a minimum flow of 1 $m^3 \cdot s^{-1}$ was found sufficient to reach the target level of <10% dewatering of nests in most years in our study period, whereas a flow of 2 $m^3 \cdot s^{-1}$ would reduce dewatering to a minimum in all years. Accordingly, the amount and period of water releases have been adjusted through the study period, resulting in the last nine years having the lowest registered mortality values. Although more work is needed to develop a "best practice" flow management plan for the Bjoreio River, the present results provide a valuable baseline for managers and stakeholders to discuss costs and benefits for various flow regimes.

5 | CONCLUSION

Dewatering of nests during low flow periods in winter may cause substantial mortality in Atlantic salmon and brown trout, but incubation mortality may be effectively mitigated by incorporating adequate minimum flow levels that keep nests submerged during the incubation period. Critical minimum flow requirements may be quantified by locating the depth level of nests, as in this study. Whereas the relationship between nest dewatering and flow in this study was developed using a simple model incorporating water level and discharge, it is possible to include similar data with more complex hydraulic models for modelling the relationship with more detail on different sites and river reaches. This relationship provides an important baseline for evaluating the requirements for minimum flow levels during the incubation period of eggs and nests, and for determining management targets concerning nest dewatering.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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