


Exploring sensitivities to hydropeaking in Atlantic salmon parr using individual-based modelling

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Abstract

Hydropeaking (the release of water pulses at hydropower plants) results in temporary reductions in river channel water-covered area downstream, which may cause fish mortality through stranding. We used a mechanistic modelling approach to examine how both the form of the hydropeaking cycle and the characteristics of the affected fish control how hydropeaking may cause stranding mortality of fish. We modelled the response of Atlantic parr to hydropeaking in a regulated watercourse in central Norway (the River Nidelva) using an individual-based population model designed explicitly to examine fish behaviour and stranding mortality during hydropeaking. A response to hydropeaking, involving migration from the riverbanks towards the mid-channel on down-ramping and a return to the riverbanks on up-ramping, was based on individuals being parameterized to migrate to habitat properties that spatially changed throughout the hydropeaking cycle. We found that stranding mortality was strongly dependent on both the form of the hydropeaking cycle and on the fish response. Total stranding mortality was more dependent on the down-ramping speed than the duration of the minimum flow period. Total stranding mortality was greatest when there was a low movement speed, leading to individuals being stranded, combined with a high probability of dying per unit of time when stranded. Given the sensitivity of mortality to the fish response and the lack of detailed field studies quantifying this, we conclude that this area requires further controlled studies for parameterizing models used to predict effects of hydropeaking on fish. Simulation-based modelling, where there is a 100% control of and knowledge of fish characteristics, where a range of deterministic functions can be evaluated and in which boundary conditions can be easily controlled, may be a useful research tool to complement empirical studies.

KEYWORDS

Atlantic salmon juveniles, fish mortality, fish movement, hydropeaking, individual-based modelling

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1 | INTRODUCTION

Hydropeaking—the release of pulses of water to increase energy production at hydropower plants (HPPs) to meet short-term energy demands—is a common practice in hydroregulated rivers (Bin Ashraf et al., 2018). Hydropeaking affects flow conditions in the watercourse downstream of the HPP. The most immediate impact is an induced rapid change in river discharge during both down-ramping (reduction in discharge) and up-ramping (increase in discharge), which has a corresponding effect on downstream flow properties and water-covered area. Reductions in water-covered area (dewatering) may cause stranding (beaching) of fish present in areas that are dewatered, potentially leading to subsequent fish mortality (Nagrodski et al., 2012).

Total stranding mortality within a single hydropeaking event is affected by properties of the event such as the minimum flow on down-ramping, speed of down-ramping and duration of the minimum flow period. The minimum flow affects the total area that is dewatered, the down-ramping speed affects the ability for fish to temporarily migrate to parts of the river that remain water-covered and the duration of the minimum flow period affects the probability of survival for stranded fish. Fish stranded in temporarily dewatered areas typically do not experience 100% mortality because there are often small sources of water available, for instance in interstitial spaces between coarse bed material, so short periods of dewatering may not always result in mortality. Given that mortality is dependent on the hydropeaking flow regime, a range of recommendations have been made to mitigate effects including modifying operational regimes (Moreira et al., 2019) and installation of hydraulic structures such as buffer reservoirs and retention basins (Reindl et al., 2022). Additionally, mitigation technologies including the Air Cushion Underground Reservoir (ACUR) (Storli, 2017; Storli & Lundström, 2019) that uses compressed air to dampen changes in downstream flow conditions during hydropeaking have recently been investigated.

Fish behaviour also affects stranding mortality. Studies in controlled experiments within rivers have shown that stranding mortality depends on the state of the fish (size, age or life-stage), and the time of day and year when hydropeaking is conducted (Halleraker et al., 2003; Saltveit et al., 2001). This is typically related to differences in how the fish respond to hydropeaking. Older fish tend to be more mobile, so are better able to find areas that remain water-covered during minimum flows. Atlantic salmon (*Salmo salar* L.) parr (juveniles) tend to be less active during winter than summer, particularly during daytime (Valdimarsson & Metcalfe, 1998), so are more susceptible when hydropeaking occurs in winter during daytime. The exact manner in which down-ramping affects fish depends on how compensatory responses are constrained by characteristics of the habitat. If fish are in a part of the channel that is dewatered on down-ramping but which is in proximity to a deep part of the channel that remains water-covered, fish may temporarily migrate to the deeper location until the down-ramping event is over. Localized fish movements have indeed been identified during down-ramping: Scruton et al. (2003) found mean and maximum distances of movements of

Atlantic salmon parr of ≈ 14 m and ≈ 25 m, respectively, while Boavida et al. (2017) found a median movement distance of ≈ 16 m. However, if deeper locations that remain water-covered on down-ramping are absent, this opportunity will not be present, so mortality will be higher. Given this, the spatial distribution of potential fish habitats, and the ability of fish to migrate between them, may have a large effect on stranding mortality.

Field studies can provide useful information on how hydropeaking causes stranding mortality, but they are limited in scope and in what they can measure. First, field studies are often limited in scope. For example, Saltveit et al. (2001) used a single net enclosure when examining the stranding mortality of Atlantic salmon parr. Results from such experiments only apply to habitat conditions at the experimental site, so may provide biased estimates if used to predict for locations with different characteristics. Second, field studies do not measure all system properties but typically rely on observations of the fish population before and after hydropeaking events. Information that may be required to understand system behaviour, such as how fish movements change in response to hydropeaking, is often absent. An approach that can be integrated to be used alongside field studies is the use of dynamic, process-based modelling. If the model is successfully calibrated and validated using empirical data, it may be possible to use the model, as both a predictive and an analytic tool, that complements the empirical research. For example, stranding effects can be expanded from individual, empirically characterized locations, and sensitivities to exactly how channel morphology, hydropeaking regime and fish behaviour interact to cause the observed mortality can be examined.

In this study, we use a mechanistic individual-based modelling approach to investigate how the effect of hydropeaking on Atlantic salmon parr is influenced by (1) the form of the hydropeaking cycle (down-ramping speed and duration of the minimum flow period) and (2) characteristics of the parr (how quickly they migrate to optimal habitat, their territory size and their susceptibility to mortality on stranding). We conduct a sensitivity analysis to determine how the total stranding mortality in the population is dependent on the interaction between controlling parameters with the objective of (1) identifying optimal ramping regimes and (2) identifying the influence of parameters of the fish response so that future empirical studies can be better targeted.

2 | MATERIALS AND METHODS

In the following, we describe the procedure used for modelling hydropeaking-induced stranding mortality. We first describe an individual-based model (IBM), developed to simulate fish behaviour and stranding mortality under conditions of hydropeaking. We then present a case study—a site within the River Nidelva, Central Norway—that we use to identify influences on the total stranding mortality during hydropeaking. We describe the procedure used for estimating hydraulic conditions throughout the hydropeaking cycle, including habitat suitability and water-covered area. Finally, we

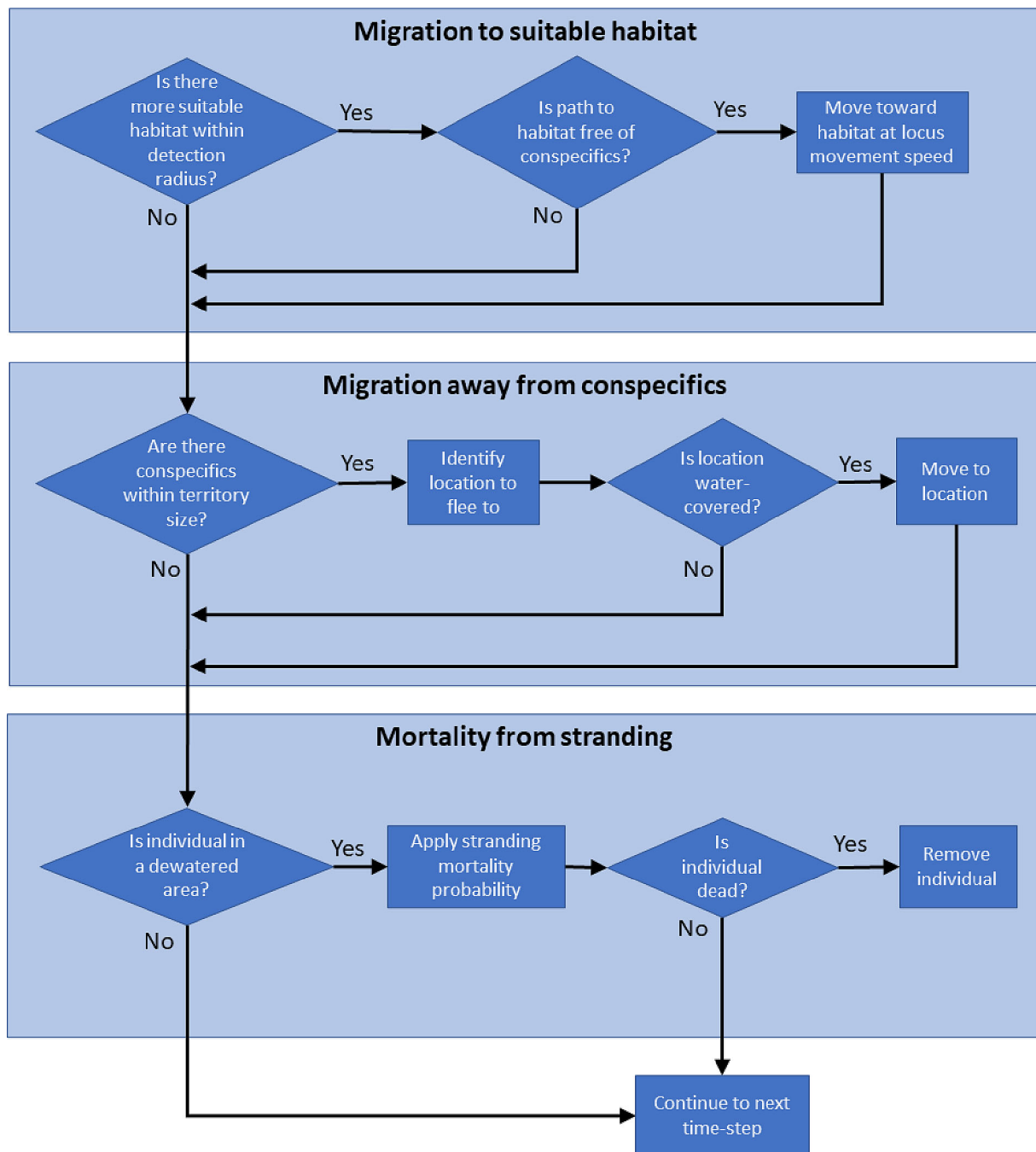


FIGURE 1 Schematic of SalStrand-IBM model routines

describe the simulation parameterization, including a full sensitivity analysis that allows the gauging of relevant features of the ramping regime and the fish behaviour/response.

2.1 | Individual-based model

An individual-based population model (*SalStrand-IBM*) was developed to evaluate the response of Atlantic salmon parr to hydropeaking-induced flow changes and consequent stranding mortality in stranded

individuals. This model, alongside a description complying to the Overview, Design concepts and Details protocol (Grimm et al., 2020), is available at GitHub (<https://github.com/HedgerNINA/SalStrand-IBM>). The model was developed using the modelling package NetLogo, a multiagent programmable modelling environment (Wilensky, 1999). The model is run with a time-step length of 10 min. Physical habitat characteristics (habitat suitability and whether a location is water-covered or dewatered) are modelled on an orthogonal grid of 1×1 m grid cells. At each time-step, the model sequentially selects each parr individual using a random selection order, and three

routines are applied (see Figure 1). The model has two routines describing the parr behaviour. First, parr migrate to the most hydraulically suitable habitat available to them. Second, parr migrate away from one another, based on parr's inherent territoriality (see Valdimarsson & Metcalfe, 2001). These two routines produce behaviours that counterbalance one another, with the former causing parr to cluster in and around suitable habitat and the latter dispersing them and limiting the numbers present in suitable habitat. The routine for migration to suitable habitat implements a response to hydropeaking-induced down-ramping because it means that parr migrate away from areas that are becoming dewatered (very shallow and very low velocity areas are parameterized as being unsuitable). An additional routine implements a stranding mortality probability for those parr that remain in dewatered areas. Three key parameters controlling the parr are (1) the *locus movement speed*, specified as the movement in the locus position (the average holding position of the individual) over the 10 min time-step interval when migrating to suitable habitat; (2) the *territory size*, specified as the diameter of a circle centred on the individual, for which a behavioural response to conspecifics (other individuals) occurs should this territory overlap with that of other conspecifics; and (3) the *stranding mortality probability*, the probability of mortality for a stranded individual over the 10 min time-step interval.

2.1.1 | Migration to suitable habitat

The parr individual identifies the location that has highest habitat suitability within a range of 5 m and moves towards that location at the locus movement speed, if (1) the suitability of that location is greater than the suitability of the current location the individual occupies and (2) the path between the individual and that location is free from conspecifics within the radius of the individual's territory size. Implicit in this routine is that parr individuals are able to detect suitable habitat in their proximity (radius of 5 m). To do this, it is assumed that the individual will be swimming around its locus position averaged across the 10 min time-step of the model: These short-term, sub-10 min movements are not explicitly modelled to minimize computational time. The requirement for a path that is free of conspecifics is included because it is assumed an individual will not migrate through an area inhabited by conspecifics.

2.1.2 | Migration away from conspecifics

The parr individual identifies if conspecifics are present within its territory size. If one or more conspecifics are present, the individual moves in the opposite distance from the average position of these conspecifics by this territory size. For example, if the territory size is 1 m, and there are two conspecifics in close proximity (<1 m), one conspecific will move away from the other by a distance of 1 m. The result is that the minimum distance of separation between the conspecifics' locus positions will be 1 m.

Migration to suitable habitat or away from conspecifics only occurs if the parr individual is in a water-covered location. Parr individuals may become stranded in areas that have become dewatered on down-ramping, and such individuals become stationary and subject to stranding mortality, until the area becomes water-covered again on up-ramping.

2.1.3 | Mortality from stranding

The parr individual experiences a mortality probability each time-step that it is occupying a dewatered location, defined as a stranding mortality probability. Locations become dewatered, depending on channel bathymetry and hydraulic conditions. Stranding mortality probability is defined in the model as a probability for a 4 h period ($P(M_{4h})$, corresponding to the length of a typical stranding event) but converted within the model to be applied at the model 10 min time-step, $P(M_{ts})$, using the relationship $P(M_{ts}) = 1 - \left((1 - P(M_{4h}))^{1/24} \right)$.

Migration to more suitable habitat and total stranding mortality in the *SalStrand-IBM* model are dependent on how the spatial distribution of suitable habitat and the spatial distribution of water-covered area change during the hydropeaking cycle. Habitat suitability in each 1×1 m cell is determined using a habitat suitability curve-based approach, based on suitability for velocity and depth (predicted externally by a hydrodynamic model), which changes according to discharge. The status of each cell in terms of the presence of water is calculated for each discharge. A depth of >0 m indicates a water-covered status. Stranding mortality is only applied to parr individuals in cells with a dewatered status (depth = 0 m).

2.2 | Case study: River Nidelva

The IBM was used to investigate hydropeaking-induced stranding mortality in Atlantic salmon parr in a short stretch of the River Nidelva, a regulated salmon river in west-central Norway (63.4°N, 10.4°E). The salmon-supporting stretch of this river lies in the lowest 9 km reach, downstream of an HPP (Nedre Leirfoss) (Figure 2a). This reach is characterized by a low change in elevation, from 11 masl immediately downstream of Nedre Leirfoss falling to ≈ 2 masl 3.75 km downstream. Flows in this reach are subject to rapid change due to hydropeaking. While the hydropeaking regime is flexible in terms of frequency, magnitude and duration, hydropeaking usually involves one cycle per day, discharges typically range between 30 and $135 \text{ m}^3 \text{ s}^{-1}$ and minimum flows last for 3–4 h (Figure 2b). Down-ramping reduces water-covered area: For example, Arnekleiv et al. (2013) estimated a reduction in wetted area of 17.8% when flows were reduced from maximum to the minimum. Rapid reductions in water flow from hydropeaking have been associated with adverse effects on the Atlantic salmon population since the 1980s due to stranding and mortality of juveniles (Hvidsten, 1985). The study site in the Nidelva where effects of hydropeaking on parr were considered was a 700 m long river meander (Figure 2a). This area consists of a

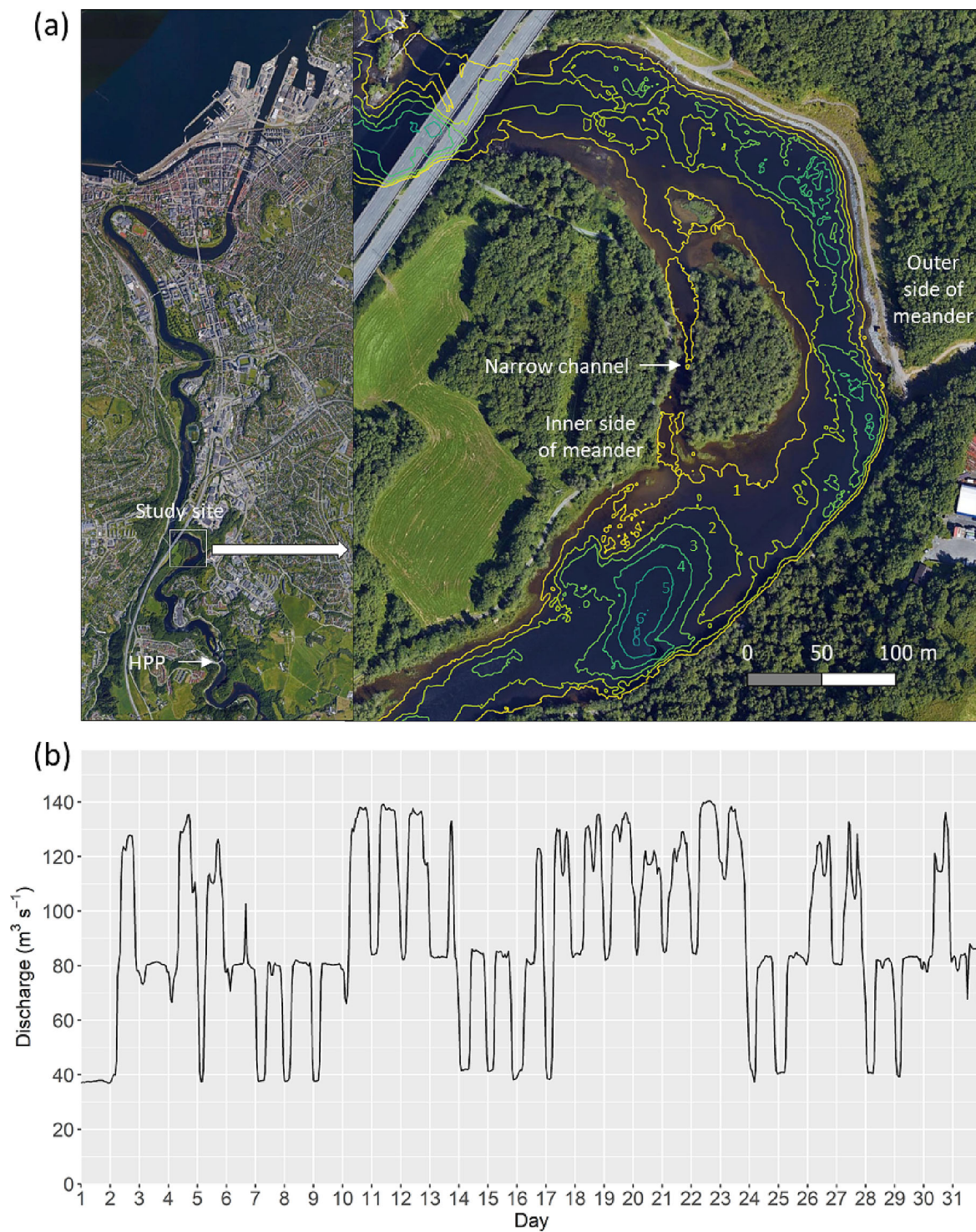


FIGURE 2 The River Nidelva: (a) study site and (b) measured discharge downstream of Nedre Leirfoss HPP during a month when hydropeaking was applied (January 2018). In (a), contours show depths at a 1 m interval from the hydrodynamic simulation at discharge $Q = 135 \text{ m}^3 \text{ s}^{-1}$.

meander containing pool, glide and run mesohabitats (see Borsányi, 2006) and is characterized by predominantly gravel-pebble substrates. Current speeds and depths are faster towards the deeper outer side of the meander than on the shallower inner side. Parts of the channel on the inner side of the meander, and particularly in parts

of a narrow channel that intersects the meander, are often dewatered during the minimum flow period after down-ramping. The study site has relatively high densities of Atlantic salmon parr and has been used for previous empirical studies of hydropeaking-induced stranding mortality (Saltveit et al., 2001).

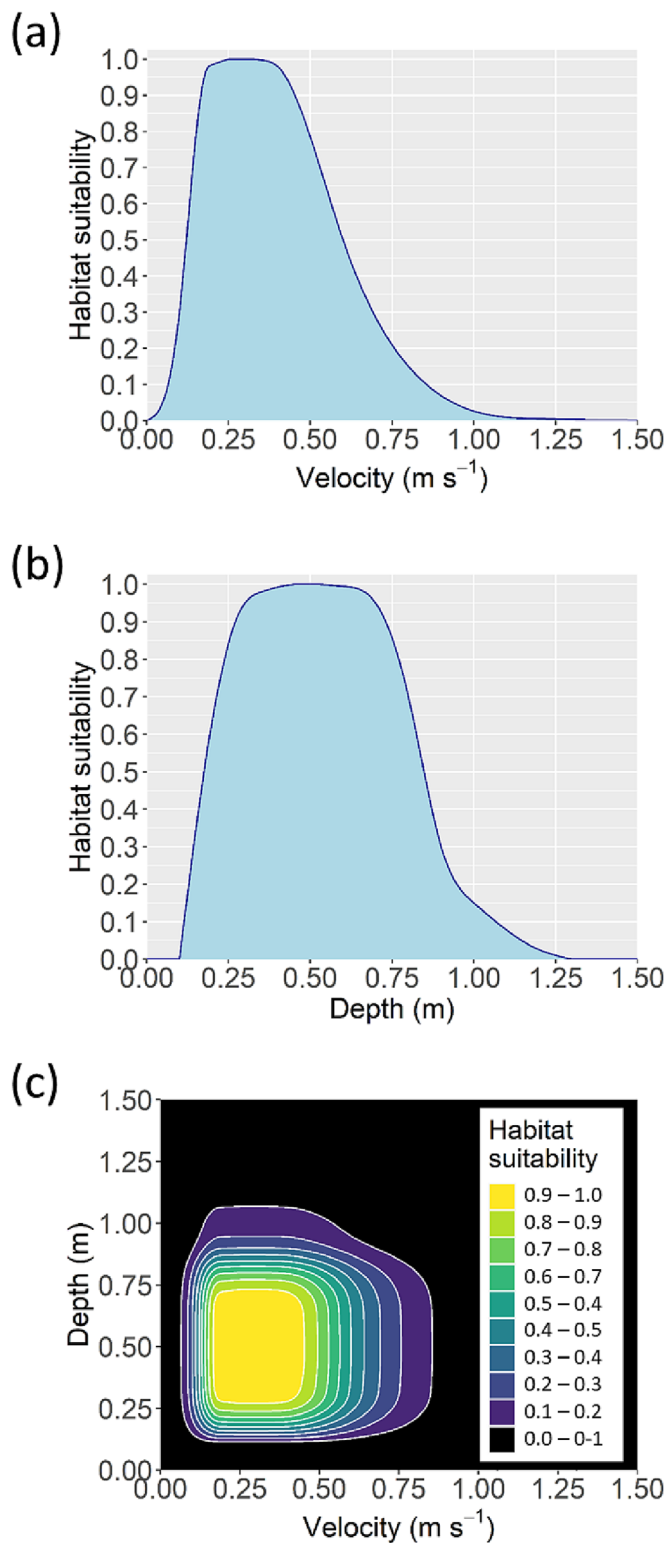


FIGURE 3 Habitat suitability relationships for Atlantic salmon parr: (a) velocity, (b) depth and (c) velocity and depth combined

Hydraulic conditions at a range of discharges throughout the reach downstream of Nedre Leirfoss HPP were predicted using hydrodynamic modelling. Velocity and depth were simulated across a finite-difference grid (cell size = 0.5×0.5 m) using the

hydrodynamic model HEC-RAS 5.0.7 (Brunner, 2016) and upscaled to the 1×1 m resolution of the IBM. The hydrodynamic model bathymetry grid was derived from remote sensing and survey data including LiDAR, Acoustic Doppler Current Profiler surveys and RTK-GPS measurements. The hydrodynamic model was calibrated by adjusting the Manning roughness coefficient and validated using 42 RTK-GPS water level measurements taken at discharges $Q = 85 \text{ m}^3 \text{ s}^{-1}$ and $Q = 97 \text{ m}^3 \text{ s}^{-1}$. Steady state conditions were achieved at 15 discharges (at $5 \text{ m}^3 \text{ s}^{-1}$ intervals between 30 and 85 and at 100, 115 and $135 \text{ m}^3 \text{ s}^{-1}$). A discharge of $135 \text{ m}^3 \text{ s}^{-1}$ corresponded to the maximum permitted within the salmon-supporting watercourse plus the full production in the hydropower plant, at which the river was bankfull; $30 \text{ m}^3 \text{ s}^{-1}$ corresponded to that occurring at minimum flow after down-ramping. Habitat suitability for supporting Atlantic salmon parr in each 1×1 m cell was then determined using a habitat suitability curve-based approach, based on velocity and depth as predicted by the hydrodynamic model for each discharge. Available Atlantic salmon survey data within the Nidelva were too sparse and too restricted in range of environmental properties to establish habitat suitability relationships specific to the Nidelva, so we relied on curves for velocity and depth habitat suitability that were based on those found by Heggenes and Saltveit (1990) (see Figure 3a,b). The final habitat suitability per cell, used to control the distribution of parr, was calculated as the product of velocity and depth habitat suitabilities (Figure 3c). This ranged between zero (the cell was completely unsuitable for parr) to one (the cell had maximum suitability for parr).

2.3 | Simulations

Given that IBMs that incorporate a stochastic element can generate different results for the same set of model conditions, each simulation was run three times, and the mean of the three outputs was used for further analyses. Simulations were initiated with a burn-in period, which allowed the parr to distribute themselves according to the habitat suitability spatial distribution found at maximum discharge, followed by the implementation of ramping scenarios.

2.3.1 | Burn-in period

All simulations were initiated with a period (length = 1 day) where discharge was set at a maximum ($Q = 135 \text{ m}^3 \text{ s}^{-1}$). Simulations were initialized with 3,000 parr individuals, randomly assigned to locations within the study site that had a habitat suitability of ≥ 0.9 . This gave an approximate initial density of 1.1 parr m^{-2} , which is consistent with the maximum parr density observed for this location in an electrofishing survey (1.4 m^{-2} ; see Arnekleiv et al., 2013). During this period, parr individuals moved location based on the routines for (1) migration to more suitable habitat and (2) migration away from conspecifics.

TABLE 1 Model parameters of baseline simulation and sensitivity analysis simulations

Parameter	Symbol	Baseline value	Values used in sensitivity analysis
Ramping speed ($\Delta m^3 s^{-1}$)	R	6	3.0, 3.6, 4.2, ... 9.0
Duration of minimum flow period (h)	D	4	2.0, 2.4, 2.8, ... 6.0
Locus movement speed ($m 10 \text{ min}^{-1}$)	L	1.0	0.5, 0.6, 0.7, ... 1.5
Territory diameter (m)	T	1.0	0.5, 0.6, 0.7, ... 1.5
Stranding mortality probability (for a 4 h dewatering event)	M_{4h}	0.5	0.25, 0.30, 0.35, ... 0.75

2.3.2 | Ramping

Ramping scenarios were defined so that discharge ranged between a maximum ($Q = 135 \text{ m}^3 \text{ s}^{-1}$) and a minimum ($Q = 30 \text{ m}^3 \text{ s}^{-1}$) once per day. Down-ramping was initiated at the beginning of the day (time = 00:00 h) and proceeded with a constant speed (ramping speed, $\Delta m^3 \text{ s}^{-1}$) until the minimum discharge was reached. This was followed by a period of minimum flow, before up-ramping at an equivalent speed to that used during down-ramping until maximum discharge was reached.

Two sets of simulations were run: (1) a baseline simulation, parameterized using a ramping regime typical of that found in the river and parameter values of parr movement and stranding mortality probability that were representative of those found in reality, and (2) a quantitative sensitivity analysis, conducted both locally (addressing sensitivity to pairs of variables together) and globally (addressing sensitivity to all variables simultaneously). Total stranding mortality (% of the initial population) was used to assess effects of simulation parameters.

The baseline simulation was run with a ramping speed and duration of the minimum flow period corresponding to a typical hydropeaking cycle within the Nidelva (ramping speed = $6 \Delta m^3 10 \text{ min}^{-1}$, minimum flow period duration = 4 h; Table 1). Baseline values for parr characteristics—locus movement speed, territory size and stranding mortality probability—were based on the literature. The baseline locus movement speed ($1 \text{ m } 10 \text{ min}^{-1}$) was chosen so that it approximated movements identified by Scruton et al. (2003), who found that during a down-ramping time of 2 h, there was a mean movement distance of 14 m, which would correspond to a movement speed of $\approx 1.2 \text{ m } 10 \text{ min}^{-1}$. The baseline territory size (diameter) was set to 1 m. Under this, two conspecifics near to one another would move to a distance of separation of 1 m (or for each individual, a radius of 0.5 m). Assuming a circular territorial range around the individual, this would give a territory area of $\approx 0.78 \text{ m}^2$, which approximated that found in the literature for parr. For example, Steingrímsson and Grant (2011) found modal territory sizes of 0.5–1.0 m^2 , and Venter et al. (2008) found median territory sizes of between ≈ 0.4 and 1.4 m^2 in young-of-the-year parr. Detailed, controlled studies of mortality from stranding are not available. A field study by Saltveit et al. (2001) conducted in the Nidelva presented stranding mortality results from two down-ramping events (expressed as the proportion of those stranded found dead) of ≈ 25 and 75%. An experimental study by Puffer et al. (2017) found a

low mortality from stranding in summer: a total of 13 individuals identified as dead out of an initial 60 ($\approx 20\%$ mortality) after two beaching events. Based on these estimated mortalities, a baseline mortality probability of 50% ($M_{4h} = 0.5$) was established, representing an approximate mid-point among their observed range.

The sensitivity analysis was used to examine the effect of ramping regime (ramping speed and duration of the minimum flow period) and parr characteristics (locus movement speed, territory size and stranding mortality probability). In the sensitivity analyses, parameter values were altered around the baseline value by 10% intervals from -50% to 50% . Local sensitivity analyses were first conducted exploring combinations of ramping regime properties and parr characteristics. A global sensitivity analysis, examining the relative influence of all parameters together, was then conducted using beta regression (using the `betareg` function of the `betareg` package in R). The effect of the parameters—ramping speed, duration of minimum flow period, locus movement speed, territory size and stranding mortality probability—on the total stranding mortality was assessed additively.

3 | RESULTS

3.1 | Simulation of river hydrodynamics and habitat suitability

The hydrodynamic model simulated flows during hydropeaking that were consistent with those measured: simulated and measured water levels were highly correlated ($r^2 = 0.99$), and there was only a 3% difference between simulated and measured water-covered area (see Alfredsen et al., 2022). Water-covered area and water velocity and depth predicted by the hydrodynamic model greatly differed between maximum ($135 \text{ m}^3 \text{ s}^{-1}$; Figure 4a) and minimum ($30 \text{ m}^3 \text{ s}^{-1}$; Figure 4b) discharges. At minimum discharge, $\approx 15\%$ of the study site channel was dewatered relative to that at maximum discharge, particularly on the gentle slope on the inner side of the channel, and in the narrow channel that intersected the meander. Velocities and depths were lower across the study site at the minimum discharge. The spatial distribution of habitat suitability changed in concordance with the change in velocities and depths. During maximum discharge, optimal habitat was predicted to be situated around the banks on the inner side of the meander, resulting from the inner side having relatively low velocities and depths. Conditions towards the mid-channel were

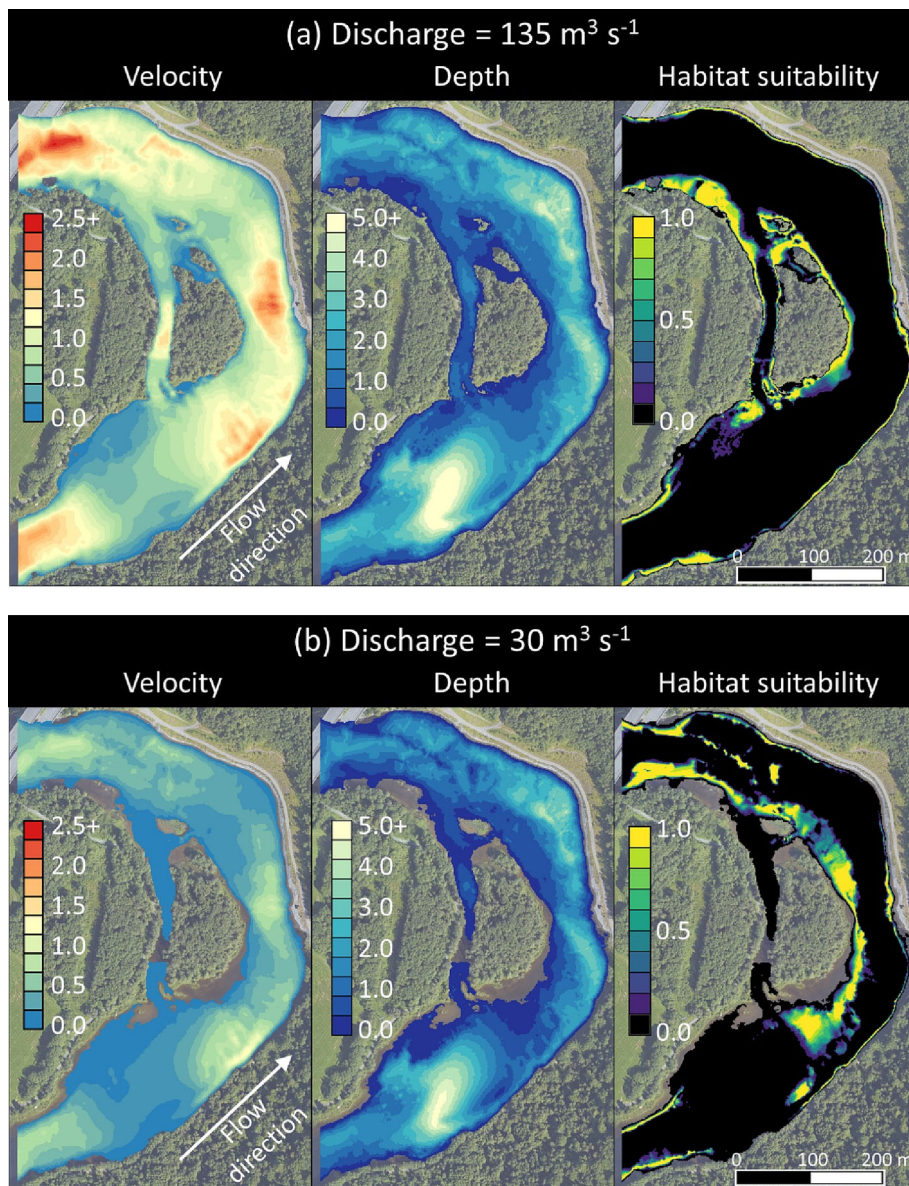


FIGURE 4 Predicted velocity, depth and parr habitat suitability during (a) maximum discharge ($Q = 135 \text{ m}^3 \text{ s}^{-1}$) and (b) minimum discharge ($Q = 30 \text{ m}^3 \text{ s}^{-1}$)

sub-optimal due to them having high velocities and depths. During minimum discharge, optimal habitat was more distributed towards the middle of the channel where velocities and depths had fallen towards those preferred by the parr, and areas around the banks that were previously optimal habitat were now either dewatered or suboptimal due to having very low velocities and depths. These conditions represented the extremes experienced during the hydropeaking cycle used to model parr responses to hydropeaking.

3.2 | Parr responses to hydropeaking

3.2.1 | Baseline simulation

Parr changed their spatial distribution in response to the change in the spatial distribution of habitat suitability throughout the hydropeaking cycle. Prior to the initiation of down-ramping, parr were

distributed in small patches along the channel banks in areas of high habitat suitability where velocity and depth were relatively low ($0.2\text{--}0.5 \text{ m}$ and $0.25\text{--}0.75 \text{ m s}^{-1}$, respectively). They were particularly prevalent on the inner side of the meander (Figure 5a). On down-ramping, the most suitable habitat moved out into the mid-channel (Figure 5b). Velocities and depths near the banks were too low, whereas those in the mid-channel were closer to those more suitable for parr, so they consequently migrated away from the channel banks towards the mid-channel. Throughout the minimum flow period, parr continued to migrate towards the mid-channel, leading to their distribution being more centred to the mid-channel by the time that up-ramping was initiated (Figure 5c). During up-ramping, the location of suitable habitat moved back towards the channel banks, and there was a subsequent return of parr towards the banks by the start of the maximum flow period. By the end of the hydropeaking cycle, the distribution of parr was similar to that at the initiation of the cycle (Figure 5d). Most parr migrated during the hydropeaking cycle: during

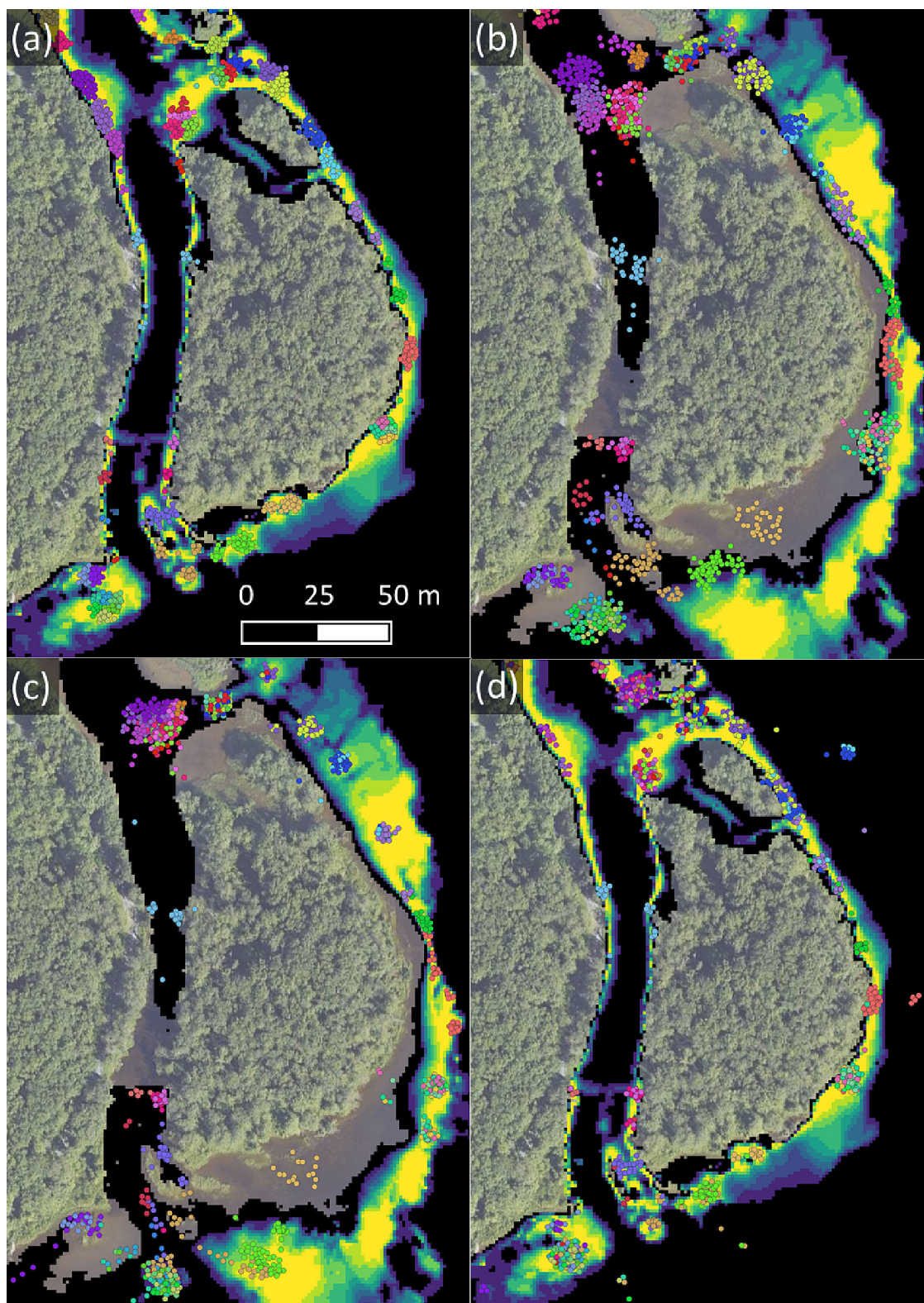


FIGURE 5 Spatial distribution of parr during a single hydropeaking cycle: (a) initial distribution (time-step = 1); (b) distribution at termination of down-ramping (time-step = 19); (c) distribution at initiation of up-ramping (time-step = 41); (d) distribution after up-ramping (time-step = 144). Filled circles show parr positions (colours have been randomly assigned to clusters and remain constant in all panels). Background colours indicate habitat suitability, following the same colour scheme as in Figure 4, with the habitat suitability shown being that calculated for the discharge of the respective part of the hydropeaking cycle.

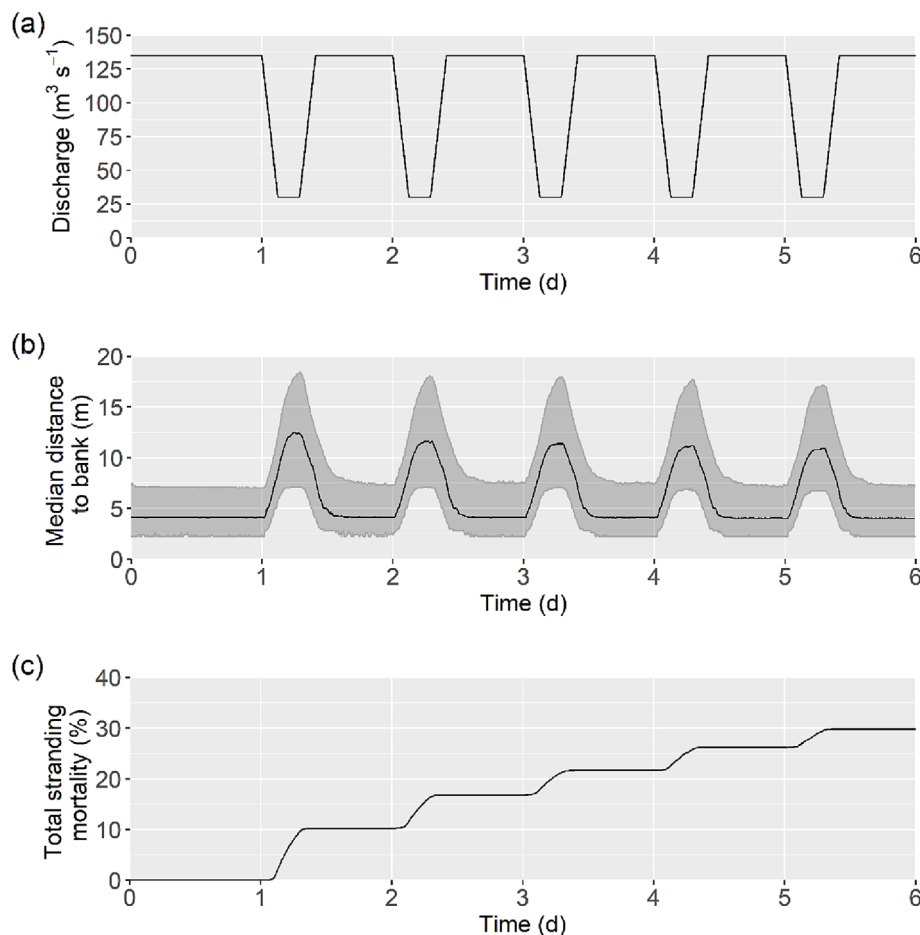


FIGURE 6 Discharge (a), median distance to bank of non-stranded parr (b) and total stranding mortality (c) during hydropeaking in the baseline simulation. In (b), distance to the bank is calculated as the Euclidean distance between the individual and closest bank (depth = 0 m); the median distance is shown by the solid line, and the interquartile range is covered by the shaded area.

down-ramping and up-ramping phases, when parr were redistributing themselves towards the changing pattern of optimal habitat, a median of 85% of non-stranded parr were moving towards optimal habitat during each time-step of the simulation. The non-stranded parr that did not migrate on a given time-step happened to be in optimal habitat relative to their neighbourhood.

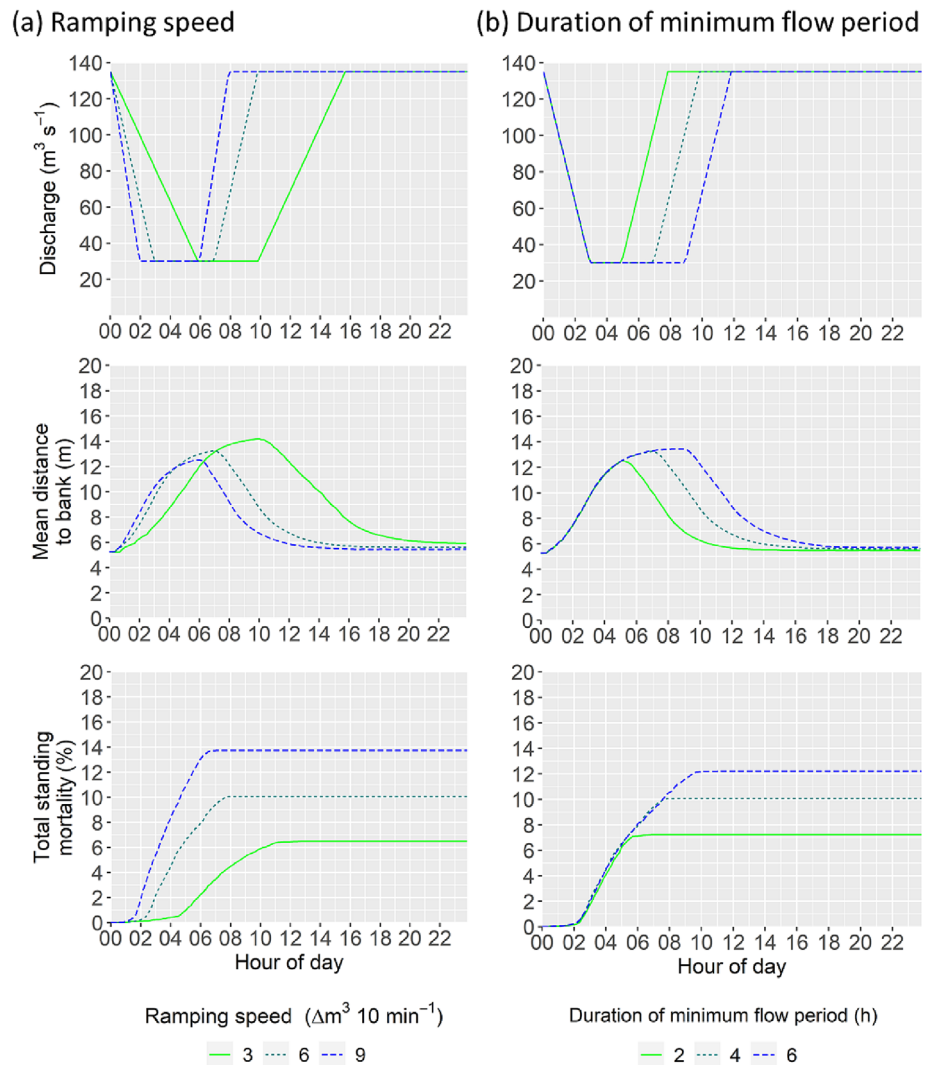
The temporal pattern of discharge across the hydropeaking cycle (Figure 6a) controlled the pattern of parr distances to the banks (Figure 6b) and parr mortality (Figure 6c). Individual distances to the bank ranged between 1 and 39 m, but parr moved an average of ≈ 7 –8 m further away from the banks towards the mid-channel on down-ramping, before returning towards the banks on up-ramping (Figure 6b). The distribution became more dispersed during down-ramping and the minimum flow periods: 50% of parr were found from ≈ 2.5 –7.5 m before down-ramping but from ≈ 7.5 –18.5 m immediately before initiation of the up-ramping cycle. This resulted from the change in distribution of optimal habitat (which was very constrained at the riverbank before down-ramping and occurred over a larger area at minimum flow) and the redistribution of parr to new areas of optimal habitat. Parr that became stranded in dewatered areas were subject to stranding mortality (Figure 6c). This stranding mortality occurred predominantly on the down-ramping phase and minimum flow period of the hydropeaking cycle, although some occurred in the initial part of the up-ramping phase before dewatered areas had

become water-covered again. Approximately 10% of existing parr died in each hydropeaking cycle. Given that this percentage remained constant and that the number of parr remaining at the beginning of a hydropeaking cycle declined with number of preceding cycles, the absolute number dying in each cycle declined with each successive cycle.

3.2.2 | Sensitivity to ramping regime

Movement patterns and total stranding mortality were strongly dependent on ramping regime (Figure 7). Increasing the ramping speed (Figure 7a) from $\Delta 3$ to $\Delta 9 \text{ m}^3 \text{ 10 min}^{-1}$ caused a sharper and earlier change in discharge, which reduced the mean distances parr moved away from the banks after down-ramping from 14 to 12.5 m, and caused an earlier return towards the banks on up-ramping. High ramping speeds resulted in rapid dewatering around the banks so more parr became stranded ($\approx 14\%$ mortality for a $\Delta 9 \text{ m}^3 \text{ 10 min}^{-1}$ ramping speed). Low ramping speeds allowed a greater proportion of the parr population to migrate towards suitable habitat in the mid-channel by the beginning of the minimum flow period; this, in turn, resulted in a reduction in stranding mortality ($\approx 6.5\%$ mortality for a $\Delta 3 \text{ m}^3 \text{ 10 min}^{-1}$ ramping speed). Increasing the duration of the minimum flow period (Figure 7b) from 2 to 6 h

FIGURE 7 Discharge, mean distance to bank of non-stranded parr and total stranding mortality during a single hydropeaking cycle for (a) different ramping speeds and (b) different durations of the minimum flow period



caused an increase in the distances parr moved from the bank from a mean of 12.5 m to a mean of 13.5 m and an extended, 4 h increased in the period of movements towards the mid-channel, before parr began to return to the bank. Long minimum flow periods allowed a greater proportion of the population to reach the optimal habitat that was situated mid-channel during the minimum flow period. This, however, also extended the period over which stranding mortality was applied for those individuals that had been unable to move away from dewatered locations, resulting in an increase in total mortality ($\approx 7\%$ and $\approx 12\%$ for minimum flow durations of 2 and 6 h, respectively). Total stranding mortality was greatest with ramping regimes that included both a high ramping speed and a long duration of the minimum flow period (Figure 8): Total stranding mortality was 17.0% with the highest ramping speed and longest duration of the minimum flow period, over three times greater than with the lowest ramping speed and shortest duration (stranding mortality = 5.3%). Of these two parameters, ramping speed had slightly greater effect: For example, total stranding mortality varied from 5.3% to 9.8% over the range of ramping speeds tested for the shortest minimum flow duration, whereas it only

varied from 5.3% to 7.5% over the range of minimum flow durations tested for the slowest ramping speed.

3.2.3 | Sensitivity to parr characteristics

Total stranding mortality declined with an increase in locus movement speed and increased with an increase in territory size and stranding mortality probability (Figure 9). The decline in total stranding mortality with an increase in locus movement speed was caused by parr being better able to migrate away from areas that were becoming dewatered to optimal habitat situated towards the mid-channel on down-ramping. The increase in total stranding mortality with an increase in territory size was caused by a greater territory size leading to an increase in the spread of individuals, such that some were in very shallow areas, very close to the bank, that were more prone to rapid dewatering. As expected, total stranding mortality increased with the probability of a stranded individual dying per unit time. Among the pairwise interactions, total stranding mortality was greatest when high territory sizes were combined with

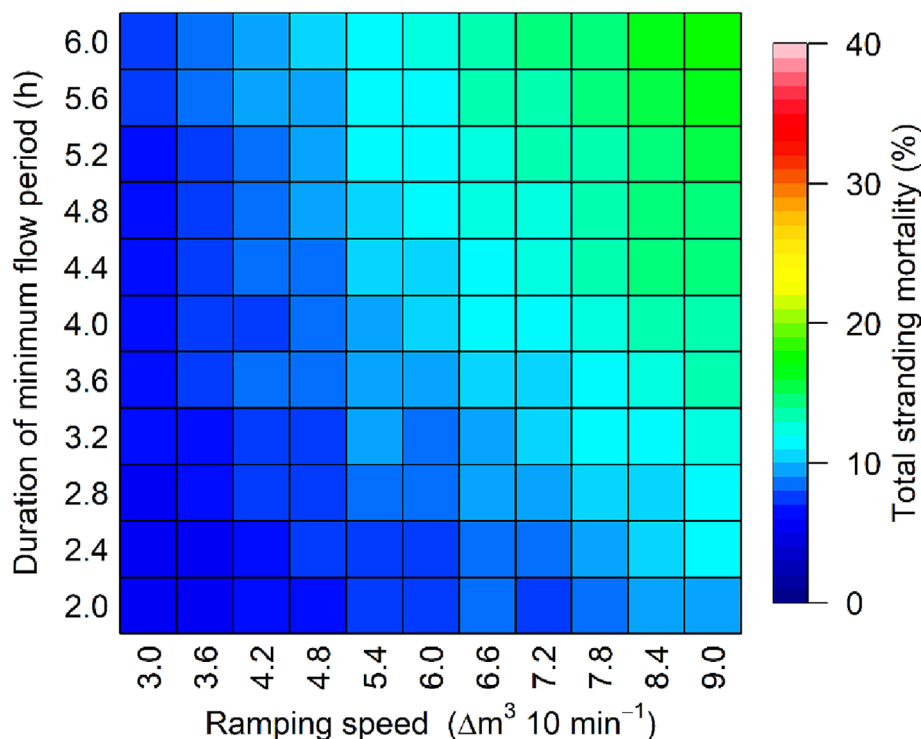


FIGURE 8 Effect of ramping speed and duration of minimum flow period on total stranding mortality after a single hydropeaking cycle (24 h after initiation)

low locus movement speeds (maximum total stranding mortality = 23.9%, Figure 9a), when high stranding mortality probability was combined with low locus movement speed (maximum total stranding mortality = 32.6%, Figure 9b), and when high stranding mortality was combined with high territory size (maximum total stranding mortality = 17.0%, Figure 9c).

3.2.4 | Interaction between ramping regime and parr characteristics

Total stranding mortality was strongly dependent on the interaction between the ramping regime and parr characteristics (Figure 10). Within the pairwise interactions involving ramping speed, total stranding mortality increased when high ramping speed was combined with a low locus movement speed (Figure 10a.1), a large territory size (Figure 10a.2) and a high stranding mortality probability (Figure 10a.3). Within the pairwise interactions involving duration of the minimum flow period, total stranding mortality increased when a long duration was combined with a low locus movement speed (Figure 10b.1), a high territory size (Figure 10b.2) and a high stranding mortality probability (Figure 10b.3). Overall, greatest mortalities were found when fast ramping speeds or long durations of the minimum flow period were concurrent with low locus movement speeds. When considering the additive effect of all parameters together, locus movement speed had the strongest effect on total stranding mortality, followed by (in descending order) stranding mortality probability, ramping speed, territory size and duration of the minimum flow period (Table 2). A 1% increase in locus movement speed increased the “odds” of the stranding mortality ($\hat{p}/(1-\hat{p})$) by a factor of 0.9819

(i.e., a relative reduction of -1.81%), whereas a 1% increase in duration of the minimum flow period increased the odds by a factor of 1.0051 (i.e., a relative increase of 0.51%).

4 | DISCUSSION

Total stranding mortality was dependent on the form of the hydropeaking cycle, the behaviour of the parr (locus movement speed and territory size) and the stranding mortality probability. As expected, total stranding mortality increased with ramping speed and duration of the minimum flow period: increases in ramping speed led to more individuals becoming stranded in dewatered areas where they were subject to stranding mortality; increases in duration of the minimum flow period led to longer periods of stranding and therefore increased mortality of stranded individuals. Stranding mortality declined with an increase in locus movement speed (more individuals escaped stranding in dewatered areas) but increased with an increase in territory size (dispersion of individuals from conspecifics caused more to be present in areas that were subsequently dewatered). Finally, total stranding mortality was (as expected) dependent on stranding mortality probability—the probability that a stranded individual would die per unit of time. The locus movement speed, however, had strongest effect on total stranding mortality. In the following, we discuss the implications of these findings for predicting effects of hydropeaking on parr. We begin by discussing model development issues, we then explore key findings of the research and, finally, we discuss these issues within the context of both current research on stranding mortality and programmes to ensure environmentally acceptable hydropeaking regimes.

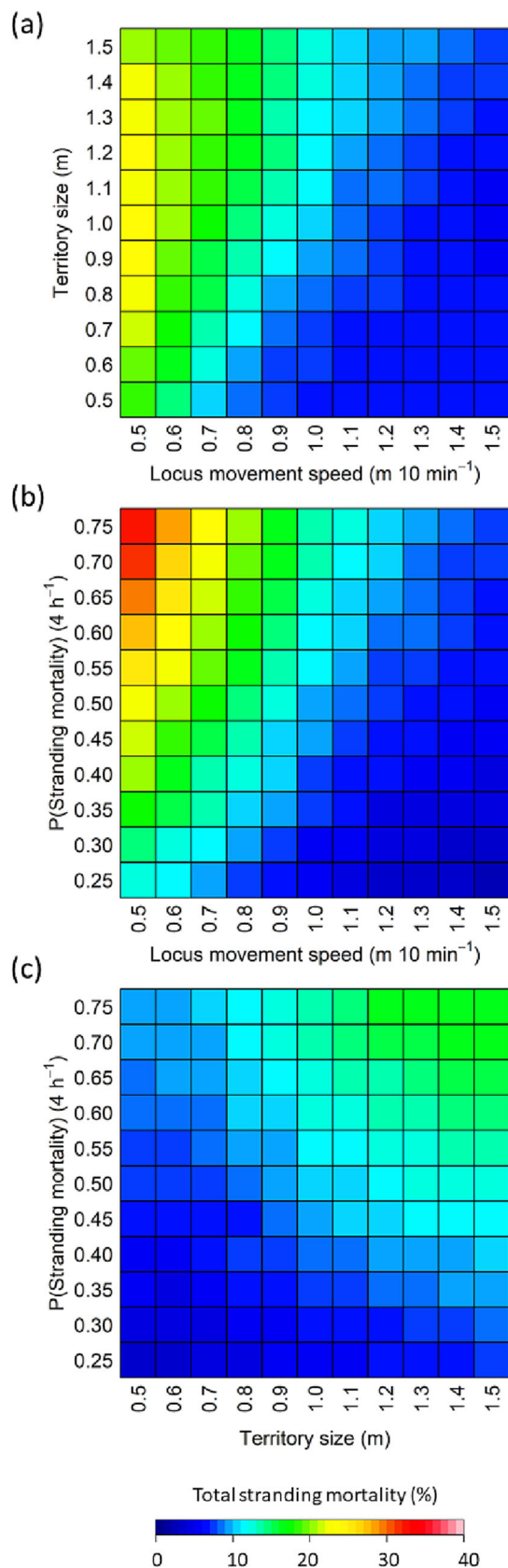


FIGURE 9 Effect of locus movement speed, territory size and stranding mortality probability on total stranding mortality after a single hydropeaking cycle (24 h after initiation). Pairwise combinations: locus movement speed and territory size (a), locus movement speed and stranding mortality probability (b) and territory size and stranding mortality probability (c).

4.1 | Model development

Results are dependent on how the model was developed. In the following, we consider how the model setup with regard to (1) model boundary conditions, (2) model formulation and (3) model parameterization may affect the reliability of model predictions.

4.1.1 | Model boundary conditions

The main driver for parr migration and total stranding mortality was the change in hydraulic properties during the hydropeaking cycle. While the hydraulic model provided a realistic simulation of river hydraulics under steady-state conditions, the simulation of dewatering and re-watering during the down- and up-ramping phases of the hydropeaking cycle used by the IBM was a simplification of that which would be found in reality. Water levels within the simulation declined or ascended at the same rate regardless of location, whereas in reality, a river's water level changes as a wave that perturbs downstream of the power plant, resulting in both an increasing lag and a decreasing rate of change with distance downstream (Burman et al., 2021). However, given the shortness of the stretch that was studied, and the proximity of this stretch to the HPP, we consider that modelling water fluctuations based on steady-state simulations would be an acceptable approximation of a full wave simulation.

4.1.2 | Model formulation

The IBM was developed to allow for analysis of the relative effects of ramping regime and fish characteristics (locus movement speed, territory size and stranding mortality probability) on the total stranding mortality of parr, and in the interest of parsimony, model development was constrained to only include processes that were considered to be most pertinent to simulate this. Mortality was only applied to individuals that were within dewatered cells, and we did not consider adverse effects from stress (see Flodmark et al., 2002) experienced by individuals in adverse conditions (such as very shallow water), which might impact them, either directly in single down-ramping events, or over the long term. Additionally, biological properties were not parameterized to vary among individuals, so there was no individual variation in terms of habitat suitability, locus movement speed, territory size or stranding mortality probability. While variation among conspecifics always exists in reality, it was not considered necessary to include this to determine system sensitivity to, for example, ramping

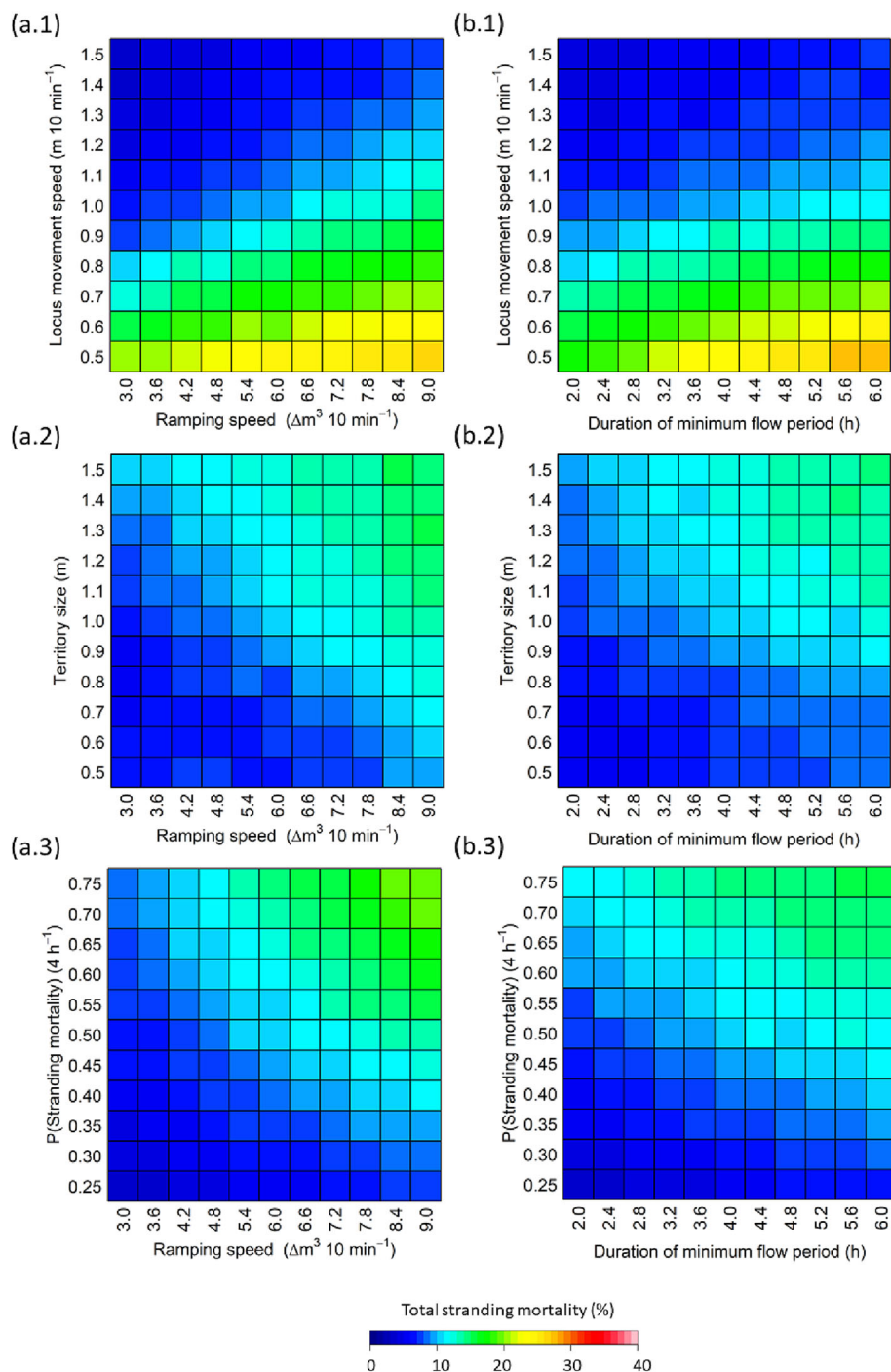


FIGURE 10 Effect of ramping regime (ramping speed and duration of minimum flow) and parr characteristics (locus movement speed, territory size and stranding mortality probability) on total stranding mortality after a single hydropeaking cycle (24 h after initiation). Pairwise combinations: ramping speed and locus movement speed (a.1), territory size (a.2) and stranding mortality probability (a.3); duration of the minimum flow period and locus movement speed (b.1), territory size (b.2) and stranding mortality probability (b.3)

regimes. The three model routines that were used to examine impacts on total stranding mortality—migration to suitable habitat, migration away from nearby conspecifics and the mortality probability from a stranding event—were formulated based as much as possible on phenomena identified in past research. Dispersion among conspecifics and stranding mortality are established phenomena, so the functions developed for the model are strongly grounded in reality. The routine for migration to more suitable habitat, as a means of governing how parr respond to rapid changes in water flow, is less well supported by empirical research. This manifested within the model by parr migrating

away from bank-side areas that were becoming very slow flowing and shallow on down-ramping and returning to these areas on up-ramping. A variety of alternative approaches could be used: For example, the parr response could be to the rate of change in habitat conditions in their location, acting as a warning to the individual that “something is wrong” and that it needs to look for a refuge. Additionally, where parr move to may depend upon flow direction, rather than just flow velocity and depth. The habitat suitability curve approach used here, based solely on velocity and depth, did however generate a spatial distribution that was biologically feasible (individuals clustered in fairly

TABLE 2 Relationship between total stranding mortality (proportion of population) and percentage change from baseline value for ramping speed, duration of the minimum flow period, locus movement speed, territory size and stranding mortality probability as derived through a beta regression model.

Parameter	Estimate	Std. error	z value	p	Exp (estimate)
(Intercept)	-2.2054	0.0032118	-686.647	<0.001	0.1102
Ramping speed	0.0073	0.0001518	48.3061	<0.001	1.0074
Duration of minimum flow period	0.0050	0.0001519	33.1695	<0.001	1.0051
Locus movement speed	-0.0183	0.0001505	-121.4081	<0.001	0.9819
Territory size	0.0061	0.0001519	40.3142	<0.001	1.0061
Stranding mortality probability	0.0098	0.0001516	64.5911	<0.001	1.0098

slow, shallow waters around the bank during high-flow conditions). This study has shown that it is possible for the fish to change location in response to hydropeaking in such a way that mortality is reduced, where the *only* causative link between the fish and the hydraulics is the fish moving to more suitable habitat within its immediate neighbourhood: That is, it is not necessary for there to be a more complex response to temporal changes in hydraulics experienced by the fish for them to act. Finally, movements were only modelled with regard to migration to suitable habitat and avoidance of conspecifics. Movements away from dewatered areas at low flows in this part of the Nidelva have been observed by Berland et al. (2004), consistent with the current study, but they also observed larger-scale movements of parr, over a distance in the order of ≈ 1 km over a 2 week period. Migration patterns in the current study were therefore somewhat simplified in comparison to reality.

Basing the habitat suitability model solely on hydraulic properties (velocity and depth) and ignoring other controls on fish distribution such as substrate size is a potential weakness. Substrate size, which is a known element of Atlantic salmon parr habitat (see Armstrong et al., 2003), was not included within the habitat suitability model as this has not been quantitatively mapped throughout the Nidelva. However, inspection of the study site has shown the prevalence of suitable substrate types (gravel, pebbles and cobbles) for supporting salmon juveniles. The high flows and moderate gradients at the study site suggest that this is not an area where the bed material will be dominated by deposited unsuitable sandy substrates. Given this, it is possible that hydraulic properties, rather than substrate types, are the limiting conditions for the availability of suitable habitat in the study site.

4.1.3 | Model parameterization

The selection of baseline values for function parameters was based on findings within the literature. Migration away from nearby conspecifics was parameterized best because of the relatively large amount of quantitative data on territoriality in salmonids. Producing a reliable estimate for locus movement speed was more difficult. Typical swimming speeds of Atlantic salmon parr are ≈ 0.5 m s⁻¹ (Peake et al., 1997), so all parr should be able to swim out of stranding zones

during down-ramping. The fact that stranding mortality is found in salmon parr proves that not all move out of zones that are subject to dewatering and that there is some preference to holding position even when hydraulics change. The baseline locus movements speed was therefore parameterized so that it corresponded to that established in a field experiment (Scruton et al., 2003), but there is much less certainty in the selection of this parameter than in the determination of territory size. Selection of a baseline mortality for stranded individuals was also difficult due to the lack of field studies quantifying this. We relied on results of Saltveit et al. (2001) and Puffer et al. (2017), but these studies did not look at mortality under a range of stranding conditions, so our parameterization of stranding mortality in the baseline simulation was not particularly robust. The sensitivity analysis extended the values of model parameters considered to $\pm 50\%$, so examined ramping speeds and minimum flow durations, which were realistic for typical hydropeaking regimes. Properties such as the locus movement speed, defining how quickly a fish moves away from a holding area, are much less certain, however.

4.2 | The controls on stranding mortality

Controls on stranding mortality will be specific to the characteristics of the river channel. For the river stretch modelled in the current study, a gentle gradient on the inner side of the meander meant that the amount of the channel that was dewatered on down-ramping was relatively large, and the movement speed of the boundary between the dewatered and water-covered area was relatively fast. Thus, stranding mortality was high. A stretch with a more “U”-shaped profile could potentially have less stranding mortality if the down-ramping only occurs within the limbs of the “U” shape. Under these circumstances, the area dewatered, and the speed at which the dewatered/water-covered boundary moves will be relatively low, leading to a lower stranding mortality. This will impact on the findings of a sensitivity analysis. For instance, if there is minimal distance between optimal habitat areas during high-flow conditions and water-covered areas during low-flow conditions, the importance of locus movement speed will be reduced.

Controls on total stranding mortality will also depend on how quickly the fish swim, how territorial they are, how prone they are to

mortality and their preferences for different habitat characteristics (defined in the model by habitat suitability). All of these variables will be population specific and will vary according to age and activity status. The current study suggests that older and more mobile parr will be less prone to stranding mortality (other factors being equal), something that is consistent with observations in the Nidelva that the 0+ age group has been particularly affected relative to older age groups (Arnekleiv et al., 1994). The habitat suitability curve used in the current study was based on findings in a Norwegian Atlantic salmon population and is broadly consistent with other reported Atlantic salmon parr habitat suitability indices: See, for example, Dunbar et al. (2002), Guay et al. (2000) and Heggenes et al. (1995). Suitability was parameterized to be highest for relatively shallow and slow flowing waters—areas that were near the bank during high discharges—so parr were prone to being stuck in dewatered areas, near the bank, on down-ramping. The habitat suitability approach as used here has come under some criticism, however, because the distribution of fish may be affected by the spatial distribution of habitat over large scales (see Railsback, 2016). Parr may also be found in deeper water, nearer to the mid channel, and such parr would be less prone to mortality on down-ramping.

The relative strength of the controls on stranding mortality identified in this study is therefore specific to the ranges of the properties investigated—whether related to characteristics of the channel or those of the population. Our findings, based on simulations calibrated for the Nidelva, do not necessarily apply to those in other specific hydropeaked rivers. Thus, for a robust estimate of how hydropeaking impacts on stranding mortality, field work to define the specific characteristics of the watercourse and the population under investigation needs to be conducted.

4.3 | Use of dynamic modelling in future research and management

Many studies have been conducted on stranding mortality associated with hydropeaking, but most have been descriptive and few have used controlled conditions. Studies on movement patterns in hydropeaked rivers exist, but these have mainly only documented aggregate effects on changes in the overall spatial distribution of fish in response to hydropeaking, rather than quantifying distances and directions of individual fish movement. Information on movements can be derived in a variety of ways including camera observation for examining movements in bulk, or PIT tagging (Johnston et al., 2009) for examining individual movements, but there is a lack of research using these methods to assess hydropeaking effects in rivers. To the authors' knowledge, no studies have quantified how stranding mortality is dependent on the length of dewatering. Given the sensitivity of total stranding mortality to biological parameters, more research in this area is required. Studies under more controlled conditions can be supplemented with the type of agent-based modelling used here. The advantage of this approach is that it allows the modelling of the interaction of controls on total stranding mortality.

Information from this dynamic modelling approach can also be used to improve management of the watercourse, such as establishing trade-offs between operational objectives of the HPP managers and environmental objectives with regard to sustaining fish populations. For example, this study suggests that parr mortality is less susceptible to the duration of the minimum flow period than the down-ramping speed. If equivalent or more power could be generated by increasing the minimum flow period rather than the down-ramping speed, the former would therefore be advisable as a “win” for both power-production and fish population sustainability. This ability to examine effects of the hydropeaking cycle is particularly important for predicting the outcomes of new technology (for instance, ACUR technology which reduces the down-ramping speed) before its implementation in the HPP.

5 | CONCLUSION

We have shown that the potential effect of hydropeaking-induced stranding mortality in Atlantic salmon parr is strongly dependent on how the parr react to flow changes during the hydropeaking cycle. Stranding mortality may be strongly reduced if the fish migrate, even over short distances, away from the dewatered zone to deeper parts of the channel. Total stranding mortality is also dependent on interactions among conspecifics (dependent on territory size) and the likelihood of mortality per unit time when stranded. For the conditions analysed in this study, total stranding mortality was more sensitive to characteristics of the parr than to the duration of the minimum flow period. Detailed, quantitative research on how fish respond to rapid changes in flow during hydropeaking are sparse, with most studies reporting aggregate population effects in uncontrolled conditions. However, fish responses will depend on a range of factors such as fish species, age and activity status, so generalizing from individual studies may not provide robust models. Given the increasing emphasis now given on implementing hydropeaking regimes that minimize adverse effects on fish populations, we suggest that more research is required focusing on biological responses. This would allow for evaluation of potential hydropeaking regimes within the context of the characteristics of the affected fish population. Field-based or laboratory-based studies are essential for this. However, simulation-based modelling, in which there is a 100% control of and knowledge of fish characteristics, in which a range of deterministic functions can be evaluated and in which boundary conditions such as bathymetry and flow characteristics can be easily controlled, may be a useful research tool to complement such studies.

SIGNIFICANCE STATEMENT

River flow fluctuations associated with hydropeaking cause stranding mortality in fishes. Investigation of stranding mortality through field studies, however, typically provides little information on the way in which fish respond to flow variations, and findings may have limited

generalizability. Here, we use an individual-based modelling approach to examine sensitivities to the parameters controlling stranding mortality, both those of the hydropeaking regime—ramping speed and duration of the minimum flow period—and those of the fish biology—movement speed, territory size and probability of mortality on stranding. This approach may be used in the planning of new hydropeaking regimes, and as an exploratory tool for identifying the relative influence of parameters, allowing the focusing of further field studies.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in GitHub (at <https://github.com/HedgerNINA/SalStrand-IBM>).

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