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RESEARCH ARTICLE

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Adaptive responses of freshwater pearl mussels, *Margaritifera margaritifera*, to managed drawdowns

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Abstract

1. Alterations to water management practices, in response to a growing demand to maximize energy production from renewable sources, threaten to exacerbate anticipated future water shortages caused by severe drought episodes, brought on by climate change.
2. Across Scotland, many highly managed systems are inhabited by some of the last remaining reproductively viable populations of the freshwater pearl mussel, *Margaritifera margaritifera*. A lack of empirical evidence concerning mussel responses to alterations in flow is inhibiting the development of effective conservation management practices to prolonged drought.
3. This study addressed this knowledge gap by examining the response of *M. margaritifera* to controlled water level drawdowns in laboratory and field settings. Using a laboratory flume, the responses of *M. margaritifera* from two different populations (a regulated system versus an unregulated system) were compared across rates of drawdown and density treatments. An analogous field trial was undertaken to examine the responses of *M. margaritifera* in a regulated system, with a hydroelectric dam facilitating a controlled drawdown.
4. The study showed that *M. margaritifera* can detect alterations in flow depth, which culminate in the emersion of mussel beds, and respond by undertaking vertical and horizontal movements to mitigate the risk of prolonged aerial exposure. Results from the field trial corroborated findings from the flume experiments, with 80% of mussels shown to avoid emersion successfully by tracking receding water levels.
5. Findings from this study support the role of controlled drawdowns in regulated rivers to reduce mortalities associated with receding water levels during prolonged low-flow episodes. Differences between populations in response highlight a need to adopt a context-dependent approach to conservation efforts.

KEYWORDS
behaviour, conservation, dams, drought, freshwater mussels, movement

1 | INTRODUCTION

The freshwater pearl mussel, *Margaritifera margaritifera*, is one of the most threatened and widely researched unionid species (Bauer & Wachtler, 2001; Arvidsson, Karlsson & Österling, 2012; Cosgrove et al., 2016), with evidence to suggest that it fulfils the criteria for an indicator, flagship, umbrella, and keystone species (Geist, 2010). Studies examining the ecology of *M. margaritifera* are likely to be important to the conservation of oligotrophic stream ecosystems (Boon et al., 2019) and are applicable to wider conservation efforts concerning unionid species.

In the European Union populations of this rare, long-lived freshwater bivalve are protected by the European Habitats Directive (Ziuganov et al., 1994; Geist, 2010), which provides for safeguarding of the species via designated Special Areas of Conservation (Council of the European Communities, 1992), and yet declines across populations persist (Geist, 2010; Cosgrove et al., 2016; Lopes-Lima et al., 2016).

Scotland remains one of the last strongholds for the species, with river systems in the Scottish Highlands continuing to support large reproductively viable populations (Cosgrove et al., 2016), defined by their ability to be self-sustainable without requiring the addition of new genetic material originating from outside the system (British Standards Institution, 2017). Many of these important populations inhabit regulated rivers, managed for hydroelectric energy production. Attempts to address the causes of decline and implement long-term conservation strategies for freshwater mussels have frequently highlighted the importance of hydrological management schemes (Layzer & Madison, 1995; Gosselin, 2015; Araujo & Álvarez-Cobelas, 2016; Geist, 2021).

The regulation of rivers for hydroelectricity has been attributed as the cause of substantial losses to populations of unionid mussels globally (Campbell & Hilderbrand, 2017; Wegscheider et al., 2019; von Proschwitz & Wengström, 2020), with studies often referring to the fragmentation of populations caused by the inhibition of the migration of their host species (during the parasitic phase of the life cycle), together with altered river flow, sediment, and temperature regimes as key threats to freshwater mussels emanating from the presence of impoundments (Winemiller et al., 2016; Araujo et al., 2018; Modesto et al., 2018; Ferreira-Rodríguez et al., 2019).

In Scotland, water environment regulations apply regulatory controls on the environmental flow practices in regulated rivers to minimize the potential impact of impoundments on the ecology of associated ecosystems (Scottish Environment Protection Agency, 2018). These regulations define a constant minimum discharge value, termed compensation flow, for impoundments, with operations often exceeding such values but never allowed to drop below this minimum. However, recent drought conditions have led to negotiations between hydroelectric dam operators and government agencies on greater flexibility in reducing the statutory minimum compensation flow during extended low run-off conditions. Despite this, there are concerns that this may not be sufficient to mitigate the impacts of more severe droughts anticipated in future climate scenarios. A key component of the desire to uphold the minimum discharge values concerns the potential aerial exposure of *M. margaritifera* and subsequent population mortality under drought conditions.

From a conservation perspective, it is important to understand how species such as *M. margaritifera* respond to more extreme flow events. Desiccation, resulting from low flow discharge, represents a clear threat to efforts to maintain and improve the population health of mussel species such as *M. margaritifera* (Hastie, Boon & Young, 2000; Hardison & Layzer, 2001; Hauer, 2015; Randklev et al., 2018; Sousa et al., 2018; Lymbery et al., 2020). Within Scotland, more frequent periods of low summer discharge are anticipated as a result of extended episodes of low precipitation, in addition to lower levels of groundwater, with extreme drought events expected to increase from 1:20 years to 1:3 years (Cosgrove et al., 2021; Kirkpatrick, Partridge & Spray, 2021). Regulated systems are not exempt from the threats of extreme flow events, with one element of their management being the need to ensure that their operation assists in providing ecological resilience to the increased incidence of floods and droughts resulting from climate change, while also meeting operational requirements (Schneider et al., 2013; Sundt-Hansen et al., 2018). However, without the empirical evidence to inform how *M. margaritifera* responds to alterations in managed flows, the effects of changes in dam operation are unknown.

Despite the frequency with which impoundments are attributed as potential inhibitors of successful *M. margaritifera* conservation in the literature, few studies have examined the effects of dams on freshwater mussels (Sousa et al., 2020). Those that have undertook observational studies using correlative approaches to discern the potential factors governing the spatial variation and abundance of populations, accounting for the presence and proximity of impoundments (Addy, Cooksley & Sime, 2012; Sousa et al., 2020), with no direct examination of *M. margaritifera* responses to alterations in flow characteristics resulting from dam operation.

The current conservation management of *M. margaritifera* is grounded in the principle that individuals are sedentary, and hence unable to use the surrounding environment to adapt to changes in flow. There is a growing body of evidence, however, to suggest that mussels do respond to alterations in environmental characteristics: mussels exhibit movement seasonally for reproductive purposes (Amyot & Downing, 1997), and in response to alterations in the hydrological environment (Johnson & Brown, 2000; Bartsch et al., 2010; Block, Gerald & Levine, 2013; French & Ackerman, 2014; Clements, 2015; Hamstead et al., 2019), with suggestions that burrowing may also assist in the avoidance of *Dreissena polymorpha* (zebra mussel) infestation (Burlakova & Karatayev, 2007). There is a need, therefore, to investigate whether such responses are also displayed by *M. margaritifera*, with potential repercussions for conservation management strategies.

Recent studies observing the response of other freshwater mussel species inhabiting drought-prone systems have provided evidence to suggest that individuals adopt behavioural strategies to avoid or mitigate the effects of emersion by tracking receding water levels (horizontal movement) or burrowing (vertical movement) further into the river-bed substratum (Gough, Gascho Landis & Stoeckel, 2012; Lymbery et al., 2020). Similar research has also been conducted within regulated systems to examine the response of two freshwater mussel species (*Amblema plicata* and *Lampsilis cardium*) to controlled drawdowns (Newton, Zigler & Gray, 2015), yielding similar results; however, such studies are yet to determine whether these responses are population specific.

The extent to which individuals prioritize the expression of particular behavioural traits is thought to vary between conspecifics and across populations, presenting potential variation in response depending on the physiology of the individual and the environment that they inhabit (Allen & Vaughn, 2009; Dingemanse et al., 2009; Gough, Gascho Landis & Stoeckel, 2012; Daniel & Brown, 2014). The magnitude of a stressor is also likely to influence the response of individuals, with Newton, Zigler & Gray (2015) postulating that larger movements by freshwater mussels are prompted by greater levels of stress. However, no known study has assessed whether the rate at which emersion occurs effects the response of freshwater mussels. Thus, any research concerning the response of freshwater mussels to alterations in flow regime must account for variation across individuals and populations, as well as variation in the rate of drawdown.

The purpose of this study was to investigate the responses of *M. margaritifera* to alterations in flow depth that risk emersion. The work aimed to provide empirical evidence to inform the mitigation of the effects of hydropower operational regimes, in addition to impacts from climate change, on populations in regulated systems. To do so, this study used field and laboratory approaches to test the following four hypotheses: (i) *M. margaritifera* shows a behavioural response to receding water levels (drawdown) in the form of horizontal and vertical movements; (ii) the movement of mussels shows a quantitative response to different rates of drawdown; (iii) the movement of mussels in response to drawdown varies across populations inhabiting regulated and unregulated systems; and (iv) the movement of mussels in response to drawdown varies with proximity to conspecifics.

2 | MATERIALS AND METHODS

2.1 | Flume study

Laboratory based experiments (Figure 1) were designed to compare the behavioural responses of individuals from two different populations (regulated and unregulated) to reductions in flow depth that incur partial aerial exposure of the gravel bed.

2.1.1 | Mussel collection

Margaritifera margaritifera mussels were collected, under licence (100197), in the summer of 2017 from a disused mill lade, hydrologically connected to the main channel of the River South Esk, Scotland. This unregulated system presented relatively homogeneous flow regimes, less turbulent than those experienced in the main channel. However, regular alterations in flow depth were expected, and desiccation of the remaining population occurred in the summer of 2019. (See Table S2 for annual flow discharge recordings for the River South Esk.)

A group of *M. margaritifera* mussels were collected, under licence (141417), in the summer of 2019 from the River Lyon, Scotland, which is a regulated system controlled by two hydroelectric dams situated approximately 6 km apart (Figure 2). The collections were from habitat located approximately 19 km downstream from the nearest impoundment in the main channel of the river, which experienced heterogeneous turbulent flow regimes. The River Lyon is a 391-km^2 headwater catchment of the River Tay, the largest river in Scotland, and comprises one of the most intensely regulated catchments in the UK (Geris et al., 2015). (See Table S1 for annual flow discharge recordings for the River Lyon.)

Adult mussels were removed by hand and stored in aerated cool boxes, lined with substrate and filled with water from the corresponding system. Collected individuals were held in two tanks (one for each population) at the Scottish Centre for Ecology and the Natural Environment (SCENE). Each tank contained washed gravel (0.1–25 mm) to a depth of 100 mm, fed with water from Loch Lomond at ambient temperature, 14 °C ± 4.2 (annual mean temperature ± SD), to a depth of 200 mm, and with a flow rate to mimic the conditions of the respective habitats. Each mussel was marked on the shell using correction fluid and given a unique identification number, and then weighed and measured for shell length, width, and height.

2.1.2 | Experimental set-up

Experiments were conducted in a controlled, recirculating flume system, with a viewing chamber (Figure 1a) located at SCENE. The 0.6-m wide channel supports flows of 0.4 m in depth at a maximum flow rate of 0.2 m s^{-1}. Flow is controlled by an adjustable electrical propeller. The system was fed with untreated water from Loch Lomond. Flow velocity was kept constant (0.1 m s^{-1}). The water input rate was maintained at 0.001 m^3 s^{-1} (Figure 1a). The water temperature reflected the ambient levels observed in the loch.

A step-gradient foundation, perpendicular to the flow direction, was formed using cement blocks (Figure 1b). Layers of water-worked fine gravel (median = 20 mm) covered the cement blocks to a minimum depth of 100 mm, providing conditions often highlighted as favourable for burrowing by unionid mussels (Hastie, Boon & Young, 2000; Geist & Auerswald, 2007). The structure (0.6 × 0.27 × 6.2 m) comprised two sections of flat river bed (0.08 × 6.2 m), defined as the upper and lower plateau, separated by a 33° slope (0.44 × 6.2 m). An acoustic doppler velocimeter probe (ADV Vectrino II; Nortek AS, Rud, Norway) recorded flow profiles across the artificial bed to identify a test section (1.4 m × 0.6 m) downstream from the inception of the artificial bed, where hydraulically rough, turbulent flow was fully developed at the point of shell placement (Figure 1a). Two high-speed commercial video

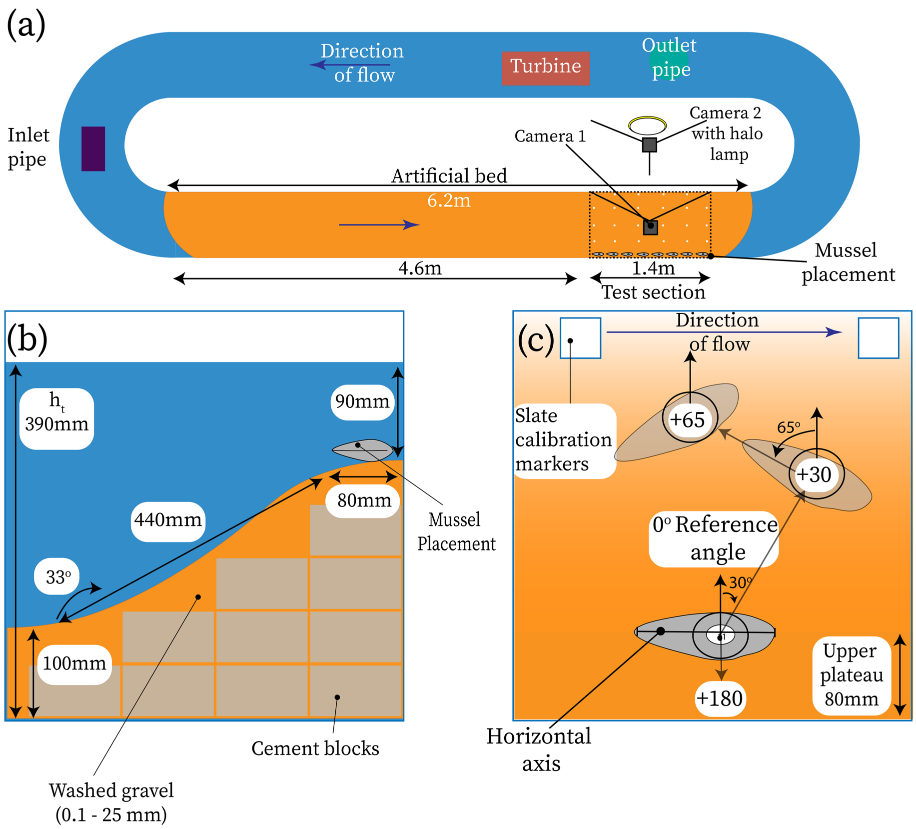

FIGURE 1 (a) Flume experiment set-up, highlighting the location of the test section. (b) Cross section of the artificial river bed. (c) View from above the test section, as seen in images captured by camera 1, providing an overview of the method used to determine the direction of mussel movement. The direction of movement was defined as a positive angular displacement from the reference direction (0° reference angle), based on the individual's orientation at the beginning of the trial: perpendicular to the horizontal axis of a mussel, pointing down the gradient of the river bed

cameras operating at 60 frames per second (GoPro Hero 8 Black; Gopro Inc., San Mateo, CA, USA) were positioned at the centre of the experimental area to capture mussel movement (Figure 1a). Square slate pieces (20 mm × 20 mm) were painted white with correction fluid and placed across the experimental test section to aid image calibration (Figure 1c). A halo lamp was placed behind the second camera to provide an ultra-bright light source.

2.1.3 | Experimental overview

Fifty mussels (25 from each population) were randomly selected for the experiment. Each individual mussel was exposed to three different drawdown rates, calculated from an analysis of annual (2018) flow depth in a regulated Scottish river, inhabited by a large functional *M. margaritifera* population: 50 mm h^{-1}(Δy_{50}), 30 mm h^{-1} (Δy_{30}), 15 mm h^{-1} (Δy_{15}) (mean drawdown of a regulated river (150 mm) over 3, 6, and 24 hours, respectively). Two mussel density treatments were tested for each of the three drawdown rates: low density (D1, with individuals placed 140 mm apart) and elevated density (D2, with individuals placed 10 mm apart). An individual experienced six trials, one for each drawdown rate and density treatment combination.

Each trial was conducted on eight mussels simultaneously, with each mussel experiencing the same drawdown rate and density treatment. At the start of a trial, the mussels were placed in a line perpendicular to the flow direction across the elevated plateau of the study site in the predefined density arrangement (Figure 1a). The flow depth (*y*, the distance from the top of the river-bed substrate to the surface of the water) at the plateau was 90 mm (Figure 1b) and circulated at an average velocity of 0.1 m s^{-1} (SD 0.03 m s^{-1}). A trial comprised three sequential experimental periods: (i) a pre-drawdown period, comprising a 2-hour settling period (with constant *y*); (ii) a drawdown period (with *y* reduced by 150 mm at the pre-determined drawdown rate); and (iii) a post-drawdown period of 12 hours (with *y* kept constant at the reduced level). Throughout each trial the flow velocity was kept constant at 0.1 m s^{-1} (SD 0.05 m s^{-1}). The cameras recorded time-lapse footage at 30-s intervals throughout the trial. Following the trial, each mussel was randomly assigned a period of rest ranging from 1 to 8 weeks, before undergoing another trial, to understand how fatigue may affect their responses.

An analysis of the mussel responses to drawdown was undertaken using tracking software, examining when the mussels moved, how far they moved, and in which direction they moved (see section 2.3 for details).

2.2 | Field study

A field experiment was designed to examine whether the results from the flume trials could be replicated within a regulated river system. Here, the behavioural responses of 18 individuals, collected from the corresponding river system, were analysed in response to a reduction in flow depth that incurred a partial aerial exposure of the river bed.

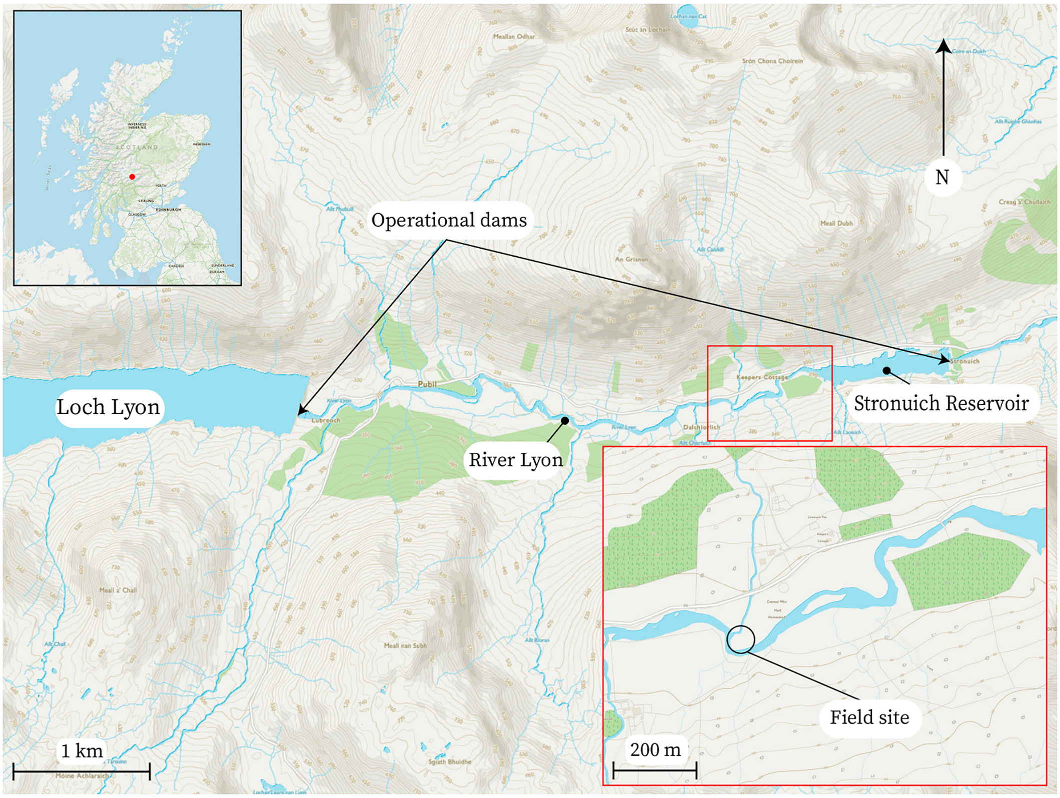

FIGURE 2 A map of the site used in the field study, noting the location of the two operational dams and the location of the field site, with reference to a map of Scotland, and the river reach downstream of Loch Lyon, where mussel movement was examined in relation to a controlled drawdown

The experiment comprised a single trial, using a target drawdown rate of 30 mm h^{-1} (Δy_{30}) and a low-density arrangement. The experiment was undertaken in early November 2020.

2.2.1 | Location

The test site was located approximately 2 km upstream of the impoundment at Stronuich and 4 km downstream of the impoundment at Loch Lyon (Figure 2). The impoundment on Loch Lyon provided adequate control of the hydrodynamics at the test site in the absence of significant catchment effects (for annual flow discharge recordings for the River Lyon, see Table S1). The test site was located on a point bar, comprising a gentle slope of relatively homogeneous gravel (median size = 28 mm), completely submerged during high flow regimes.

2.2.2 | Mussel collection

A sample of 18 *M. margaritifera* mussels were collected, under licence, 22 km downstream of the impoundment at Stronuich, from the main channel of the river. Individuals were marked, using fluorescent pink aquarium-grade spray paint, and given a unique number for identification, and were then weighed and measured for shell length, width, and height. Mussels were placed in mesh plastic crates and positioned in the water at the test site 24 h before the trial.

2.2.3 | Experimental set-up

A scaffold structure was built and placed within the river (Figure 3a). Two high-speed commercial video cameras (GoPro Hero 8 Black) and one halo light were fixed to the structure. A measuring stick was placed on the outer support beam to record alterations in flow depth.

A cool box was attached to the inner support beam and contained two 12V batteries running in parallel connected to an invertor, which powered the cameras and light throughout the experiment. Thin slate squares (20 mm × 20 mm) were painted, using white aquarium-grade spray paint, and placed across the experimental test section to aid image calibration (Figure 3b).

2.2.4 | Experimental overview

The trial was conducted on 18 mussels simultaneously. At the start of the trial a target flow of 16 $m^3 s^{-1}$ was released from the

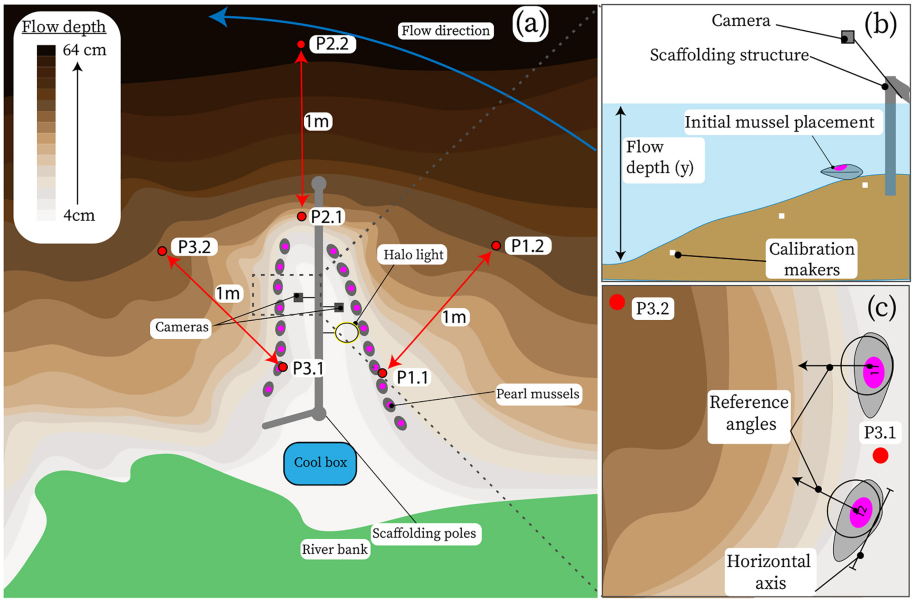

FIGURE 3 (a) Field experiment set-up, highlighting the location of the test site, located on a point bar on the inside bend of a meander, with the locations of the initial mussel placement, scaffold structure, and locations for taking acoustic doppler velocimeter (ADV) measurements: three locations around the scaffold structure (P1.1, P2.1, P3.1) and three corresponding locations at 1 m downgradient (P1.2, P2.2, P3.2). The grey dotted box and grey dotted lines show: (b) the cross section of the ridge; and (c) the overview of the method used to determine the direction of mussel movement, which defined the direction as a positive angular displacement from the reference direction, pointing perpendicular to the mussel's horizontal axis directly down the river-bed slope to the nearest refuge from emersion

impoundment at Loch Lyon, with an average water temperature of 7 °C. Flow depths within a 1 m radius of the scaffold structure were recorded to ascertain the gradient of the slope. Flow profiles were recorded at six locations (Figure 3a) using a handheld acoustic doppler velocimeter probe (Flowtracker 2; Sontek, San Diego, CA, USA) across the test site: at three locations across the ridge where the scaffold structure was located (P1.1, P2.1, P3.1) and at three corresponding locations within 1 m of each point on the ridge that presented the largest recorded flow depths (P1.2, P2.2, P3.2).

Mussels were placed horizontally on the bed at the top of the ridge, facing down the gradient, at either side of the scaffold structure, (y = 120 mm): nine at P11, facing the flow travelling into the meander, and nine at P31, facing the flow travelling away from the meander (Figure 3a). Mussels were subsequently left undisturbed for 3 h during a pre-drawdown period. Following this, three incremental reductions in flow were conducted over 6 h during the drawdown period (y reduced by 200 mm). Flow profiles were recorded at the six locations, 30 min after each incremental reduction in flow, providing four flow profiles at each location. A post-drawdown period was then undertaken, with the final flow regime maintained for a further 8 h after which normal operations at the dam on Loch Lyon resumed.

Again, an analysis of the mussel responses to drawdown was undertaken using tracking software, examining when the mussels moved, how far they moved, and in which direction they moved (see section 2.3 for details).

2.3 | Behavioural analysis

After each trial, video footage stored on the microSD of the camera was downloaded, compiled, and edited using ADOBE PREMIER PRO® (Adobe, San Jose, CA, USA) to remove image distortion and enhance visibility. Image sequences were organized into three groups corresponding to the three sequential experimental periods. Images were imported into FIJI (Schindelin, Arganda-Carreras & Frise, 2012) and analysed using the MTRACKJ plug-in (Meijering, Dzyubachyk & Smal, 2012), where mussel movements were tracked. The following variables were quantified for each individual mussel in a trial: (i) total distance of movement (cm); (ii) average direction of movement from the reference angle (°); (iii) initial response (see below for description); and (iv) final resting position.

The 'direction of movement' pertained to the average angular change of an individual's displacement vector (pointing from the previous point to the present point on an individual's track) relative to a reference coordinate system of the image (with the origin taken as the previous point). Angle values ranged from 180° to 0°, where 0° refers to a movement that runs parallel in the direction of the reference angle, and 180° refers to a movement that runs parallel in the opposite direction of the reference angle (Figure 1c). The reference coordinate system of an image was based on the individual's orientation at the beginning of the trial: perpendicular to the horizontal axis of a mussel, pointing down the gradient of the river bed. For flume trials the reference coordinate system was the same for all individuals in a given trial owing to the homogeneous conditions, with the reference angle running perpendicular to the flow direction (Figure 1c). However, for field studies this varied with individual positioning, yet the reference angle always constituted the shortest linear direction an individual would need to move to arrive at the deepest part of the river bed, within 1 m of the scaffold structure (Figure 3c).

The 'initial response' comprised the categorization of the extent to which a mussel was exposed to air when their first movement was recorded: fully exposed (<10% water contact); partially exposed (10–90% water contact); and fully submerged (>90% shell submerged in water).

The 'final resting position' described the extent of mussel burial in the substrate at the end of the trial, with mussels recorded as having burrowed if they had an angle to the sediment of at least 45° and with sediment covering the shell to the umbo or higher (in accordance with Lymbery et al., 2020). The three categories for final resting position were: (i) fully exposed to the flow and horizontal on the bed (100% shell exposed); (ii) partially buried (20–80% shell exposed); and (iii) completely buried (<20% shell exposed).

2.4 | Statistical analysis

Four statistical approaches were used to examine the successful avoidance of aerial exposure by individual mussels in laboratory conditions. Three statistical approaches were used to examine the successful avoidance of aerial exposure by individual mussels in field conditions. Data analysis was executed in R 3.5.3 (R Core Team, 2020). For details of the statistical approaches used, in addition to the variables explored, see Table S2.

3 | RESULTS

The results from both flume and field trials found that mussels displayed horizontal and vertical movements in response to drawdown events. In all trials, mussels were shown to increase their movements to avoid emersion (Figure 4), with more frequent movements observed during the drawdown and post-drawdown periods compared with the pre-drawdown settlement period (Figure 5). During the flume trials, the use of these movements to successfully avoid emersion varied with respect to the drawdown rate and the population (Table 1). A few individuals repeatedly demonstrated successful emersion avoidance across the six flume trials, with differences observed between populations (Table 2). A comparison between flume and field trials found that successful emersion avoidance was higher in the field trials: 72% of individual mussels successfully tracked receding water levels to avoid prolonged aerial exposure in the field trial, compared with 46% for individuals from the same system experiencing the same density and drawdown conditions in the flume study.

3.1 | Flume data

3.1.1 | Successful avoidance

Initial analysis of the success or failure in avoidance of aerial exposure by individual mussels revealed significant differences across populations and drawdown rates, and no significant effect of density treatment. An examination of differences between populations found contrasting responses to the same drawdown rates, with variation across the three drawdown rates specific to the population (Table 1). For both populations there were no significant differences between the Δh_{15} and Δh_{30} trials, only when comparing these trials with those

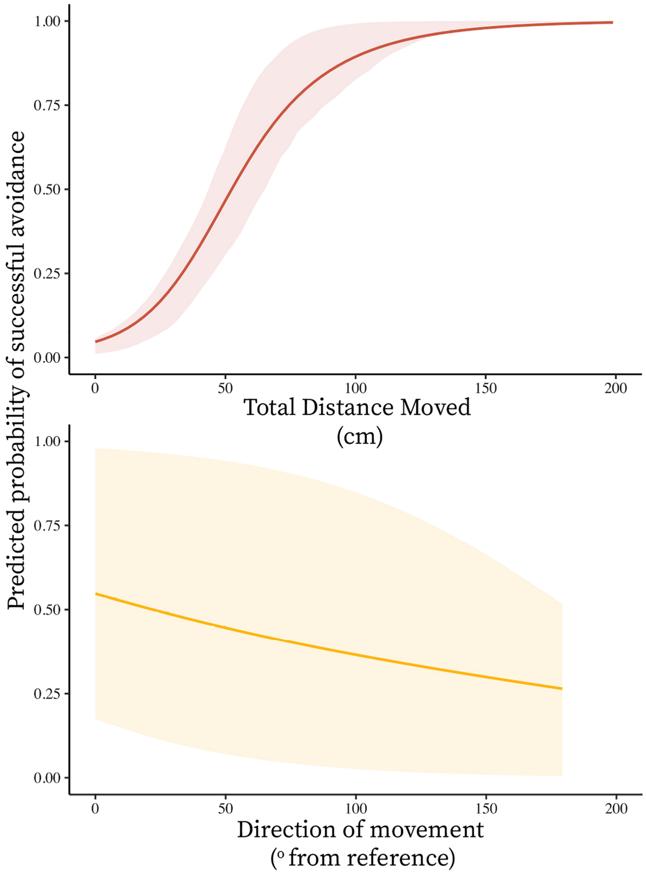

FIGURE 4 The average marginal predicted probability of successful avoidance of emersion associated with alterations in the length and direction of mussel movement, with the upper and lower quartiles displayed

undertaken using a Δy_{50} drawdown rate. The second stage of the analysis, expanding on the initial model with more predictor variables, revealed further variation in avoidance success in response to the total distance of movement, with marginal effects from the direction of movement and initial response. Results from the final optimal model are presented in Table 2.

3.1.2 | Repeatability of avoidance

The proportion of total variance accounted for by differences among individuals was found to be relatively low ($R = 0.221$, $P < 0.05$), with consistent successful avoidance across the three drawdown rates shown to be rare for individuals in both populations (Table 3). However, it appears that consistency in successful avoidance is greater in individuals from the unregulated system (Table 3).

3.1.3 | Presence of movement

Examination of the presence or absence of individual movement revealed differences across drawdown rate, experimental period,

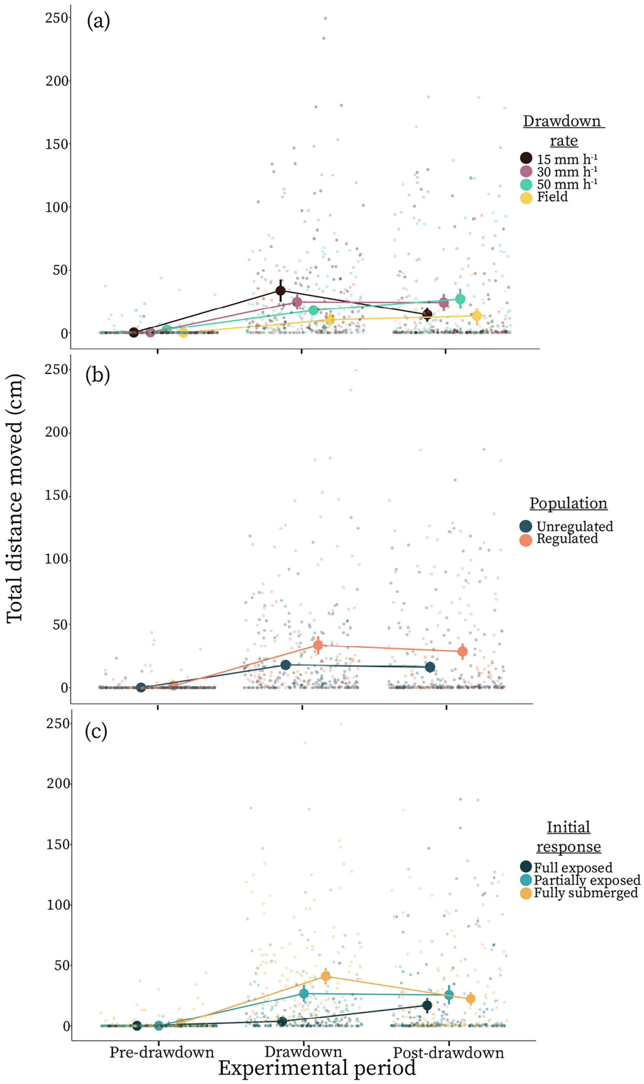

FIGURE 5 Variation in the total distance mussels covered during a trial, accounting for differences across: (a) drawdown rate; (b) population; and (c) the extent to which mussels were emersed when they first displayed movement in a trial. Differences in the distance covered are presented across the three experimental stages of a trial (pre-drawdown, drawdown, post-drawdown). Raw values for each individual are plotted as individual points. The mean total distance (± SE) of all individuals for a given drawdown rate, population, or initial response are presented across the three experimental periods. Lines have been added to connect mean data points and aid visualization, and are not representative of a continuous trend in the data set

group success, population, density, and initial response. The occurrence of movement was significantly higher during and following a drawdown event across all three drawdown rates. Individuals were also found to move more when a greater proportion of individuals in the trial successfully moved down the river-bed gradient to avoid emersion. Comparisons across populations found that during the post-drawdown period, individuals from the regulated system were marginally more likely to display movement than individuals from the

TABLE 1 A comparison of the proportion of individuals that successfully avoided aerial exposure for a given drawdown rate and population

Population	Drawdown rate (mm h^{-1})	Successful avoidance (%)	
		No	Yes
Unregulated	15	57	43
	30	58	42
	50	80	20
Regulated	15	46	54
	30	60	40
	50	42	58

unregulated system following a drawdown event. Movement was significantly more frequent during experiments with mussels placed at an elevated density compared with the low-density treatment. During the drawdown period, mussels that displayed an initial response when fully submerged, or partially exposed, were significantly more likely to move than individuals that displayed their initial response when fully exposed. Results from the final optimal model are presented in Table 4.

3.1.4 | Total distance moved

Examination of the factors determining how far individuals moved revealed differences across experimental period, drawdown rate, population, initial response, and direction of movement. The distance moved by an individual significantly increased during and following a drawdown event across all three drawdown rates (Figure 5). Comparisons across populations (Figure 5) found that individuals from the regulated system moved further than those from the unregulated system during the post-drawdown period. Individuals that initially responded to a drawdown event while partially or fully submerged moved significantly further than those that failed to respond until fully emersed (Figure 5). The distance moved by individuals was significantly larger when the direction of movement was closer to the reference angle for the individual (Figure 6). Results from the final optimal model are presented in Table S3.

3.1.5 | Direction of movement

Examination of the factors determining the direction that individuals moved revealed differences across experimental period, drawdown rate, population, initial response, and lengths of movement. Mussels were found to be more direct in their movements during drawdown events compared with before and after these events across all three drawdown rates (Figure 7). For all mussels, directionality was greatest during trials with a drawdown rate of Δy_{30}. Differences in

TABLE 2 Summary statistics from the optimal binomial mixed-effects model, which sought to define the key variables affecting emersion avoidance by *Margaritifera margaritifera*

Primary response variable	Predictors	Estimate	SE	P
Presence/absence of successful emersion avoidance by individual mussels	(Intercept)	−1.877	0.991	0.058•
	Direction of movement (°)	−0.015	0.008	0.070•
	Distance of movement (cm)	0.085	0.017	<0.001***
	Population (regulated)	−0.270	0.820	0.741
	Drawdown rate (Δy_{30})	−0.139	0.551	0.800
	Drawdown rate (Δy_{50})	−2.425	0.784	0.002*
	Initial response (partially exposed, PE)	1.225	0.704	0.082•
	Initial response (submerged, S)	0.088	0.890	0.921
	Δy_{30}: regulated	−0.646	0.929	0.486
	Δy_{50}: regulated	1.930	1.097	0.078•
	Distance: PE	−0.027	0.015	0.074•
	Distance: S	0.016	0.020	0.414
	Distance: regulated	−0.027	0.015	0.069•

Significance levels: •$P < 0.1$; *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$

TABLE 3 The repeatability of individual mussel avoidance of aerial exposure during laboratory experiments, with comparisons between drawdown rates and across populations. The percentage of individuals that avoided aerial exposure in both (or all) corresponding drawdown rates is shown (% repeated avoidance). Of the individuals that repeated avoidance, the percentage of those that were sampled from a regulated system or unregulated system is given (between populations). Of all the individuals sampled from a population that successfully avoided aerial exposure in at least one experiment with a corresponding drawdown rate, the percentage of those that displayed repeated avoidance is shown (within populations)

Comparison		Between populations		Within populations	
drawdown rates (Δy_A:Δy_B)	% repeated avoidance	% regulated	% unregulated	% regulated	% unregulated
Δy_{50}:Δy_{30}	69	56	44	68	69
Δy_{50}: Δy_{15}	59	70	29	50	79
Δy_{30}: Δy_{15}	64	35	64	68	57
Δy_{15}:Δy_{30}:Δy_{50}	22	40	60	17	38

the directionality of movement between populations were highlighted when comparing drawdown rates, initial responses, and experimental stages. Mussels from the regulated system were more direct in their movements during trials with a drawdown rate of Δy_{50}, compared with mussels from the unregulated system (Figure 7). Comparisons across populations also found that mussels from the regulated system were more direct in their movements during the drawdown period compared with mussels from the unregulated system. Mussels from the regulated system that initially displayed a response when partially submerged were found to be the most direct in their movements, contrasting significantly with their counterparts in the unregulated system (Figure 7). The direction of movement was significantly closer to the reference angle for individuals that moved greater distances during a trial (Figure 6). Results from the final optimal model are presented in Table S4.

3.1.6 | Extent of burial

Examination of the factors determining the position that individuals adopt following a response to drawdown revealed differences across drawdown rates and population, as well as for the total distance and direction of movement ($\chi^2(12) = 177.14$, $P < 0.001$, McFadden $R^2 = 0.23$). Individuals were more likely to burrow completely at drawdown rates of Δh_{30} ($P < 0.05$) and Δh_{50} ($P < 0.01$), compared with Δh_{15}. Individuals from the regulated system were more likely to burrow completely ($P < 0.001$) and were marginally more likely to burrow partially ($P = 0.064$) than individuals from the unregulated system. Individuals that moved greater distances were more likely to burrow partially ($P < 0.001$) and burrow completely ($P < 0.001$) than remain fully exposed to the flow. Individuals that moved in a direction closer to the reference angle were marginally more likely to burrow completely ($P = 0.06$).

TABLE 4 Summary statistics from the optimal binomial mixed-effects model, which sought to define the key variables affecting the presence or absence of movement in *Margaritifera margaritifera*

Primary response variable	Predictors	Estimate	SE	*P*
Presence/absence of movement	(Intercept)	−1.258	0.550	<0.05*
	Population (regulated)	−0.227	0.314	0.450
	Drawdown rate (Δy_{30})	−1.142	0.612	0.062•
	Drawdown rate (Δy_{50})	0.827	0.568	0.147
	Initial response (partially exposed, PE)	0.104	0.363	0.774
	Initial response (submerged, S)	0.261	0.333	0.433
	Density (elevated, D2)	0.672	0.171	<0.001***
	Group success (%, GS)	−2.663	0.992	<0.01**
	Experimental stage (drawdown, D)	5.014	0.699	<0.001***
	Experimental stage (post-drawdown, PD)	3.017	0.500	<0.001***
	Δy_{30}:GS	3.0866	1.113	<0.01**
	Δy_{50}:GS	2.6192	1.089	<0.05*
	D:PE	1.2604	0.533	<0.05*
	D:S	2.7558	0.662	<0.001***
	PD:regulated	0.780	0.411	0.058•

Significance levels: •$P < 0.1$; *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$

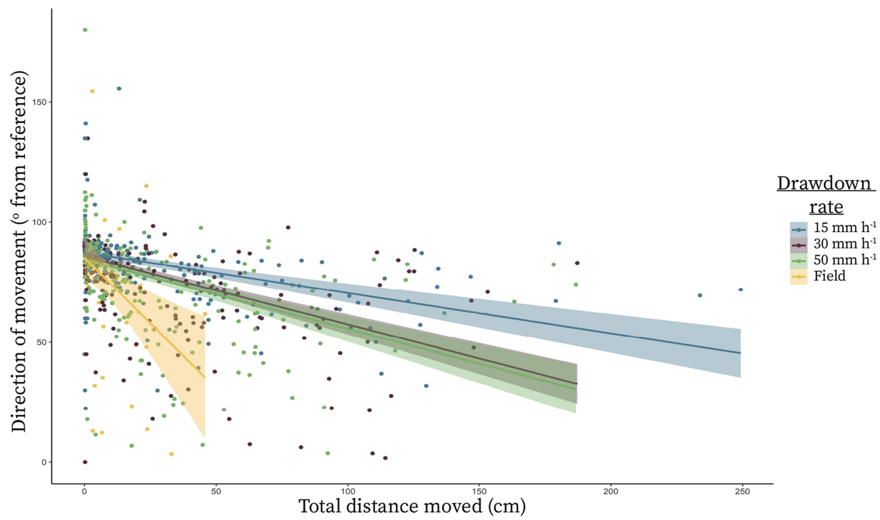

FIGURE 6 Variation in the average direction of movement in association with differences in the total distance covered by individual mussels during a trial, accounting for variation across drawdown rate. Estimates of the conditional mean function for the three drawdown rates used in the flume studies, and the target 3 cm h^{-1} drawdown rate used in the field trial, are presented with corresponding 95% confidence intervals

3.2 | Field data

3.2.1 | Successful avoidance

Analysis revealed variation in avoidance success in response to the length of movement and direction of movement; however, neither variable was found to have a significant effect.

3.2.2 | Presence of movement

Examination of the presence or absence of individual movement revealed differences across experimental period and initial response. The frequency of movement did not significantly alter across experimental periods. Individuals that displayed an initial response when fully submerged were marginally ($P = 0.054$) more likely to

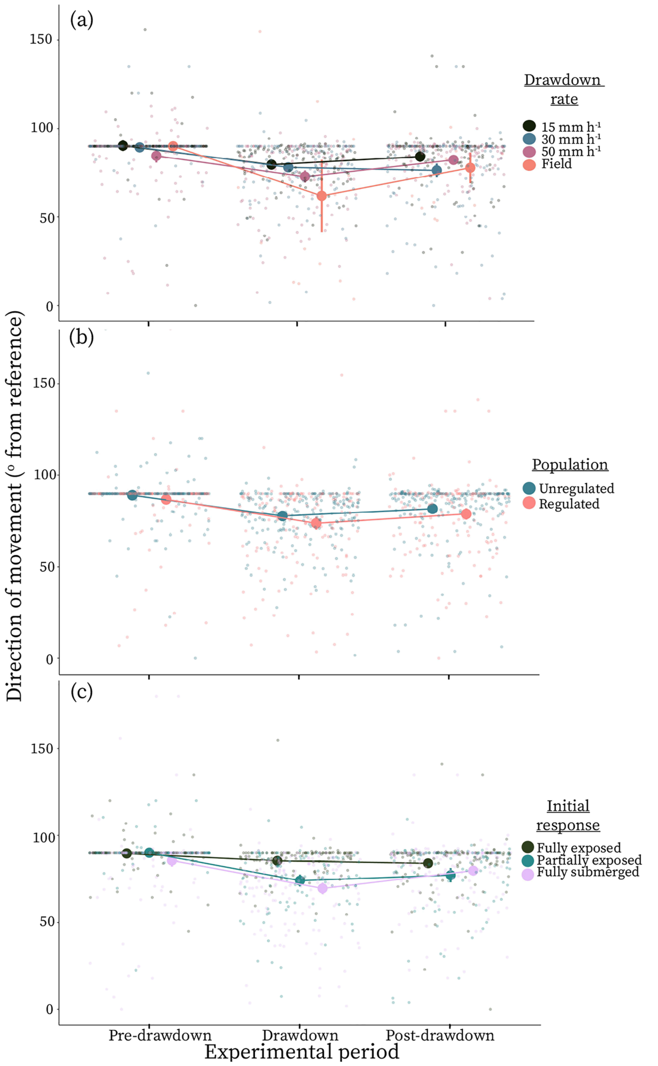

FIGURE 7 Variation in the average direction of movement displayed by individual mussels during a trial, accounting for differences across: (a) drawdown rate; (b) population; and (c) the extent to which mussels were emersed when they first displayed movement in a trial. Differences in average direction of movement are presented across the three experimental stages of the trial (pre-drawdown, drawdown, post-drawdown). Raw values for each individual are plotted as individual points. The mean direction of movement (± SE) of all individuals for a given drawdown rate, population, or initial response are presented across the three experimental periods. Lines have been added to connect mean data points and aid visualization, and are not representative of a continuous trend in the data set

display movement compared with those that responded while partially or fully exposed to the air. No other significant predictors of movement were found.

3.2.3 | Total distance moved

Examination of the factors determining how far individuals moved revealed differences across experimental period, morphology, and direction of movement. Individuals moved significantly further during the drawdown ($P < 0.05$) and post-drawdown ($P < 0.05$) periods, compared with the pre-exposure period. No significant difference in total distance moved was observed between the drawdown and post-drawdown period. Individuals that were larger moved significantly further ($P < 0.05$). Individuals that moved in a direction closer to the reference angle also moved significantly further ($P < 0.05$) (Figure 6). No other significant predictors of how far individuals moved were found.

3.2.4 | Direction of movement

Examination of the factors determining the direction individuals moved revealed differences across morphology, initial response, flow depth differential, and total distance moved. Individuals that displayed an initial response when fully submerged were significantly ($P < 0.05$) more likely to display a direction of movement closer to the reference angle compared with those that responded while partially or fully exposed to the air (Figure 7). Individuals that were larger were marginally ($P = 0.061$) more likely to display a direction of movement closer to the reference angle compared with those that responded while partially or fully exposed to the air. Individuals that were placed in an environment with greater differences in flow depth were significantly ($P < 0.05$) less likely to display a direction of movement closer to the reference angle. Individuals that moved further were significantly ($P < 0.05$) more likely to display a direction of movement closer to the reference angle (Figure 6). No other significant predictors of the direction individuals moved were found.

3.2.5 | Comparisons with flume study

The avoidance success of individuals in the field experiment was significantly higher than the avoidance success of individuals from the same population experiencing the same drawdown rate with the same density arrangement in laboratory experiments ($\chi^2 = 11.077$, $P < 0.001$).

4 | DISCUSSION

The data presented in this article demonstrate, for the first time, the responses of *M. margaritifera* to reductions in water depth that risk emersion, with evidence from both laboratory and field trials. Previous studies have established the potential for freshwater mussel species to identify alterations in the hydrological environment and consequently undertake behavioural responses to mitigate the risk of prolonged aerial exposure (Balfour & Smock, 1995; Gough, Gascho Landis & Stoeckel, 2012; Lymbery et al., 2020). However, these have been consigned to species inhabiting intermittent freshwater systems within arid and semi-arid climates, with no consideration towards species within temperate environments that are likely to experience more extreme hydrological alterations resulting from future climate change. Overall, the results presented here illustrate how *M. margaritifera* displays similar behavioural responses to those of fellow unionid species: exhibiting a propensity to detect reductions in flow and move down a gradient in the river bed to avoid emersion (hypothesis i), which alters in response to modifications to the rate of drawdown (hypothesis ii). The study also revealed substantial intraspecific variation at the population and individual level (hypothesis iii), with differences in the arrangement of individuals (hypothesis iv), with respect to conspecifics and the environmental conditions, also determining the successful avoidance of prolonged aerial exposure.

4.1 | Behavioural responses to emersion

The successful avoidance of emersion by *M. margaritifera* during controlled reductions in water depth was observed in all trials. However, the proportion of mussels that successfully avoided prolonged aerial exposure during trials varied significantly across different rates of drawdown (hypothesis ii). For a given population and drawdown rate, the highest emersion avoidance success rate was 58%, compared with a low value of 20% (Table 1). A key component of this study was to examine the behavioural traits used by *M. margaritifera* in response to reductions in water depth, which may mitigate potentially lethal prolonged aerial exposure, and examine the potential factors that drive variation in successful avoidance across individuals and trials.

The results of this study strongly suggest that horizontal movement is an important behaviour adopted by *M. margaritifera* to track receding water levels and consequently avoid prolonged aerial exposure (hypothesis i). Traditionally, freshwater mussels have been viewed as a relatively sedentary species; however, results from this study and similar research suggest that individuals may move significant distances across the river bed (Schwalb & Pusch, 2007; Negishi et al., 2011; Gough, Gascho Landis & Stoeckel, 2012; Lymbery et al., 2020). In this study, mussels moved significantly more during and after a drawdown event compared with before the drawdown event (Figure 5), suggesting that receding water levels provided a stimulus for movement. Mussels were shown to move up to 3 m during a single trial, conducted over a 24-h period, with evidence from the literature showing that this is not uncommon. For example, over the course of a year *Elliptio complanata* were found to move up to 46.2 m in a small stream (Balfour & Smock, 1995). The results of this study suggest that greater extents of horizontal movement across the river bed confer survival benefits to the respective individuals, with the probability of successful emersion avoidance increasing with an increase in the total distance individuals covered over the course of a trial.

Further examination of the movement patterns showed a divergence from previously held views that the direction of movement exhibited by mussels is predominantly random (Balfour & Smock, 1995; Schwalb & Pusch, 2007). Instead, results from this study indicated that individual movements occur mainly during and following a drawdown event, with individuals often displaying movement that directed them to lower gradients in the river bed over the shortest distances. In addition, the individuals that covered greater distances in their movement were also those that moved in a more direct manner to reach deeper water. Thus, it appears that the successful tracking of receding water levels, by moving down the river-bed gradient in a horizontal motion, following the water's edge, provides a positive stimulus for greater movement. This strong directionality of movement is a result shared by similar studies (Newton, Zigler & Gray, 2015).

The results from this study also identified vertical movement as a common behavioural response to drawdown (hypothesis i). Previous studies have noted this behaviour in other freshwater mussel species in response to drought, conferring greater survival, but it does not appear to be universal to all (Amyot & Downing, 1997; Negishi et al., 2011). Gough, Gascho Landis & Stoeckel (2012) proposed three different behavioural strategies undertaken by three different freshwater mussel species: species with low physiological tolerance to emersion moved horizontally to track receding water levels; species with high physiological tolerance to emersion displayed minimal horizontal movement, and instead burrowed immediately when emersed; and species that are semi-tolerant to emersion tracked water levels and then burrowed. Other studies have yielded results to support this hypothesis (Newton, Zigler & Gray, 2015; Lymbery et al., 2020). Here, *M. margaritifera* were often shown to mimic the responses of a semi-tolerant species, with vertical movement usually displayed by mussels that tracked receding water levels and subsequently avoided emersion.

The tolerance of *M. margaritifera* to desiccation remains largely unknown. The endangered status of the species may have prevented the acquisition of licensing to undertake such work. However, results from this study indicate that brief exposure, of up to 24 hours, elicits some degree of stress in individuals. Mussels afforded more than 2 months rest between trials appeared more likely to respond to emersion by moving than those who had less than a week between trials, but the results could not provide conclusive evidence of this trend. Thus, it appears mussels experienced some degree of fatigue from a drawdown event, with full recovery potentially requiring 4–8 weeks. Curley et al. (2021) reported similar results when inducing aerial exposure in *M. margaritifera*, with observed variation in recovery dependent on the metabolic scope of an individual.

Variation in individual response was prevalent across the trials in this study, epitomized by the significant differences in the initial responses of mussels to drawdown, which appeared to indicate the extent of movement anticipated for an individual in response to receding water levels. Individuals that displayed initial movement while fully or partially submerged were far more likely to respond to a drawdown event and successfully avoid prolonged aerial exposure. The movements displayed by these individuals appeared to increase in response to faster drawdown rates, implying a heightened behavioural response to increased extents of stress – a common observation in studies concerning behavioural responses to stress in freshwater mussel species (Robson et al., 2009; Hasenbein et al., 2015; Hartmann et al., 2016).

Mussels that refrained from movement while fully or partially submerged often displayed no movement throughout the duration of a trial, and instead remained horizontal on the river bed with their valves closed. This behavioural response could assist in sealing in any moisture and avoiding substantial water loss (Newton, Zigler & Gray, 2015). However, the effectiveness of such strategies would be marginal in circumstances with prolonged aerial exposure, as this necessitates anaerobic respiration and the subsequent accumulation of toxic metabolic by-products (Robson et al., 2009; Collas et al., 2014). The physiology of individuals may drive this variation in response, with some individuals appearing more alert to alterations in their environment. Observations during the trials also noted the use of the foot by individuals as a potential means of detecting stimuli for movement during the initial response: mussels appeared to extend their foot in search of water, moving in the direction of the water's edge where the foot made contact or closing their shell aperture if no contact was made. Research conducted by Yeager, Cherry & Neves (1994) reported the use of pedal feeding by juvenile rainbow mussels, *Villosa iris*, whereby cilia on the foot facilitate particle ingestion, thus highlighting the use of the foot by freshwater mussels for purposes other than horizontal and vertical movement. Nonetheless, studies concerning the use of the foot as a sensory organ are unknown and may warrant investigation.

Previous studies have often noted the role of thermal regimes in governing the response of freshwater mussels (Archambault, Cope & Kwak, 2013; Denic et al., 2015; Bolotov et al., 2018). Indications from this study suggest that temperature may affect the potential for *M. margaritifera* to avoid emersion, with lower temperatures appearing to be correlated with higher rates of success in the avoidance of prolonged aerial exposure: the highest success rates were observed in the field, with an average water temperature of 7 °C. However, as a result of the study design, it was difficult to discern the true effect of temperature: the lowest temperatures recorded during the trials with mussels from the regulated system were at the highest drawdown rate (Δy_{50}), and the highest temperatures recorded during trials with mussels from the unregulated system were also at the highest drawdown rate (Δy_{50}). It is unclear, therefore, whether the higher temperatures prompted a reduced success rate in the unregulated population, indicating differences across populations, or whether a threshold in mussel response was evoked at significantly higher drawdown rates.

4.2 | Variation across populations

In addition to substantial individual variation in response to receding water levels, this study also revealed significant differences across populations (hypothesis iii). The findings presented here represent the first known study of intraspecific variation in the behavioural responses of unionid mussels originating from different populations to alterations in the hydrological environment.

Examination of differences in the behavioural responses to drawdown found that individuals from the regulated system demonstrated greater horizontal and vertical movements than those from the unregulated system. Within the flume studies these differences in the extent of movement did not translate into a higher frequency of successful evasions of emersion, except for trials conducted at the highest drawdown rate (Δy_{50}). For all flume trials, the gradient was less than 0.5 m in length. It is anticipated that reductions in the water level *in situ* may confer a greater extent of emersion across the river bed, with mussels required to move more than 0.5 m to avoid prolonged aerial exposure (Newton, Zigler & Gray, 2015). Therefore, the response of individuals from the regulated system may present substantial survival benefits over their unregulated counterparts in such circumstances.

Further analysis of differences between populations at the highest drawdown rate revealed a significant deviation in response to the highest rate of drawdown, with individuals from the regulated system proving more successful at avoiding emersion. The prevailing environmental characteristics within an animal's habitat are known to accentuate the importance of particular traits (Cook, Wells & Herbert, 2011; Killen et al., 2013); thus, individuals from the regulated system may be more adept at responding to a recession in the water level, given that such conditions are more likely to occur in their habitat. The adaptation of life history traits by populations of *M. margaritifera* has been alluded to in previous studies, with Preston et al. (2010) highlighting significant differences in shell morphology across populations, linked to the hydrological characteristics of their habitats.

Population-specific responses were further evident when examining the repeatability of responses across drawdown rates. Despite displaying a higher frequency of successful avoidance overall, individuals from the regulated system were seemingly less consistent in their response. Only 17% of individuals that successfully avoided aerial exposure in at least one trial managed to replicate this success across all six trials, compared with 38% for the unregulated system (Table 2). Further assessment of the conditions that may have caused this decrease in consistency for mussels from the regulated system showed a significant drop in repeatability between trials with a drawdown rate of Δy_{30} compared with Δy_{15}. This was correlated with an overall reduction in the proportion of individuals successful in avoiding prolonged emersion, when comparing trials with drawdown rates of Δy_{30}, Δy_{15}, and Δy_{50}. The reasons for this are unclear and deviate from the negative linear response to increasing drawdown rate observed within the unregulated population. Further study with a larger subsample of the population may be needed to dissect and understand this perceived trend. Nevertheless, the results from the analysis of repeatability revealed the presence of individuals more capable of responding to changes in the hydrological environment within both populations.

Observed differences in response across populations, highlighted in this study, are probably driven by an amalgamation of phenotypic plasticity, genetic determination, and habitat characteristics. Phenotypic plasticity is thought to be crucial in ensuring an organism's survival when exposed to environmental perturbations (Piersma & Drent, 2003). This notion is particularly relevant to lotic systems, which are inherently dynamic across temporal and spatial scales. A study conducted by Tuttle-Raycraft & Ackerman (2020), examining the extent to which phenotypic plasticity develops in unionid species and consequently governs behavioural responses and physiological function, found that clearance rates of juveniles of the same species from the same source population, reared in different conditions, respond differently to the same stressor (Tuttle-Raycraft & Ackerman, 2020). These differences are likely to be driven by local adaptations in gill structure (Vanden Byllaardt & Ackerman, 2014), such as gill surfaces that are more dense and larger palp structures (Tuttle-Raycraft & Ackerman, 2019), representative of the prevailing hydrogeomorphological conditions (Silverman et al., 1997; Dutertre et al., 2009; Troost et al., 2009; Ouellette-Plante et al., 2017). However, there are likely to be limits to the extent that phenotypic plasticity governs freshwater mussel responses to environmental perturbations, with temporal and spatial alterations in habitat conditions, in addition to genetic variation, influencing the response of organisms. Furthermore, this study represents the only known research into behavioural differences in locomotion across populations of the same unionid species. Therefore, more work is required to discern the potential physiological differences that may drive these responses, in addition to how and when they develop.

4.3 | Findings from the field

Assessment of the results from the field component of this study revealed a significantly higher success rate in the avoidance of emersion by individual mussels, compared with their counterparts in the flume trials. Given the relatively low sample size and high proportion of successful avoidance it was hard to disentangle the main drivers for successful avoidance. However, as seen in the laboratory studies, individuals that displayed an initial response while fully or partially submerged were likely to display greater directionality in their movements and move greater distances, resulting in a higher likelihood of success in avoiding emersion.

Despite conveying broad similarities with the flume studies, the field trials discerned two key factors governing mussel response that had not previously been identified: first, the effect of individual morphology, with larger mussels shown to move further and display greater directionality; and second, the effect of the river-bed slope, from the channel bank towards the centre of the channel (transverse slopes), with more pronounced shifts in flow depth reducing the directionality of movement.

The perceived variation in mussel response to dewatering, resulting from morphological differences, appears to contribute further to contrasting accounts in the literature. Some studies suggest an absence of a morphological effect on a mussel's response (Schwalb & Pusch, 2007; Lymbery et al., 2020), whereas others have insinuated that smaller individuals are more susceptible to drought (Sousa et al., 2018). Morphology is expected to affect the individual response to alterations in the hydrological environment, with increasing size found to increase the metabolic scope of individuals (Curley et al., 2021), thus enabling them to cope with the energetic requirements of movement. However, differences in movement attributed to morphological dissimilarities are likely to be compounded by more significant effects pertaining to variation across populations, species, and stressors; hence, the reason morphology was not shown to be a significant driver of response in the flume trials.

Observations of mussel movement with regards to their positioning showed a greater variation in the movement patterns of mussels when positioned on steeper transverse slopes. Newton, Zigler & Gray (2015) postulated that highly sloped surfaces may cue the directional movement of mussels and provide easier access to areas with greater flow depth. Steeper slopes are also likely to present more stable conditions for movement (Lamb, Dietrich & Venditti, 2008), yet more dynamic near-bed flows are expected on steeper slopes (Armanini & Gregoretti, 2005), which may govern the mussel response and cause substantial alterations in the direction of movement over shorter distances. Furthermore, the river bed predominantly consisted of homogeneous gravel substrate, without larger pebbles and boulders, in both laboratory and field settings for this study. The composition and structure of river-bed substrate is likely to dictate the extent to which mussels can move, either by presenting obstacles to movement or by an absence of suitable medium in which to move. For example, armoured bed layers often lack the fine gravels necessary to permit vertical movements by adult and juvenile freshwater mussels (Addy, Cooksley & Sime, 2012). Thus, further study is required to understand the potential hydrogeomorphological processes in the near-bed environment that determine a mussel's successful tracking of receding water levels.

4.4 | Implications for conservation and river regulation

Within Scotland, extreme drought events are anticipated to increase in frequency in the future, with extended episodes of low summer discharge resulting from reduced precipitation in the spring and summer months (Kirkpatrick, Partridge & Spray, 2021). Despite fears that such events may culminate in large-scale mortalities across *M. margaritifera* populations (Morales, Peñín & Lizana, 2011; Santos et al., 2015; Cosgrove et al., 2021), citing the immobility of such species as a reason for their vulnerability (Sousa et al., 2018), few studies have attempted to examine how individuals respond to alterations in the hydrological regime.

Results from this study provide evidence to suggest a divergence from the current conservation management strategies that are founded upon the view that *M. margaritifera* are sedentary, and hence unable to respond to alterations in their environment. Here, for the first time, empirical evidence is provided to suggest that *M. margaritifera* can successfully detect alterations in flow depth that culminate in the emersion of mussel beds, and respond through vertical and horizontal movements to mitigate the risk of prolonged aerial exposure. These results build upon a growing body of literature revealing the propensity of freshwater mussel species to use behavioural strategies to avoid or mitigate the effects of emersion (Amyot & Downing, 1997; Negishi et al., 2011; Gough, Gascho Landis & Stoeckel, 2012; Ganser, Newton & Haro, 2015; Lymbery et al., 2020). Furthermore, the results presented here reveal variation in response across individuals and populations, suggesting that individual physiology and habitat characteristics shape the extent to which mussels evoke behavioural strategies to avoid emersion. Thus, attempts to discern the risk of populations to recession in water level must adopt a context-dependent approach, with drawdown experiments on sample populations advised in order to predict population response and expected mortality reliably.

It is recommended that flume-based studies should be undertaken with a subset of the corresponding *M. margaritifera* population. Responses to water-level recession should be tested in association with variation in river-bed gradient, mussel arrangement, and drawdown rate. The three drawdown rates used in this study appeared adequate to identify differences within and between populations, although drawdown rates of greater than 50 mm h^{-1} and lower than 15 mm h^{-1} may be useful for a further examination of thresholds in response. In field settings, it is suggested that the distance between the water's edge on the river bank at the start and at the end of a drawdown should not exceed 50 cm in a 24-hour period, with smaller incremental changes of less than 20 cm likely to evoke more successful responses in mussels. In cases where the habitat conditions are deemed unsuitable to facilitate the successful tracking of the water level by horizontal movements (e.g. in densely packed mussel beds), mussels may have to be translocated by hand. Evidence presented in this paper suggests that no mortality is expected in cases where emersion is negated after 24 hours.

Future work should examine the phenotypic plasticity in locomotion behaviour, building upon explorations of plasticity in feeding behaviour (Tuttle-Raycraft & Ackerman, 2020). Alterations in flow regime within juvenile rearing facilities could be used to examine whether a divergence in locomotion behaviour develops within juveniles sampled from the same population. Flume studies could then discern whether different flow regimes have facilitated a shift in the response of individuals to drawdowns, and whether these differences are more prevalent at different life stages of *M. margaritifera*. Research into the physiology and genetic histories of respective individuals would assist in teasing apart the role of hydrogeomorphological habitat conditions in defining mussel development and responses.

In addition to providing pathways for future research, results from this study advocate for the greater assimilation of water level management as a tool for the conservation of freshwater mussel species. Data presented here indicate that the management of water levels during drought conditions could assist in the preservation of populations, with controlled drawdowns facilitating mussel movement into safer regions of the river bed. However, recent alterations in management practices in Scotland permit storage reservoirs to be drawn down to levels significantly lower than previously, to maximize energy production and prevent uncontrolled spill when hydroeletric generation is halted. These practices risk inhibiting the active management of regulated systems during drought conditions.

Results from this study support an integrative approach to the management of regulated systems, favouring the provision of more natural flow regimes and offering practitioners clear operational guidelines founded upon scientific evidence (Geist, 2021). This would assist in harbouring greater population resilience to alterations in flow regime, a view echoed in similar studies (Newton, Zigler & Gray, 2015; Sousa et al., 2020). With an increase in demand for renewable energy sources resulting in a shift towards increasing support for small hydropower plants, and more exploitative management practices, it is crucial for future research and corresponding conservation management strategies to examine further the response of freshwater mussels to river regulation. These strategies should place greater consideration on sustainable water abstraction that retains the ability to mitigate the effects of severe climatic conditions. Attempts to bridge the gap between conservation management and river regulation are likely to facilitate improved conditions for aquatic species within the associated systems, and may also provide a tool to buffer populations against the effects of climate change.

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CONFLICT OF INTEREST

The authors declare that they have no conflicts of interest associated with this work.

DATA AVAILABILITY STATEMENT

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

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