DOI: 10.1111/1365-2664.14387

## RESEARCH ARTICLE

## River infrastructure and the spread of freshwater invasive species: Inferences from an experimentally-parameterised individual-based model

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#### Funding information

Engineering and Physical Sciences Research Council, Grant/Award Number: EP/L01582X/1; European Horizon 2020 AMBER Project, Grant/Award Number: 689682

Handling Editor: Paulo S. Pompeu

## Abstract

- Invasive species and river infrastructure are major threats to freshwater biodiversity. These stressors are commonly considered in isolation, yet the construction and maintenance of river infrastructure can both enhance and limit the expansion of invasive species. Spatial and temporal limitations of laboratory and field studies, coupled with little consideration of population-level responses (e.g. invasion rate), have limited understanding of the efficacy of infrastructure for long-term, catchment-scale containment of invasive species.
- 2. This study utilised an individual-based model (IBM) to investigate the ability of a partial riverine barrier to contain the spread of invasive species at large spatio-temporal scales, using American signal crayfish *Pacifastacus leniusculus* as a model species. The base model (no barrier) accurately recreated longitudinal expansion rates of signal crayfish reported in existing literature. A virtual riverine barrier was added to the base model, with passage at the structure parameterised using existing literature and the results of an experiment that demonstrated no clear relationship between crayfish density and passage efficiency at a Crump weir.
- 3. Model outputs indicated a weir downstream of the release point had no effect on longitudinal expansion of crayfish, whereas an upstream barrier slowed the invasion rate for 6.5 years after it was first encountered. After the invasion rate had recovered to pre-barrier levels, the invasion front was 2.4 km further downstream than predicted in the absence of a barrier, representing a 1.73 year delay in longitudinal range expansion.
- 4. Synthesis and applications. Despite substantial negative impacts on native biodiversity, river infrastructure can also delay the spread of freshwater invasive species, representing a trade-off. This demonstrates the need to consider positive ecological consequences of river infrastructure when designing prioritisation techniques for barrier removal and mitigation (e.g. selective fish passage), and suggests that in some cases barriers may provide a useful integrated pest management tool.

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### KEYWORDS

agent-based model, dispersal, in-stream engineering, low-head barriers, non-native species, range expansion, river engineering, signal crayfish

## 1 | INTRODUCTION

Invasive species are among the greatest threats to global biodiversity (Blackburn et al., 2019; Olden et al., 2004). Fresh waters are considered the most degraded and threatened of all ecosystems (Albert et al., 2021) and are particularly vulnerable to invasive species due to a variety of unregulated transport vectors and high levels of endemism induced by biotic separation of basins (Moorhouse & MacDonald, 2015). Freshwater invasive species negatively affect native communities through competition, niche displacement, hybridisation, predation, and disease transmission (Mooney & Cleland, 2001), substantially reducing abundance and diversity (Gallardo et al., 2016). These ecological impacts negatively affect provisioning ecosystem services (Pejchar & Mooney, 2009) and cause substantial economic loss (Haubrock et al., 2021).

In addition to invasive species, freshwater ecosystems are threatened by extensive engineering, particularly high densities of river infrastructure such as dams, weirs, and culverts (Belletti et al., 2020). These structures disrupt longitudinal, lateral and vertical connectivity (Ward & Stanford, 1995), degrading and fragmenting essential habitats (Fuller et al., 2015), obstructing critical migrations (Sheer & Steel, 2006), and modifying hydrogeomorphological processes (Petts & Gurnell, 2013). These changes manifest in substantial impacts on native fish (Liermann et al., 2012), macroinvertebrates (Linares et al., 2018) and plants (Jansson et al., 2000); as such, the removal or mitigation of river infrastructure is viewed as a critical aspect of river restoration (Brown et al., 2013; Mouchliantis, 2022).

While the impacts of invasive species and river infrastructure are commonly considered in isolation, they frequently interact, either to magnify negative effects (e.g. Havel et al., 2005), or diminish them through contradictory mechanisms, such as limiting abundance (Miehls et al., 2020) and delaying range expansion (e.g. Jones et al., 2021; Rahel, 2013). There are many examples of the latter, including impeded upstream movement of invasive fish due to rock filled gabions (e.g. van der Walt et al., 2019 for smallmouth bass Micropterus dolomieu in South Africa), culverts (e.g. Thompson & Rahel, 1998 for brook trout Salvelinus fontinalis in Wyoming, USA), and low-head dams (e.g. Hasegawa, 2017 for brown trout Salmo trutta in Japan). Structures can also limit upstream movements of invasive decapod crustaceans, including American signal crayfish Pacifastacus leniusculus (Rosewarne et al., 2013), and red swamp crayfish Procambarus clarkii (Dana et al., 2011). Such observations have led some to propose that the installation and maintenance of river infrastructure may provide a viable integrated pest management

(IPM) technique to contain the spread of freshwater invasive species (e.g. Jones et al., 2021; Rahel, 2013).

Investigations into the value of river infrastructure as an invasive species management approach generally quantify passage at individual barriers (i.e. at a limited spatial scale: Rosewarne et al., 2013; Hasegawa, 2017), or survey presence and absence of invasive species at large spatial scales over short time periods (i.e. a limited temporal scale: Dana et al., 2011; Kerby et al., 2005). Although this indicates the potential for barriers to contain invasions, the spatial and temporal bias limits understanding of their long-term efficacy at a catchment level. Furthermore, these studies rarely quantify population-level responses (e.g. invasion rate) or the influence on invasion dynamics. Individual-based models (IBMs) incorporate complex interdependent factors (e.g. growth, reproduction, movement, and mortality), allowing populationlevel impacts of management techniques to be explored at larger spatio-temporal scales (Grimm et al., 2005). However, they depend on high quality data for parameterisation and validation (Grimm et al., 2005), and studies examining drivers of barrier passage rarely consider the importance of population-level factors such as density, despite strong associations with dispersal (Altwegg et al., 2013).

This study developed an IBM to determine the impact of river infrastructure on the spread of an aquatic invasive species at a large spatio-temporal scale, using the American signal crayfish as the model. Signal crayfish are the most widespread invasive crayfish in Europe (Kouba et al., 2014), and once established they have overwhelmingly negative impacts on native biodiversity (Galib et al., 2021) and hydromorphology (Harvey et al., 2014). River infrastructure limits their upstream movements under laboratory (Frings et al., 2013; Kerr et al., 2021) and field (Rosewarne et al., 2013) conditions, with some suggesting that riverine barriers provide the most effective method of controlling their spread (Krieg & Zenker, 2020). Furthermore, high-quality data on population dynamics (e.g. Guan & Wiles, 1999), movement (Bubb et al., 2004) and drivers of barrier passage (Rosewarne et al., 2013) are available for IBM parameterisation. However, the influence of conspecific density on barrier passage remains unclear, despite its known associations with dispersal (Galib et al., 2022), and therefore additional experimentation was required prior to IBM development. Consequently, the objectives were to: (1) experimentally investigate the impact of crayfish density on barrier passage; and (2) formulate an IBM to assess the impact of a partial riverine barrier on the longitudinal spread of crayfish.

## 2 | MATERIALS AND METHODS

## 2.1 | Experimental evaluation of the effect of density on passage

#### 2.1.1 | Crayfish collection, maintenance and tagging

Crayfish were collected from Castle Mill Stream (51°45′41.2″N 1°16′31.8″W; n = 272) and Crampmoor Fish Farm (51°00′01.2″N 1°27′01.4″W; n = 88) using six prismoidal and six cylindrical traps baited with cat food. Traps were collected after 10–24 h, and the crayfish transported in containers holding water obtained from the site of capture to the International Centre for Ecohydraulics Research facilities at the Boldrewood Innovation Campus, University of Southampton. On arrival, crayfish were randomly allocated to one of two aerated and filtered 1000L indoor holding tanks at an average temperature of 17.8°C (range = 16.6–19.1°C). Crayfish trapping was conducted under licence from the UK Environment Agency (Permit References EP-EW094-L-209/16097/01 and EP/EW002-I-426/16416/02), and with appropriate permission from local land owners.

Twenty-four hours prior to use in experimental trials, the carapace of each crayfish was marked with a number using white nail varnish, and a 12 mm half-duplex PIT tag was attached to the carapace with cyanoacrylate glue. During tagging, mass (mean = 37.7 g, SD = 20.57), sex (females = 191, males = 169), carapace (mean = 49.36 mm, SD = 10.40) and chela length (mean = 39.54 mm, SD = 13.24) were recorded. These morphological metrics did not vary between treatments (Table S1.1).

## 2.1.2 | Experimental setup

A model Crump weir (length = 2380mm, width = 60mm, height = 340 mm) constructed of 18 mm thick plywood was installed in an indoor recirculating flume (length = 16m, width = 0.6 m, depth = 0.8 m) at the University of Southampton Boldrewood Innovation Campus (Figure 1). A removable screen was placed at the foot of the weir to create a 1 m<sup>2</sup> 'acclimation zone' where crayfish acclimatised to conditions in the flume. To track the movements of crayfish within the experimental area, four PIT antennas were placed laterally in the flume, with two antennas installed in the acclimation zone, one on the downstream face of the weir, and one on the upstream face (Figure 1a). Downward facing infrared CCTV cameras (Swann Pro A850) were mounted 0.7 m above the acclimation area, on the downstream weir face, and weir crest to record crayfish behaviour.



FIGURE 1 (a) Side view of a recirculatory flume used in an experiment to determine influence of crayfish density on upstream passage at a model Crump weir (dark grey). Location of PIT antennas (dashed lines) and their detection distance (light grey shaded area), removable screen (double line) and release location of the crayfish (cross) are depicted. (b) Plan view of recirculatory flume illustrating flow velocities in the experimental area. Grey circles indicate locations of measurements taken using an electromagnetic flow meter (Valeport Model 801; measurements averaged over 10s). From left to right, white lines denote the downstream extent, crest and upstream extent of the weir.

Two comparable studies of crayfish passage under flume conditions have been conducted, although the observed passage success differed substantially (Frings et al., 2013 observed no successful passage at weir crest velocities above 0.65 ms<sup>-1</sup>; Kerr et al., 2021 found that 14% of crayfish passed crest velocities of 0.74 ms<sup>-1</sup>). However, the crayfish used here were sourced from the same population as Kerr et al. (2021), and therefore the experimental setup (Figure 1a) and flow conditions (Figure 1b) were chosen to replicate this study. A full description of the experimental setup is available in Supporting Information S1.2.

## 2.1.3 | Experimental procedure

Four density treatments (1, 5, 10 and 20 crayfish m<sup>-2</sup>), comparable to those observed in the wild (Table S1.2), were selected. Signal crayfish are nocturnal (Thomas et al., 2016), and therefore 40 night-time (19:30–05:00) trials were conducted between the 17th and 28th of August 2019, with one trial per density treatment conducted in a random order each night until 10 trials per treatment were completed (*n* crayfish = 360).

Twenty-four hours prior to use in the trials, test crayfish were placed into 20L aerated acclimation tanks at the treatment densities. Prior to the start of each trial, the crayfish were transferred to the acclimation zone at the downstream end of the experimental area (Figure 1a) and acclimatised for 30 min. On removing the screen, the crayfish could access the experimental area for 1h before the trial was terminated. Individual crayfish movements during the acclimation of PIT telemetry and video. Each crayfish was used once only. Flume water temperature (mean =  $20.7^{\circ}$ C, SD = 0.78) was within the range in which signal crayfish maintain normal performance (13.7–30.1°C; Rodríguez Valido et al., 2021) and did not differ between treatments (One-way ANOVA:  $F_{3,36} = 1.554$ , p = 0.217). All experimental procedures were sanctioned by the University of Southampton Ethical Review Board (ERGO ID: 51963).

### 2.1.4 | Behavioural analysis

PIT telemetry data was used to calculate four metrics: (1) *Proportion* of attempts, (2) *Proportion of passes*, (3) *Time to first attempt* and (4) *Time to first pass* (Table 1). Where PIT telemetry data was unavailable (n = 6 trials), the metrics were calculated using video analysis, with the location of PIT antennas providing reference points. To prevent overrepresentation of individuals that spent long periods within the PIT antenna detection zone, only observations separated by greater than 30s were treated as individual detections.

### 2.1.5 | Data analysis

Generalised linear models (GLMs) with a binomial error structure and a 'logit' link function were used to investigate the influence of **TABLE 1** Key metrics used to assess crayfish movementbehaviour when passing a model Crump weir at different densities.

Metric name	Definition
Proportion of attempts	The proportion of individuals in each trial that attempted to pass the weir. An attempt was defined as detection at PIT antenna 3 located at the downstream extent of the high velocity region at the weir crest.
Proportion of passes	The proportion of individuals within a trial that successfully passed the crest of the weir. Passage was defined as detection at PIT antenna 4 located upstream of the weir crest.
Time to first attempt	The time interval between the removal of the screen at the foot of the weir and the first recorded attempt (i.e. detection at PIT antenna 3) for each individual.
Time to first pass	The time interval between the removal of the screen at the foot of the weir and the first recorded successful pass (i.e. detection at PIT antenna 4) for each individual.

density on *Proportion of attempts* and *Proportion of passes*. For each GLM, diagnostic plots (Residuals vs Fitted and Normal Q-Q) indicated that assumptions of homoscedasticity and normality of residuals were met.

Cox proportional hazards models were used to assess the relationship between density and *Time to first attempt* and *Time to first pass*. Goodness of fit tests to identify correlations between the Schoenfeld residuals (Schoenfeld, 1982) and time indicated that the assumption of proportional hazards was met (*Time to first attempt*:  $\chi^2 = 0.018$ , df = 1, p = 0.89; *Time to first passage*:  $\chi^2 = 0.563$ , df = 1, p = 0.45).

Data processing and statistical analysis were conducted in R studio v3.5.1 (R Core Team, 2019).

## 2.2 | Individual-based model

## 2.2.1 | Model overview

A full description of the model following the updated Overview, Design Details (ODD) reporting format (Grimm et al., 2020) is provided in Supporting Information (S2). A condensed version of the model workflow and processes is outlined below.

The IBM was coded in MATLAB (MathWorks Ltd) and reflects a homogeneous single-channel virtual river of predetermined width (2 m) and length (70 km). River depth was discounted in the model, as crayfish are benthic, and density was measured as a function of river area rather than volume. To enhance computational speed, the river was divided into 10 m sections for abundance calculations (density [number of individuals  $m^{-2}$ ]; biomass [gm<sup>-2</sup>]), and 100m sections for breeding calculations.

Individual crayfish were represented in the model, and grew, moved and interacted with conspecifics in accordance with population and movement dynamics data sourced from available literature (see Supporting Information S2) and the experiment described in Section 2.1. The model started at year 0, day of the year (DOY) 150, with 100 seed crayfish (randomly allocated as male or female at a 1:1 ratio) released into the river at river km 35. The model duration was 20 years. During each time step (1 day), seven key processes occurred:

- 1. Incrementation of time-dependent factors. Age and correlated factors (size variables: carapace length and mass) of each crayfish were incremented with each time step. Likewise, in the case of gravid crayfish, the gestation period was increased by one time step.
- 2. *Population calculations*. Crayfish density and biomass were calculated for each 10 m river section.
- Movement. The distance moved by individual crayfish during each timestep was randomly assigned based on the distribution data available in Bubb et al. (2004). Movement distances were influenced by local density, seasonal temperature changes, and predisposition to upstream/downstream movement.
- 4. Barrier passage. Crayfish were assigned a random number between 0 and 1 and determined to be able to pass the barrier during an upstream movement if the value was less than a predefined threshold. This threshold (0.22 for males and 0.12 for females) was based on the passage success values reported in (Rosewarne et al., 2013), who undertook a long-term field study of crayfish passage at a small (head drop = 1.33 m) flow gauging weir. If the number exceeded the threshold, crayfish remained downstream of the barrier. All crayfish could pass downstream over the barrier without hindrance (as in Rosewarne et al., 2013). Given that density did not influence crayfish passage behaviour under the described experimental conditions (see Section 3.1), density-dependent barrier passage was not implemented.
- 5. Mortality. The probability of mortality was calculated based on size and population density. A random number was assigned to each crayfish, and they were removed from the model if the probability of mortality exceeded the random number. Crayfish were also removed if their location was outside the maximum longitudinal extent of the river, or if they exceeded 7 years of age.
- 6. Reproduction. Females became gravid during the breeding season if they were sexually mature and there was an adult male in the same 100m breeding area. The number of eggs released was calculated as a function of carapace length.
- Population expansion. The locations of the upstream and downstream invasion fronts were calculated, along with the number of crayfish, the number of gravid females, and the mean biomass.

The location of the upstream and downstream invasion front was calculated at each time step by determining the furthest upstream and downstream river section from the release location where biomass was a quarter of the current maximum biomass in the model. This method reduced the effects of model stochasticity, as using the furthest position of any individual to delineate the invasion front produced erratic results that were heavily influenced by single individuals moving very large distances. The use of time varying maximum density rather than an absolute value ensured that dynamic changes in population density were factored into the spatial positioning of the invasion front. Upstream and downstream rates of population expansion were determined from the change in the location of the invasion fronts at each time step, and the total rate of population expansion was calculated as the sum of the upstream and downstream rates.

A single model run took approximately 2h to complete on a desktop computer (System: 64 bit; CPU: i7-2600, RAM: 32 GB). Final model results were batch processed (1 model run per core) using the University of Southampton's high-performance computing unit (IRIDIS 4).

### 2.2.2 | Model validation

To determine the validity of the model, 100 model runs were conducted with no barrier present, and the average upstream, downstream, and total linear expansion rates (TLERs) were calculated. A comprehensive literature search (excluding material used in model development) was undertaken to identify expansion rates reported under natural conditions (Bernardo et al., 2011; Bubb et al., 2005; Hudina et al., 2013, 2017; Peay et al., 2009; Sibley, 2000; Table S3.1). The mean and 95% confidence intervals (CIs) of the values reported in the literature were calculated and compared to the invasion rates predicted by the IBM over a comparable time period.

## 2.2.3 | The effect of a partial riverine barrier on crayfish dispersal

A partial barrier was integrated into the model either 10 km upstream or downstream of the release location. This distance was selected as pilot studies showed the rate of longitudinal expansion had plateaued in both the upstream and downstream direction prior to crayfish encountering the barrier. One-hundred model runs were conducted for each scenario, and temporal and spatial differences in the locations of the invasion fronts were assessed using 95% Cls.

### 3 | RESULTS

## 3.1 | Experimental assessment of the effects of density on barrier passage

Density did not influence any of the passage metrics. The *Proportion* of attempts (mean [ $\pm$ SD] = 0.70 ( $\pm$ 0.34]; *z* = -0.481, *p* = 0.631; Figure 2a), Proportion of passes (mean [ $\pm$ SD] = 0.37, [ $\pm$ 0.32]; *z* = -0.493, *p* = 0.622; Figure 2b), Time to first attempt (mean [ $\pm$ SD] = 855 ( $\pm$ 836] s; *z* = 0.006, *p* = 0.995; Figure 2c) and Time



FIGURE 2 The proportion of American signal crayfish that (a) attempted to pass, and (b) successfully passed a model Crump weir at different densities (points represent results from individual experimental trials, black line denotes model predictions and grey shading represents 95% confidence intervals), and the cumulative proportion of individuals over time that (c) attempted to pass, and (d) successfully passed a model Crump weir at different densities.

to first pass (mean  $[\pm SD] = 1393 [\pm 956]$  s; z = -0.173, p = 0.863; Figure 2d) were not affected by density.

## 3.2 | Individual-based model (IBM)

#### 3.2.1 | Model validation

For the base model (no barrier), the yearly rate of longitudinal expansion gradually increased after introduction and plateaued at approximately 1.42 and 2.14 km year<sup>-1</sup> in the upstream and downstream directions, respectively, after 8.5 years (TLER:  $3.56 \text{ km year}^{-1}$ ) (Figure 3a). Temperature-dependent dispersal resulted in annual fluctuations in invasion rate, with the maximum and minimum observed in the summer (upstream =  $2.64 \text{ km year}^{-1}$ , downstream =  $3.98 \text{ km year}^{-1}$ ) and winter (upstream =  $0.02 \text{ km year}^{-1}$ , downstream =  $0.02 \text{ km year}^{-1}$ ), respectively (Figure 3a).

The average invasion rates predicted by the model (0–10.4 years: upstream = 0.73; downstream = 1.07; TLER =  $1.83 \text{ km year}^{-1}$ ) were within the 95% CIs of the mean rates (upstream: 0.98; downstream: 1.54; TLER: 2.70 km year<sup>-1</sup>) reported in the literature (Figure 3b, Table S3.1), indicating that the model was appropriate.

# 3.3 | The effect of a riverine barrier on crayfish dispersal

Crayfish first reached the upstream barrier after approximately 12.2 years, which led to a reduction in the invasion rate from 1.42 to  $0.52 \text{ km year}^{-1}$  over a period of approximately 12 months (Figure 4a). The invasion rate recovered to pre-barrier levels

after 6.5 years (<1% difference for more than 7 days), at which point (18.7 years after release) the upstream invasion front was 2.34 km further downstream, representing a 1.73-year delay compared to the scenario in which the barrier was absent (Figure 4b).

Crayfish first reached the barrier 10 km downstream of the release point after approximately 10.1 years but it had no effect



FIGURE 3 (a) Changes in invasion rate predicted by the individual-based model over a 20-year period (solid lines denote 365 day smoothed average, and dashed lines denote 20 day smoothed averages), (b) Mean (circles) and 95% confidence intervals (error bars) upstream, downstream, and total linear expansion rates (TLER) of signal crayfish populations as reported in the literature and predicted by the individual-based model.



FIGURE 4 Predictions of the individual-based population dispersal model for the no barrier control (black lines) and upstream barrier (red lines) scenarios, showing: (a) differences in invasion rate, and (b) shift in location of the invasion front over time.

on the invasion rate or location of the downstream invasion front (Figure S4.1).

## 4 | DISCUSSION

Riverine barriers are increasingly used to control aquatic invasive species (Jones et al., 2021), but information regarding their efficacy over large spatio-temporal scales is limited. In this study, a combined experimental and individual-based modelling approach was adopted to predict the impact of a partial riverine barrier on longitudinal expansion of a population of signal crayfish. Crayfish density had no influence on barrier passage in terms of either motivation or ability to pass a model Crump weir under experimental conditions. The IBM demonstrated that a riverine barrier that partially blocks crayfish from passing upstream would temporarily (for 6.5 years) inhibit the upstream invasion rate, delaying and restricting population expansion by 1.83 years and 2.84 km, respectively. This study assessed the influence of a partial barrier on invasion rates at high spatio-temporal resolution and suggests that such barriers may play an important role in invasive species management strategies.

### 4.1 | Effects of density on barrier passage

Despite its importance as a predictor of dispersal tendency (Galib et al., 2022), density was not related to the motivation or ability of signal crayfish to pass an anthropogenic riverine barrier, suggesting that other factors are likely to be driving variation in passage success. Indeed, (Rosewarne et al., 2013) reported that sex and size respectively predicted ascent and descent of a gauging weir by signal crayfish, although relationships between morphology and passage were not observed in other studies conducted under laboratory (Frings et al., 2013) and field (Krieg et al., 2021) conditions. Upstream passage success is highly variable for signal crayfish, with reported rates of 0%-38.1% (Frings et al., 2013; Rosewarne et al., 2013; Kerr et al., 2021; Krieg et al., 2021; this study), and the low repeatability of previous studies means the factors explaining this variation remain unclear. Recent research has suggested that intrinsic behavioural differences (i.e. personality) are associated with passage in other taxa, with boldness and exploration predicting passage success in brown trout (Lothian & Lucas, 2021) and American eels Anguilla rostrata (Mensinger et al., 2021), respectively. Conversely, variation in passage may be driven by barrier characteristics such as substrate roughness, barrier slope, and flow velocity (Frings et al., 2013). Understanding the mechanisms driving barrier passage is essential for further refinement of the barrier passage parameters in the IBM, and this is recommended as a focus for future research. Additionally, it is important to note that although flume studies allow precise manipulation of the variable of interest, they may not replicate natural environments and behaviours (Rice et al., 2010), indicating further work exploring the effects of density on passage under field conditions is required.

## 4.2 | Individual-based model

The IBM reproduced the longitudinal expansion of a signal crayfish population, and highlighted several opportunities to optimise management strategies. For example, the IBM revealed that invasion rates in summer are substantially higher, indicating a period when management efforts could be focused. Similar techniques have been used in the Great Lakes, where barriers are employed seasonally to limit the access of invasive sea lamprey to spawning tributaries (Miehls et al., 2020). The IBM also suggested that the model population experienced a lag phase (Crooks, 2005), whereby the invasion rate remained low over the first 3 years (upstream =  $0.22 \text{ km year}^{-1}$ , downstream =  $0.29 \text{ km year}^{-1}$ ), before rising rapidly to a plateau after 8.5 years. Lag phases have been observed in situ for signal crayfish (e.g. Sandström et al., 2014), representing an important window for management prior to extensive spread (Crooks, 2005) and highlighting the need for methods of early detection (e.g. Robinson et al., 2018).

## 4.3 | The effect of a riverine barrier on crayfish dispersal

The IBM demonstrated the potential for a partial barrier to delay the invasion of signal crayfish, suggesting they may provide an effective invasive species management technique at the catchment scale. However, to be effective as a standalone strategy, physical barriers should prevent 100% of passage, a level that is challenging to achieve in reality, especially for aquatic species that are able to disperse via the terrestrial environment (Jones et al., 2021). Therefore, partial barriers are more likely to play an important role in IPM strategies which utilise a range of site-specific control and containment techniques. Indeed, barriers have been used successfully alongside extensive manual removal to control the abundance and distribution of invasive trout species in Wyoming, USA (Novinger & Rahel, 2003). IPM is strongly recommended for the management of invasive crayfish (Manfrin et al., 2019), and the integration of barriers into these strategies is likely to improve their efficacy (Krieg & Zenker, 2020).

The ability of riverine barriers to slow invasion rates highlights the need to consider invasive species in dam removal and mitigation planning. Rates of dam removal are accelerating, (Mouchliantis, 2022), yet facilitating the spread of invasive species by removing dispersal barriers is a common concern among managers (Tullos et al., 2016). Indeed, the removal of three dams on the Boardman River, Michigan, USA, facilitated the spread of the New Zealand mud snail *Potamopyrgus antipodarum* (Mahan et al., 2021), and there has been a recent drive to include the potential spread of invasive species in barrier removal prioritisation models (e.g. Terêncio et al., 2021). This is particularly important in megadiverse regions, where large dams are prevalent and their removal can facilitate enormous freshwater invasion events (e.g. Vitule et al., 2012). Similarly, mitigation techniques designed to improve passage for native species (i.e. fishways) can also allow the movement of undesirable species, representing an important trade-off for fisheries management (McLaughlin et al., 2013). This emphasises the importance of selective fish passage solutions, whereby connectivity is improved for native biota without facilitating the dispersal of invasive species (e.g. Kerr et al., 2021; Stuart et al., 2006).

The IBM provided a means to explore an invasive species management strategy that is difficult to test under field conditions. In the future, the model can be expanded to incorporate a variety of strategies, such as the installation of multiple barriers, trapping, and biological control, enabling synergies and trade-offs to be identified and an optimal solution to be selected. Indeed, this approach was used to explore management techniques for rusty crayfish Faxonius rusticus in the John Day River basin, Oregon, USA, where extensive trapping in the early stages of invasion was identified as the optimal solution (Messager & Olden, 2018). However, the value of IBMs to inform IPM depends on highquality data regarding the population-level impacts of the management techniques employed (Grimm et al., 2005), and this data is often lacking for other management approaches. Similarly, longterm field studies are needed to validate the conclusions of IBMs over large-spatio temporal scales, and the continued development of novel techniques such as biomonitoring (e.g. Turley et al., 2017) and eDNA monitoring (e.g. Robinson et al., 2019) may facilitate these studies in the future.

## 5 | CONCLUSIONS

Invasive species are considered among the greatest threats to aquatic biodiversity, and the identification and assessment of management strategies is essential for the preservation of fresh waters. Where eradication of invasive populations is not possible, options for controlling further spread include the maintenance of existing riverine barriers or installation of purpose-built structures. This study adopted an IBM approach informed by the results of an experimental study and available literature to demonstrate that a partial riverine barrier can delay the invasion of signal crayfish and temporarily limit the spatial extent of the invaded area. Partial barriers have the potential to form an important component of an IPM strategy, and IBMs provide a useful tool to optimise such strategies. Further work is recommended to elucidate drivers of passage success, provide data for model parameterisation, and test catchmentscale IPM strategies using the IBM.

#### AUTHOR CONTRIBUTIONS

Study conceptualised by Jack A Daniels, James R. Kerr and Paul S. Kemp; Density experiment conducted and data analysed by Jack A. Daniels; IBM developed by James R. Kerr; IBM data analysed/visualised by James R. Kerr and Jack A. Daniels; initial manuscript written by Jack A. Daniels, with all authors contributing to manuscript review and editing. All authors contributed critically to the drafts and gave final approval for publication.

### ACKNOWLEDGEMENTS

This work was funded by grant EP/L01582X/1 from the Engineering and Physical Sciences Council, UK (J.A.D) and the European Horizon 2020 AMBER (Adaptive Management of Barriers in European Rivers) Project, Grant number: 689682 (J.R.K). We thank M. Lawes for allowing access to their land for crayfish trapping. The authors acknowledge the use of the IRIDIS High Performance Computing Facility and associated support services at the University of Southampton.

### CONFLICT OF INTEREST STATEMENT

All authors declare no conflicts of interest.

### DATA AVAILABILITY STATEMENT

Data and model code is available from the University of Southampton PURE Repository https://doi.org/10.5258/SOTON/D2552 (Daniels et al., 2023).

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### SUPPORTING INFORMATION

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How to cite this article: Daniels, J. A., Kerr, J. R., & Kemp, P. S. (2023). River infrastructure and the spread of freshwater invasive species: Inferences from an experimentally-parameterised individual-based model. *Journal of Applied Ecology*, 00, 1–11. https://doi.org/10.1111/1365-2664.14387