

FACTORS INFLUENCING STRANDING OF WILD JUVENILE BROWN TROUT (*SALMO TRUTTA*) DURING RAPID AND FREQUENT FLOW DECREASES IN AN ARTIFICIAL STREAM

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ABSTRACT

To provide environmental guidelines for operation of peaking hydropower plants, stranding experiments with juvenile brown trout (*Salmo trutta*) were conducted in a 3.8 m wide and 19.2 m long artificial stream. We found a significant decrease in stranding of trout fry by reducing the dewatering speed from $>60 \text{ cm h}^{-1}$ to $<10 \text{ cm h}^{-1}$. At water temperatures around 11°C we found that less than 8% of the trout stranded during night experiments (on average for all subsets at dewatering rate $>60 \text{ cm h}^{-1}$). However, the highest stranding rate occurred at water temperatures around 7°C during rapid dewatering at night (mean = 22% stranding). Significantly more fry were stranded in the first versus the second to fifth dewatering episode (mean = 22% versus 10% stranding) at rapid daytime dewatering in 11°C water. Stranding of larger fry ($>0+$) was negligible at water temperatures around 11°C , except at rapid dewatering during daylight. Further, twice as many $0+$ trout as larger fry ($>70 \text{ mm}$ in June, $>60 \text{ mm}$ in late summer) stranded during rapid dewatering during daytime, and almost three times as many $0+$ stranded during rapid dewatering when they were mixed with trout parr compared to homogeneous $0+$ experiments. Our study showed a tendency towards an increased stranding of fry with long habituation time (<30 hours versus >30 hours with stable flow). We recommend dewatering in darkness at all times of year to reduce stranding of salmonids, and to use slow ramping rates $<10 \text{ cm h}^{-1}$. After longer periods with stable flows, a gentle drop in discharge is recommended, which might also reduce stress and possible sub-lethal effects. Copyright © 2003 John Wiley & Sons, Ltd.

KEY WORDS: artificial stream; brown trout; hydropeaking; flow decrease; stranding; de-watering

INTRODUCTION

The Norwegian electric energy supply system is based on hydropower. The deregulated energy market may lead to the increased use of hydropeaking, causing more frequent and rapid changes in flow downstream of power plants. Flow fluctuations are, however, a natural phenomenon in temperate rivers, and the dynamics itself plays an important role for aquatic organisms. For the maintenance of a natural river ecosystem, floods are important due to flushing and reshaping of the riverbed (Jensen and Johnsen, 1999), while natural droughts are bottlenecks for the aquatic biota, changing the faunal composition and the amount of different habitats (Stanford *et al.*, 1996; Poff *et al.*, 1997; Richter *et al.*, 1997). Even minor changes in discharge can dramatically affect the river habitat and biota during winter (Cunjak *et al.*, 1998). Under most natural conditions, flow decreases slowly and most of the organisms in the river are adapted to gentle changes in habitat. Regulated rivers have in general different instream flows without large variations, but hydropeaking operations are gaining increasing interest. Artificial flow fluctuations may alter the riverine habitat dramatically, and might lead to sub-lethal effects on fish due to increased energy consumption, stress, and hence reduced growth. Recent investigations by Flodmark *et al.* (2002) of stress response in brown trout caused by moderate flow fluctuations showed that juvenile trout return to normal within less than

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three days of peaking. Hydropeaking or accidental operation stops will give rapid flow changes. This may lead to dewatered riverbeds strongly affecting the riverine organisms through stranding and flushing (Cushman, 1985; Hunter, 1992).

Stranding of juvenile fish is a well-documented consequence below hydropeaking power stations (e.g. Hvidsten, 1985; Hunter, 1992; Saltveit *et al.*, 2001). Even gradual flow reduction downstream of a dam in Canada led to stranding of a large number of juvenile fish (Higgins and Bradford, 1996). They conducted a salvage programme to bring back surviving stranded or trapped fish into the main stem, but found that the cost of this was ten times higher than the monetary value of the fish. Slow dewatering was not sufficient to eliminate stranding. A number of factors are likely to influence stranding. These are dewatering speed (Monk, 1989), available cover (Vehanen *et al.*, 2000), response to falling water levels (Huntingford *et al.*, 1999) and temperature-dependent behaviour (Clarke and Scruton, 1999). Based on field experiments, Saltveit *et al.* (2001) found that the most important factors affecting stranding rates in young wild Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) were temperature, time of year, time of day and dewatering rate. The highest stranding rates were found at low water temperatures in daytime during midwinter, supported by the studies of Bradford *et al.* (1995). Bradford *et al.* (1995) advise dewatering during night in winter, and show that a slow dewatering rate minimizes stranding, but without defining any general threshold values.

Based on experiments and field observations, it is probably possible to develop guidelines for hydropeaking power stations to avoid severe negative impact on the river ecosystem (e.g. Hunter, 1992; Harby and Halleraker, 2001; Saltveit *et al.*, 2001). The Norwegian Research Council, several hydropower producers and the environmental authorities therefore established a multidisciplinary research project to focus on the impacts of hydropeaking on the riverine ecosystem and to produce guidelines for hydropeaking operation. The aims of the present study were to clarify the importance of the physical factors, i.e. water temperature, time of day, repeated fluctuations, dewatering rates and frequency, and habitat quality, on stranding of various density and size groups of juvenile brown trout. The experiments were carried out in an artificial channel with the main objective to improve the guidelines to minimize stranding of juvenile fish, and to test some of the conclusions from Saltveit *et al.* (2001).

MATERIAL AND METHODS

Characteristics of the Aqua channel

The experimental studies were conducted in an indoor 3.8 m wide and 19.2 m long artificial stream called the Aqua channel, located at SINTEF, Trondheim, Norway. Flow, water depth and light were operated automatically. Flow was provided from two impeller pumps, to perform peaking manipulations. Fresh water was constantly supplied from the municipal network, at a rate of about 1 l s^{-1} for the cold-water experiments and *c.* 0.5 l s^{-1} for the warm water experiments. Most of the water was recycled underneath the streambed (Figure 1). A gate at the end of the channel regulated the water depth. In this study the water temperature was adjusted within the range of $6\text{--}7^\circ\text{C}$ and $10\text{--}12^\circ\text{C}$, depending on the inflow of cold fresh water. Artificial light simulated night and day conditions. Day length was set to correspond to the natural photoperiod by following a sine function to ensure a gradual change between light and darkness.

The total model stream was divided into three sections (A, B and C), separated by net walls with mesh size of 4 mm (Figure 1). The streambed has a lateral slope of $4.8 \pm 1.3\%$ (mean \pm SD), with highest slope in the upstream section A, and lowest in the downstream section C. The substrate thickness varied from less than 5 cm to more than 25 cm. The stream substrate was 4.6% small pebble (1.6–3.2 cm), 73.1% pebble (3.2–6.4 cm), 13.3% small cobble (6.4–12.8 cm) and 9% cobble (12.8–25.6 cm). In addition, minor patches of river mosses (*Fontinalis* sp) were randomly spread on top of the substrate. A visual survey of embeddedness found that 23–30% of the streambed would offer good hiding possibilities in each of the sections.

The frequency regulated impeller pumps enabled discharge to vary from 1 to $>190 \text{ l s}^{-1}$, and combined with the adjustable gate, water depths from 10 to 40 cm were attainable at the deepest part of the stream. This deep part consisted of a 30 cm wide wooden longitudinal gutter without substrate or cover running along one of the long sides. The fish could use this gutter even when the water level receded. In the stranding experiments presented in this paper the flow fluctuated between 1 l s^{-1} and 140 l s^{-1} .

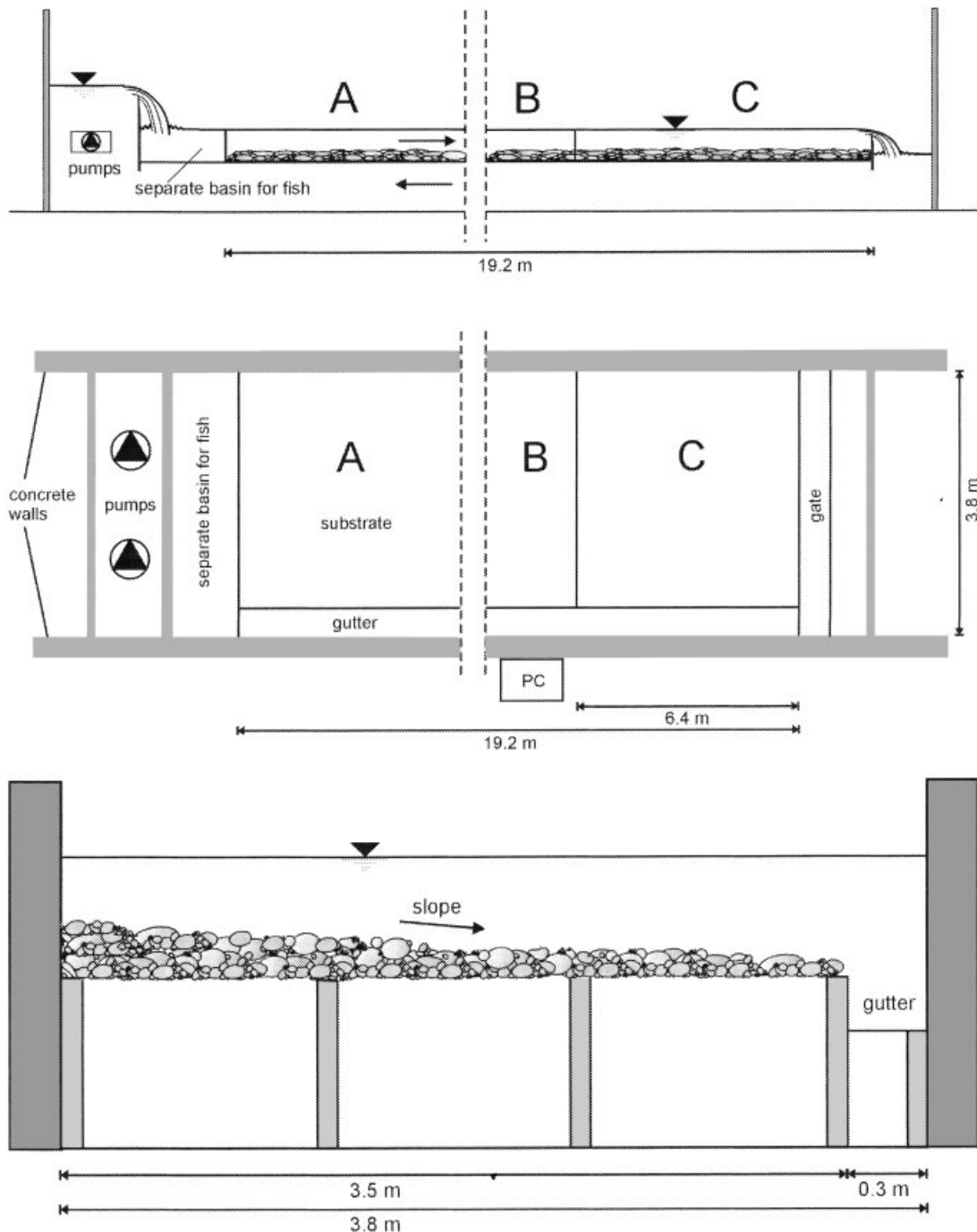


Figure 1. Schematic views of the artificial Aqua channel (top: side view, middle: plan view and bottom: cross view)

Based on high precision 3D hydraulic modelling by use of the model SSIIM, the hydraulic characteristics in 950 grid cells of the Aqua channel were described for flows of 1401 s^{-1} (maximum flow in experiments) and 401 s^{-1} (the flow just before the substrate starts to get dewatered) (Tables I and II). During the experimental period the pH was 8.1 ± 0.1 (mean \pm SD), $[\text{Ca}^{2+}]$ was $19.8 \pm 0.8 \text{ mg l}^{-1}$, conductivity was $10.5 \pm 0.6 \text{ mS m}^{-1}$ and turbidity was $0.15 \pm 0.19 \text{ FTU}$ in the tap water (unpublished data from Trondheim municipality). In 1999 the pH in the river Nidelva ranged between 7.0 and 7.3 at two stations along the river stretch where the fish were caught.

Table I. Percentage distribution of water depth (cm) in 950 cells in each section of the Aqua channel at two discharges. Depth calculated from hydraulic simulations by use of the 3D hydraulic model SSIIM after verification and calibration based on depth measurements at each discharge

Water depth (cm)	Section A		Section B		Section C	
	401 s ⁻¹	1401 s ⁻¹	401 s ⁻¹	1401 s ⁻¹	401 s ⁻¹	1401 s ⁻¹
0–5	31.6	2.9	28.9	1.4	9.9	0.0
5–10	30.8	21.2	37.2	17.8	44.8	3.5
10–15	19.8	34.8	20.5	38.9	37.6	35.8
15–20	12.0	17.1	7.9	22.0	2.3	46.5
20–25	0.0	17.2	0.0	14.2	0.0	8.9
25–30	0.0	1.6	0.0	0.4	0.0	0.0
30–35	0.0	0.0	0.0	0.0	5.3	0.0
>35	5.7	5.3	5.5	5.3	0.0	5.3

Table II. Percentage distribution of mean column velocities (m s⁻¹) in 950 cells in each section of the Aqua channel at two flows. The velocities were calculated from hydraulic simulation by use of the 3D hydraulic model SSIIM and verified by current velocity meter measurements in selected spots

Mean column velocity (m s ⁻¹)	Section A		Section B		Section C	
	401 s ⁻¹	1401 s ⁻¹	401 s ⁻¹	1401 s ⁻¹	401 s ⁻¹	1401 s ⁻¹
0.0–0.05	47.1	5.6	25.1	0.4	31.6	1.8
0.05–0.10	14.8	5.9	17.8	2.1	20.0	2.7
0.10–0.15	17.2	9.9	29.3	6.9	25.0	5.3
0.15–0.20	17.9	22.9	17.0	15.1	15.4	22.5
0.20–0.25	2.5	29.1	4.0	19.9	8.0	24.4
0.25–0.30	0.5	18.1	1.2	22.8	0.0	14.8
0.30–0.35	0.0	6.9	1.1	15.2	0.0	11.9
0.35–0.40	0.0	1.4	0.2	7.8	0.0	8.5
>0.40	0.0	0.2	4.3	9.8	0.0	8.0

Stranding experiments

Brown trout were collected from the regulated River Nidelva, Trondheim, Norway, by electrofishing. This is the same fish population used in field stranding experiments by Saltveit *et al.* (2001). The River Nidelva has been running on a partly hydropeaking scheme during recent years, so the fish populations used have already experienced rapid flow fluctuations and stranding (Hvidsten, 1985).

Fish were brought to the laboratory, measured and sorted. Fish were group tagged with minor fin clips to enable discrimination between experimental batches of fish and experiments, similar to procedures by Saltveit *et al.* (2001) and Flodmark *et al.* (2002). Fish were introduced either directly into the experimental sections of the channel or into keep nets placed in storage containers upstream of the experimental sections (Figure 1). Fish were kept up to 30 days in cold water and 25 days in the warm water experiments. Fish were not fed during any of the experiments to avoid bias of results due to preferred feeding habitats.

Studies of stress response in juvenile brown trout caused by electroshocking, transport, temperature variations and flow reductions showed that fish returned to resting values within 24 h after introduction into the stream

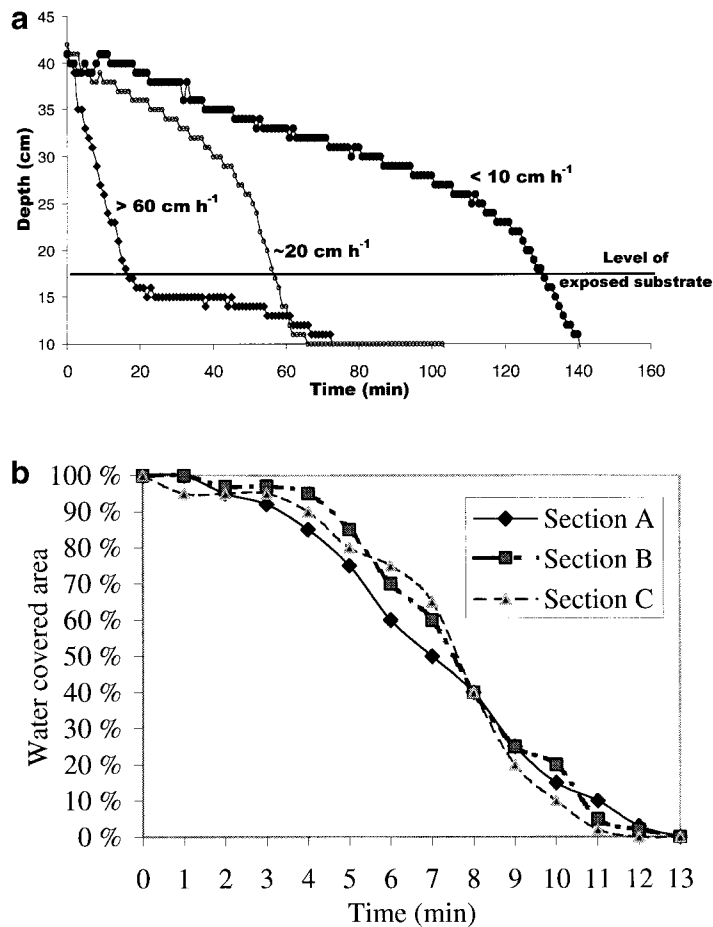


Figure 2 (a). Typical rapid, slow and ultra-slow dewatering ($>60 \text{ cm h}^{-1}$, $c. 20 \text{ cm h}^{-1}$ and $<10 \text{ cm h}^{-1}$) curves for stranding experiments in the channel used at $6\text{--}7^\circ\text{C}$ and $10\text{--}12^\circ\text{C}$, recorded as water depth measured in the deepest part (the gutter) of section C. The horizontal line represents the edge of the gutter (level when all substrate are exposed). (b) Percentage of wet area recorded by visual observations in each section during the last phase of rapid ($>60 \text{ cm h}^{-1}$) dewatering of the Aqua channel. Section A is upper, B is middle and C is downstream end

channel (Flodmark *et al.*, 2002; Arnekleiv *et al.*, unpublished data). Based on these findings, it was presumed that the experimental fish achieved natural behaviour within 24 h of stable conditions in the Aqua channel.

Fish were habituated in one of the sections or acclimatized in keep nets for three days with stable flow before each experiment. Just before the flow reductions started, the longitudinal gutter and the net walls were carefully checked for fish by visual observations in daylight experiments. Then water depth and flow were gradually reduced. The dewatering scenarios were grouped into (1) rapid ($>60 \text{ cm h}^{-1}$), (2) gentle ($c. 20 \text{ cm h}^{-1}$) and (3) slow ($<10 \text{ cm h}^{-1}$) (Figure 2). Slow dewatering ($<10 \text{ cm h}^{-1}$) was not tested in the cold water experiments. The operator followed a defined down-ramping procedure to ensure that the dewatering followed the defined dewatering scenarios. These represent dewatering scenarios relevant for hydropeaking rivers. A water level sensor (Aanderaa Instruments, Bergen) was placed in the gutter of section C to log the depth every 30 s.

All fish that escaped into the flowed gutter were identified for tags and counted after dewatering of the substrate. Headlamps were used to ensure that we caught all fish in the gutter. Each fish batch was counted several times to avoid miscounting. The substrate was not searched for stranded fish because earlier experience documented that they are very hard to find in the river substrate (Saltveit *et al.*, 2001). To avoid disturbing the substrate, only the 0.5 m adjacent to the gutter was walked on. Results for stranding are therefore based on the difference between the number of fish stocked and the number of fish found in the gutter after dewatering. Because the number of fish was limited, surviving fish were reused. The substrate was left dry for at least 4 h prior to the next experiment, to ensure

that stranded fish left in the substrate died. Those fish that eventually survived in the substrate and were found alive in one of the following experiments could be separated based on a different fin clipping. Many stranded fish were later found dead having drifted into the downstream net wall after flow increase, and were removed. Each batch of fish had at least 24 h in keep nets before they were reused.

All newly introduced fish experienced rapid dewatering in the first experiment. After the initial experiment in each series we conducted dewatering between 19 h and 64 h intervals. This is a far longer acclimatization period than the 3 h used by Bradford (1997). Before the flow was raised, new fish were gently transferred to the gutter during the *c.* 60 min it increased from 11 s^{-1} to 1401 s^{-1} .

Winter/spring time experiments

In the period 11 January to 3 March (Series 1) and 31 March to 20 April (Series 2) 2000, several series of stranding experiments simulating winter and spring conditions were conducted during both day and night time, with water temperature ranging from 6.0 to 6.8°C. The majority of the fish used were one year old (1+; hatched in 1999), the rest were two years old (2+) and had fork length 74.2 ± 4.5 mm and weight 4.5 ± 3.3 g (mean \pm SD). This length group ranging from 59 to 88 mm was treated as one batch of fish, and we did not split the fish into subgroups in the cold water experiments. In series 1 and 2 we conducted 29 comparable dewatering experiments with juvenile brown trout in one of the sections (Table III), either during day with rapid ($> 60\text{ cm h}^{-1}$) or gentle (*c.* 20 cm h^{-1}) dewatering speed, or rapid dewatering during night (in darkness).

Summer/autumn time experiments

In the period 29 May to 30 June (Series 3) and 15 August to 22 September (Series 4) 2000, several series of stranding experiments simulating summer and autumn conditions were conducted during both day and night, with water temperatures ranging from 10.0 to 12.0°C (Table III). Several size groups of brown trout were used. The brown trout <70 mm (1+; hatched in 1999) in Series 3 (June) had fork length 63.9 ± 4.8 mm and weight 2.9 ± 0.7 g (mean \pm SD); and the fish group >70 mm (2+; hatched in 1998) had fork length 77.0 ± 5.3 mm and weight 4.9 ± 1.0 g (mean \pm SD). In Series 4 (August–September) we used the following year class limits: <60 mm (0+; hatched in 2000) with fork length 49.8 ± 4.5 mm (mean \pm SD); 60–100 mm (mix of 1+ and 2+, but later refereed to as 1+) with fork length 86.5 ± 10.0 mm (mean \pm SD); and some >100 mm (2+ and 3+) with fork length 109.8 ± 6.4 mm (mean \pm SD). Several experiments with mixed size classes were combined to find the effect of mixed size variations on stranding (Table III), by stocking 0+ trout with 1+ or >100 mm trout into the same section. The stranding proportion of the 0+ trout from these experiments is described as 0+ mix in the results.

Table III. Overview of number of experiments in section A, B or C distributed on ramping rates, light conditions, fish size (see further size range for various experimental series in 'Material and method section') and season

Ramping rate (cm h^{-1})	Light	Summer/autumn (fish size)				Winter/spring
		0+	0+ mix	1+ and 2+	2+ and 3+ (> 100 mm)	Combination (59–88 mm)
Rapid (>60)	Day	27	5	29	7	12
	Night	4	2	5	1	8
Gentle (<i>c.</i> 20)	Day	7	3	7	1	9
	Night	0	0	0	0	0
Slow (<10)	Day	3	6	1	2	0
	Night	1	5	3	3	0
N total		42	21	45	14	29

Table IV. Partial and multiple regression coefficients (R) of various factors influencing stranding of brown trout based on all data (total), and split into high (10–12°C) and low (6–7°C) water temperatures. The factors are ranked by decreasing impact on the total dataset of stranded brown trout

	Total	High temp.	Low temp.
Temperature	0.281	–	–
Dewatering speed	0.234	0.258	0.146
No. of experiments	0.199	0.218	0.383
Fish size	0.185	0.258	–
Section	0.157	0.053	0.597
Fish density	0.138	0.180	0.290
Habituation	0.129	0.082	0.430
Light	0.053	0.192	0.007
Multiple (R)	0.468	0.452	0.712

Data analysis

The proportion of stranded fish in each series was analysed by use of Student's t -test, before subsets were pooled or not for further analysis, and to indicate significant differences between subsets. A multiple regression analysis of the factors shown in Table IV was conducted, and ranked for importance, based on the partial regression coefficient from these analyses. Datasets were further compared by use of box plots. The boundary of the box closest to zero indicates the 25th percentile, a line within the box marks the median, and the boundary of the box farthest from zero indicates the 75th percentile. Whiskers above and below the box indicate the 90th and 10th percentiles, and if $n > 5$ data outside this percentile range are plotted as outliers.

RESULTS

Fish behaviour

Before dewatering started, fish were rarely observed holding position in the gutter, probably due to the lack of cover and substrate. Even though we started each experiment by introducing each batch of fish into the gutter of each section, the vast majority of fish migrated rapidly into the substrate-covered shallower part of the section and established territories here. Fish tended to hide in the substrate even during the warm water experiments, and were only observed above the substrate during the final stages of dewatering.

Factor ranking

The multiple regression analysis showed that temperature (season) was the most important factor to explain the variation in stranding (Table IV). We therefore separated the results based on temperature condition. For the low water temperature condition (6–7°C) the multiple regression ranked the factors as follows: section > habituation (hours with stable flow prior to dewatering) > no. of experiments > fish density > dewatering speed (>60 or $c. 20 \text{ cm h}^{-1}$) \gg light. In high water temperature (10–12°C), the multiple regression coefficient ranked factors as follows: fish size (included mixed year classes) \approx dewatering speed (>60, $c. 20$ or $< 10 \text{ cm h}^{-1}$) > no. of experiments (days in channel) > light > fish density \gg habituation > section.

Summer/autumn simulations

Daytime. No significant difference between stranding in the three sections was observed during rapid dewatering at daytime with 0+ or 1+ brown trout in the summer/autumn experiments ($t = 0.05$ – 0.69 , $df = 16$ – 26 , $P = 0.25$ – 0.48). Hence data from all sections were pooled. There was a significantly higher stranding of 0+ than 1+ ($t = 2.98$, $df = 54$, $P < 0.01$), and a significantly higher stranding of 0+ when mixed with 1+ or 2+ trout

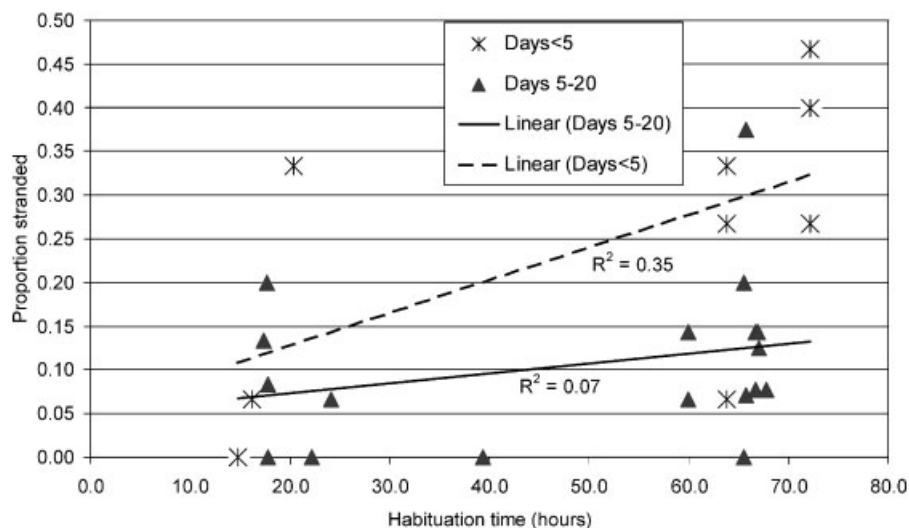


Figure 3. Proportion of stranded 0+ brown trout (50–70 mm) caused by rapid dewatering in daylight at water temperature between 10 and 12°C versus habituation time (stable flow in the Aqua channel). Data divided into fish stored in <5 days (first stranding) and 5–20 days (second to fifth stranding)

than in experiments with 0+ alone ($t = 2.11$, $df = 32$, $P = 0.02$). In rapid daylight experiments these groups are therefore treated separately. Further, there were no significant differences between stranding of <70 mm trout (hatched in 1999) from Series 3 (June) with <60 mm trout (hatched in 2000) from Series 4 (August–September) after rapid dewatering in daylight ($t = 0.01$, $df = 25$, $P = 0.50$), and these experiments were therefore pooled.

A significantly higher portion of 0+ trout <5 days in the stream (first dewatering episode) stranded than those 5–20 days in the stream (second to fifth experiment) ($t = 2.80$, $df = 24$, $P = 0.005$) (Figure 3). There was a tendency towards a decreased stranding with days in the stream (\approx number of experiments) also for the larger trout. The outliers and most of the highest proportion of stranded fish found in rapid dewatering at daytime (Figures 4–6) can be linked to the fact that this was the first dewatering episode for the fish.

Figure 3 also shows a tendency towards an increased stranding with increased habituation time, but this was not statistically significant (first rapid dewatering episodes; $t = 1.57$, $df = 7$, $P = 0.08$, second to fifth experiment $t = 0.81$, $df = 16$, $P = 0.22$). The proportion of 0+ stranding was less in rapid daylight experiments after <30 h habituation (stable flow) (mean = 0.13 for fry <5 days in the stream versus 0.08 for fry 5–20 days in the stream) than >30 hours (mean = 0.30 for fry <5 days in the stream versus 0.12 for fry 5–20 days in the stream). This tendency was not observed for any of the other subsets of fish size groups.

Nighttime. In general, there was a lower stranding frequency during night experiments than during day both for 0+ and for 1+ (Figures 4–6). Maximum median value of each 0+ subset with rapid dewatering in darkness was 0.08 (Figure 4), while in the 1+ experiments stranding was negligible in most experiments except for the rapid dewatering during daylight (Figure 6).

Ramping rates. Figures 4–6 show a clear reduction in stranding with increased ramping rate in daylight for all subsets. The 0+ mix experiments showed seven times higher stranding rate during rapid versus ultra-slow dewatering (Figure 5), while 0+ alone showed less than 50% reduction (Figure 4). However, the 0+ and the 0+ mix experiments still have some episodes with more than 0.06 proportion stranding even at the slowest dewatering rates tested. We also included trout >100 mm in the experiments, but even at the most rapid dewatering this fish size rarely stranded at all.

Winter/spring simulations

For the winter time experiments (water temperatures 6–7°C) there was a lower mean and median proportion of stranded fish in section A compared to sections B and C for both rapid dewatering during day and night, and for the

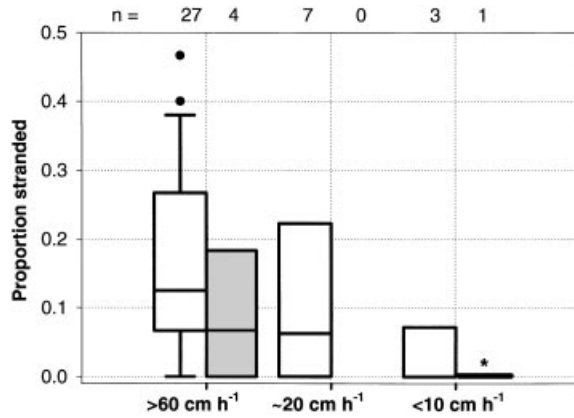


Figure 4. Box plot comparison of proportion of stranded 0+ brown trout (mean fork length 50 to 64 mm) after various dewatering rates conducted during June to September 2000 at water temperature between 10 and 12°C, with 15 to 72 hours habituation time prior to dewatering in daylight (white box/ to the left), and at night (grey box/ to the right). Asterisk indicates 0.0 stranded fish. The boxes show 25th to 75th percentile and median (the inner horizontal line in each box)

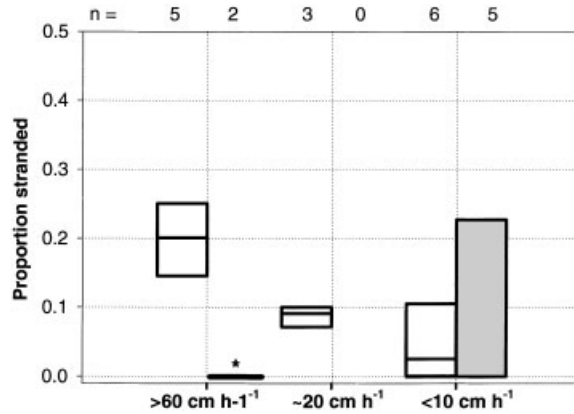


Figure 5. Box plot comparison of proportion of stranded 0+ brown trout (mean fork length 50 to 64 mm) after various dewatering rates with 0+ mixed with larger fish conducted during June to September 2000 at water temperature between 10 and 12°C, with 15 to 72 hours habituation time prior to dewatering in daylight (white box/ to the left), and at night (grey box/ to the right). Asterisk indicates 0.0 stranded fish

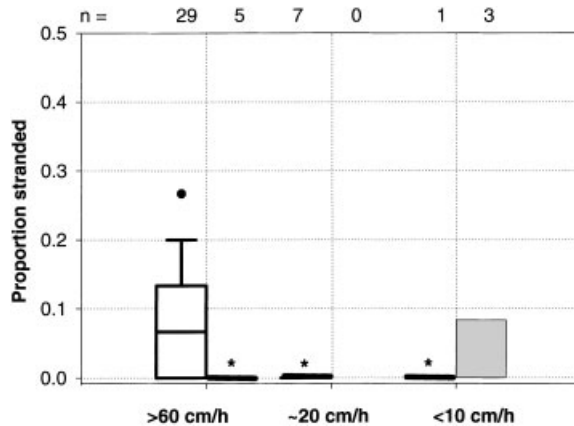


Figure 6. Box plot comparison of proportion of stranded 1+ and 2+ brown trout (mean fork length 77 to 87 mm) after various dewatering rates conducted during June to September 2000 at water temperature between 10 and 12°C, with 15 to 72 hours habituation time prior to dewatering in daylight (white box/ to the left), and at night (grey box/ to the right). Asterisks indicate 0.0 stranded fish

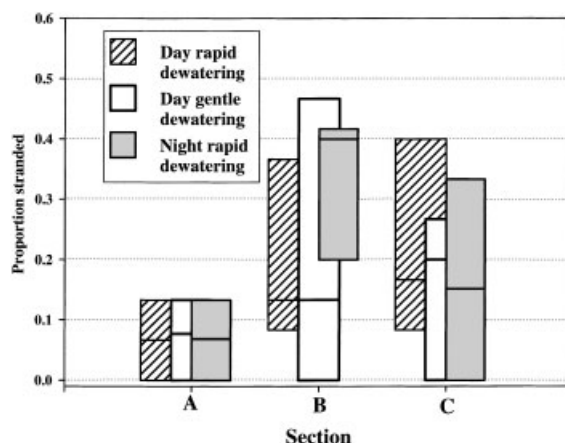


Figure 7. Box plot comparison of proportion of stranded brown trout of mixed size classes (56–88 mm) after rapid dewatering ($>60 \text{ cm h}^{-1}$) during day and night, and gentle dewatering ($c. 20 \text{ cm h}^{-1}$) during day. The results are experiments conducted in February to May 2000 at water temperatures of 6–7°C split into each section of the Aqua channel

slow dewatering rate during daytime (Figure 7). The highest stranding (median, mean and maximum proportion) was found during rapid night dewatering. There was a tendency towards a lower stranding at slow dewatering (median proportion stranded reduced from 0.13 to 0.08), but this was not statistically significant ($t = 0.78$, $df = 12$, $P = 0.22$). However, the highest stranding episode recorded during the cold water experiments was found during slow dewatering in daytime.

The size of the trout used in the experiments was different at different times of the year. The median proportion of stranded trout (mean fork length 74 mm) after rapid dewatering in daylight experiments at 6–7°C was similar to the proportion of stranded 0+ trout (mean fork length 50–64 mm) after rapid dewatering in daylight at 10–12°C (Figure 7 versus Figure 4). However, the rapid night dewatering at 6–7°C gave the highest median and inner 50% stranding rate of all the night experiments conducted (Figure 7 versus Figure 4–6), but for section B and C was not significantly higher than the daytime stranding at rapid dewatering ($t = 0.55$, $df = 11$, $P > 0.25$).

DISCUSSION

Habitat use and quality

Brown trout, but also Atlantic salmon, are the most common species in running waters in Norway, and running water habitat is central in their life history. Depth, current velocity, substrate and cover are found to be the most important physical factors affecting their selection of habitat (Heggenes, 1989; Gibson, 1993; Heggenes *et al.*, 1999). The importance of the physical variables varies between streams rivers, season and with species and fish size (Karlström, 1977; Morantz *et al.*, 1987; Heggenes and Saltveit, 1990). Furthermore, temperature and light are further driving factors for behaviour (e.g. Heggenes *et al.*, 1993; Clarke and Scruton, 1999) and habitat use (Karlström, 1977; Cunjak and Power, 1986) of salmonids. It is therefore crucial, when doing stranding experiments on these salmonids, to offer stream habitat conditions that are as natural as possible, with emphasis on the current velocity and cover (substrate composition, thickness and embeddedness).

The rate of stranded fish may be much higher under natural conditions, due to the spatial extent of dewatered riverbeds under hydropeaking in larger rivers. However, laboratory experiments offer a good way to quantify the importance of single factors under controlled conditions. This has previously been difficult in field experiments of stranding in a natural regulated river (Saltveit *et al.*, 2001), due to climatic and operational variability.

In general the experiments described in this paper were conducted in a wider channel with higher velocities, longer acclimatization times, and more variable substrate sizes and thicknesses than most other published stranding experiments with the exception of Saltveit *et al.* (2001) (Table V). Our experimental design probably led to a more substrate-seeking behaviour in the wild juvenile fish we used than other stranding experiments. However, due

Table V. Physical and biological characteristics of the Aqua channel compared to other comparable stranding studies

	Aqua channel	River Nidelva ^a	River Daleelva ^b	Exp. pond ^c	Artificial stream 1 -Canada ^d	Artificial stream 2 -Canada ^e
Size of exp. arena (m ²)	3 × 24.3	75	3 × 24	9 × 8.5	19.4	17.3
Species	Wild brown trout	Wild Atlantic salmon, brown trout	Hatchery Chinook salmon, Steelhead trout	Stocked Chinook salmon, Coho salmon	Stocked Coho salmon, rainbow trout	
Year class, fork length (mm)	45–90 (> 100) 0+, 1+, 2+, mix	45–90 0+ 1+	0+ : 44–49, 32–34	0+ : 44–49, 32–34	0+ : 40, 57 (mean)	58, 88 (mean)
Acclimatization time (h)	> 18	> 24	1–1.5	3	< 1.5	
Density (fish/ m ²)	0.56, 1.13	0.7, 1.3	1.25, 2.5	4.1, 4.7	2.6	2.9
Water depth (range, cm)	0–40	44–67	0–c. 30	13–14	13–18	4–18
Velocity (cm s ⁻¹)	< 5–40	< 5–52	Rapid	2.1–6.7	< 5–15	8–25
Substrate (dom. cm)	73% pebble (3.2–6.4)	Small cobble (mean 8.5)	Coarse	Mean: 1.4, 3 or 7 Max: 2.3, 6.2 or 20	Gravel (mean 6.5) (+ small cobble)	Gravel (mean 6.5)
Substrate thickness (cm)	5–25	Natural riverbed	Natural riverbed	12 to > 22 cm	Single layer < 10 cm	Single layer < 10 cm
Dewatering range (cm h ⁻¹)	< 10, 20 and > 60	12–90		42–240	6, 30 and 60	6, 30 and 60
Slope (%)	4 ± 1.3	2		0.9–5.1	2	2 and 6
Water temperature (°C)	6–7 and 10–12	< 4.5 and > 9	> 10	11–16.7	6 and 12	< 4

^aSaltveit *et al.* (2001).

^bEnclosure built in the Norwegian hydropeaking project (unpublished data).

^cMonk (1989).

^dBradford (1997).

^eBradford *et al.* (1995).

to the fact that fish were not fed, hunger probably intensified the search for prey animals, and the fish may have become more active by both day and night, giving bias to our results. Water temperature was not matched to real local late winter/early spring conditions, and this may also have affected the activity pattern of fish as higher water temperatures lead to higher activity levels (Clarke and Scruton, 1999).

Monk (1989) found mostly subsurface stranding of fry, and a clear relationship between increased stranding with increasing size of substrate. Based on artificial versus natural substrate in field studies (Saltveit *et al.*, 2001), the substrate or availability of suitable cover did not seem to be a controlling factor for stranding at high flow reduction rates, but was a determining factor when drawdown speed was reduced. This may be explained by the habitat selection in brown trout regarding substrate. Brown trout selection of substrate depends on fish size, with larger trout selecting larger stones (Heggenes *et al.*, 1999). Interstitial spaces function as current shelter and refugia from predators and adverse hydraulic conditions (e.g. Heggenes *et al.*, 1993). This is particularly important during low winter temperatures, because fish without sufficient cover will spend more energy in holding their position and energy reserves may be limiting for winter survival (Cunjak, 1988; Metcalfe and Thorpe, 1992; Bull *et al.*, 1996).

In our channel, we found a significant difference in stranding between section A versus sections B/C in cold water. Sections B and C had the highest velocities, and the lowest slope. This result indicates that the fish are more susceptible to stranding at high than at low velocities, probably because brown trout are more affected by higher velocities and/or good shelter in cold water (Vehanen *et al.*, 2000), and achieve low snout velocities close to or within the substrate (e.g. Heggenes *et al.*, 1993), and are therefore more easily trapped during flow reductions. Section B had the coarsest substrate while section C was coarser than section A. During cold water experiments

the highest stranding rate occurred in both sections B and C, as expected. Section A had fewer hiding places and also lower stranding. Therefore, fish not having a habitat providing sufficient shelter and resting places, seem to be less affected by stranding. We conclude that local physical conditions like slope, column velocity and shelter are more important in cold water conditions, since we did not find significant differences in stranding between the sections in the summer/autumn experiments.

It is known that the use of river margins, i.e. the shallow areas dewatered under hydropeaking, varies over the year for brown trout and Atlantic salmon (Heggenes and Saltveit, 1990), and that juvenile salmonids are less active in daylight in cold water (Heggenes *et al.*, 1993). Further, Heggenes (1988) found no significant shift in habitat use induced by short-term peaking flow in that period of the year. Based on this, we recommend that hydropower plants allocate increased flows during daylight at low temperatures, when frequently hydropeaking. This procedure may contribute to a reduction in the numbers of salmonids migrating back into river marginal habitats.

Fish size

Olson and Metzgar (1987) found evidence of a critical stranding size limit for steelhead trout based on field studies, and concluded that they exceeded the size susceptible to stranding by 1 September in the Sultan River in Washington. For Chinook salmon, Monk (1989) did not find any significant difference in stranding with size. Olson and Metzgar (1987) determined 50 mm as the critical size limit for stranding of Chinook salmon. Hvidsten (1985) suggested that the smallest brown trout stranded first due to competition, hence the smallest trout used the shallowest habitat. Despite the fact that Bradford (1997) used smaller fish (fork length *c.* 40 mm versus our smallest of 50 mm), he achieved in general very low stranding (<4% at rapid daytime dewatering) in 12°C. This is probably due to his thin substrate layer in combination with lower velocities, short habituation time and the use of hatchery fish (Table V). Hatchery fish probably do not have the same substrate-seeking behaviour as wild fish (Saltveit *et al.*, 2001).

We documented an almost two times higher stranding of 0+ than 1+ during rapid dewatering at daytime, and an almost three times higher median stranding of 0+ mixed with larger fish than 1+ fish alone during rapid dewatering. Further, stranding of 1+ is mostly negligible except for the rapid dewatering during daylight in warm water. So, a critical limit for stranding of brown trout seems to be at least 100 mm, but even this size class is susceptible to stranding in pocket waters and in low gradient river habitats with coarse substrate and good cover, thus single individuals >100 mm stranded in some of our and Hessevik's (2002) experiments.

Season

Water temperature was a major factor determining the magnitude of trout stranding in this study. Even at water temperatures above 10°C, a high incident of stranding was observed. In contrast to the findings of Bradford (1997) and Saltveit *et al.* (2001), reduction in stranding due to dewatering during night in cold water was not documented. Sheltering of juvenile trout in the substrate during winter is thought to be a daylight phenomenon, as trout may be active during night. This diurnal change in behaviour occurs when temperatures drop below 5–10°C, and is an anti-predator behaviour regulated by light (Fraser *et al.*, 1993, 1995; Heggenes *et al.*, 1993), but is also a strategy to avoid being frozen in. We link our lack of a diurnal difference during winter conditions in the present study to the fact that despite being able to simulate night conditions, 6°C was not cold enough for brown trout to become nocturnally active. Clarke and Scruton (1999) have documented a gradual increase in activity with minor increases in water temperatures in the range 3–5°C for Atlantic salmon in laboratory experiments. In addition, the lack of food may have restricted the expected nocturnal feeding behaviour at low temperatures. However, differences in diurnal winter activity are mainly found in larger juvenile fish (Heggenes *et al.*, 1993), i.e. mean sizes of 10 cm, than fish used in our experiments.

Ramping rates

Monk (1989) found no statistical difference of stranding between ramping rates of 240 cm h⁻¹ and 42 cm h⁻¹. Bradford (1997) was unable to attribute stranding rate to ramping rate between 60 and 6 cm h⁻¹. Field experiments (Saltveit *et al.*, 2001) documented no clear link between stranding and ramping rates within ramping rates of 20–78 cm h⁻¹, and time of day was more important than dewatering speed in reducing stranding of Atlantic salmon

during mid-winter in these experiments. Hence, a ramping rate slower than 20 cm h^{-1} was needed to achieve reduction in stranding.

In our study the reduction of dewatering speed from $>60 \text{ cm h}^{-1}$ to $<10 \text{ cm h}^{-1}$, decreased the stranding of trout in experiments at $10\text{--}12^\circ\text{C}$. For larger sized trout (mean fork length $77\text{--}87 \text{ mm}$) no stranding was observed in any of the seven dewatering episodes at *c.* 20 cm h^{-1} in daylight. For the smaller sized trout an increase in dewatering time from more than 60 to *c.* 20 cm h^{-1} reduced the stranding by more than 50%, and a further decrease followed at ramping rates $<10 \text{ cm h}^{-1}$. Still, even when the dewatering took more than 2 h ($<10 \text{ cm h}^{-1}$), stranding of 0+ trout during daytime experiments was not eliminated. Recent studies of the timing of migration during dewatering showed that the last part of the dewatering was critical for stranding or escapement (Hessevik, 2002).

In the $6\text{--}7^\circ\text{C}$ water temperature experiments, the impact of ramping rate was less evident, but the effects of $<10 \text{ cm h}^{-1}$ dewatering speed was not tested. However, stranding was reduced when using 20 cm h^{-1} instead of 60 cm h^{-1} to dewater the substrate also in cold water.

Habituation and repeated dewatering

The experiments showed that stranding of juvenile trout is significant even after repeated experiments with the same fish. A tendency towards increased stranding connected to a long habituation time is also found. For the smallest trout fry ($<70 \text{ mm}$) we documented a significantly higher stranding in the first versus the following dewatering episodes at rapid dewatering. This might be because some individuals left their resting positions later than others during dewatering, and hence these individuals stranded and died in the first experiments, hence stranded fish were not looked for in the substrate.

The channel was left dry for at least 4 h between each experiment. Many stranded fish were removed when they were found dead in the downstream net wall, while some subsurface stranded fish ended their days in the substrate. Olfactory cues are found to influence habitat use by Atlantic salmon (e.g. Huntingford *et al.*, 1999). The olfactory environment due to dead fish in the substrate may have caused bias in our result, thus fish may have abandoned areas with thick substrate in the end of the experimental areas.

CONCLUSIONS AND GUIDELINES

The acceptable dewatering speed to avoid stranding depends on local site characteristics, fish size, time of the year and light conditions. Water temperature (season) was the main factor determining the magnitude of stranding in brown trout juveniles. Cold water combined with coarse substrate, low gradient, and high current velocity gave the highest stranding incidents. The presence of trout parr leads to higher stranding of trout fry. Significantly fewer brown trout stranded after several dewatering episodes. A decrease in dewatering time from $>60 \text{ cm h}^{-1}$ to *c.* 20 cm h^{-1} reduced the stranding of trout fry by more than 50% in summer/autumn, and almost eliminated stranding of 1+ trout. Dewatering slower than 10 cm h^{-1} drastically decreased stranding of 0+ trout in warm water conditions. Dewatering in darkness is recommended to reduce stranding of salmonids at any time of the year, combined with slow ramping rates ($10\text{--}13 \text{ cm h}^{-1}$). For rivers dominated by coarse substrate, ultra-slow ramping rates ($<10 \text{ cm h}^{-1}$) must be achieved. Gentle drops in discharge after long stable flow periods are recommended. Allocating increased flows during daytime at low temperatures will prevent juveniles migrating back into critical marginal habitats.

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