University of Southampton

Faculty of Engineering and Physical Sciences

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The effectiveness of anthropogenic in-stream barriers as a management strategy for non-native species

By

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Thesis for the degree of Doctor of Philosophy

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University of Southampton

Abstract

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Doctor of Philosophy
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Invasive species and river infrastructure are both considered major drivers of freshwater biodiversity loss. However, there is a growing body of research suggesting that the construction, maintenance, or modification of river infrastructure (i.e., exclusion barriers) can limit the spread of invasive species, and thus may be a useful management technique. A quantitative meta-analysis conducted as part of this thesis demonstrated that current research regarding the effects of river infrastructure on the spread of invasive species is limited by ineffective experimental design, small spatio-temporal scales, and minimal consideration of invasion dynamics, meaning further assessment regarding the efficacy of exclusion barriers is essential prior to their widespread implementation.

In this thesis, individual-based modelling was used to address the limitations of previous studies due to its ability to simulate complex invasion dynamics over large spatio-temporal scales, and the American signal crayfish (*Pacifastacus leniusculus*) was identified as an appropriate model species due to its widespread distribution, rapid rate of secondary range expansion, and overwhelmingly negative ecological and socio-economic impacts.

Additional information regarding the fundamental drivers of signal crayfish dispersal and barrier passage behaviour was required for parameterisation of an individual-based model (IBM), and this was obtained through experimentation and spatial analysis. Flume-based experiments revealed that crayfish population density did not affect barrier passage behaviour, whereas individual personality was an important driver of motivation to pass in-stream structures. Spatial analysis incorporating all signal crayfish records in England demonstrated that invasion rate was affected by boating activity and water temperature, although a number of other abiotic factors (including barrier density) did not affect dispersal.

An initial version of the IBM implemented on a virtual river system demonstrated that a partial barrier could significantly delay the secondary range expansion of signal crayfish, although invasion rates recovered rapidly once the barrier had been passed. The IBM was extended to function on a real river system with multiple barriers, and used to predict the impacts of low-cost barrier modifications on the spread of signal crayfish. These predictions were then integrated with information regarding the overall costs and the impact on native fishes using multi-criteria decision analysis (MCDA). Barrier modifications substantially slowed the spread of signal crayfish, but were costly and negatively impacted habitat availability for native fishes. The combined IBM and MCDA approach effectively identified an optimal combination of modifications in the catchment (involving modifications to a single barrier) that minimised the trade-off between these three competing conservation goals.

The results presented in this thesis demonstrate that exclusion barriers can effectively slow the spread of invasive species over large spatio-temporal scales, suggesting they may perform a useful role in long-term, catchment-scale management plans. The approaches used have enhanced fundamental understanding regarding the influence of in-stream infrastructure on invasion dynamics, and will contribute to the long-term conservation of freshwater biodiversity.

Table of Contents

Abstract v

Table of Tables xi

Table of Figures xiii

List of Accompanying Materials xix

Research Thesis: Declaration of Authorship xxi

Acknowledgements xxiii

Definitions and Abbreviations xxv

- A. Referenced Nomenclature xxv
  - A.1 Families xxv
  - A.2 Species xxv
- B. Acronyms xxvii
- C. Notation xxviii
- D. General Terminology xxix

Chapter 1: Introduction 1

- 1.1 Invasive species 1
  - 1.1.1 Background 1
  - 1.1.2 Invasive species – process and definitions 1
  - 1.1.3 Invasive species – impacts and management 3
  - 1.1.4 Aquatic invasive species 6
- 1.2 River infrastructure 9
  - 1.2.1 Prevalence and uses of river infrastructure 9
  - 1.2.2 Impacts of river infrastructure 10
  - 1.2.3 Mitigation of river infrastructure 11
- 1.3 Invasive species and river infrastructure 12
  - 1.3.1 River infrastructure as a management technique 12
  - 1.3.2 Limitations of management using river infrastructure 14
- 1.4 Preliminary aims and objectives 16

Chapter 2: The effects of anthropogenic in-stream structures on non-native species: a meta-analysis. 19

- 2.1 Introduction 19
- 2.2 Methods 21
  - 2.2.1 Search protocol 21
  - 2.2.2 Screening and data collection 22
  - 2.2.3 Effect size calculation 24
  - 2.2.4 Data analysis 25
- 2.3 Results 26
  - 2.3.1 Overall effects by invasion stage 26
  - 2.3.2 Variation in overall effects 27
  - 2.3.3 Biases in current research 27
- 2.4 Discussion 31
  - 2.4.1 Overall effects by invasion stage 31
  - 2.4.2 Variation in overall effects 32
  - 2.4.3 Biases in current research 33
  - 2.4.4 Priorities for future research 34
  - 2.4.5 Conclusion 36

Chapter 3: Thesis aims and objectives 37

3.1 Aims and objectives 37
3.2 Thesis structure 37

Chapter 4: Study species and methodology 39

4.1 American signal crayfish 39
4.2 Individual-based modelling 42

Chapter 5: River infrastructure and the spread of freshwater invasive species: inferences from an experimentally-parameterised individual-based model.............45

5.1 Introduction 46
5.2 Materials and methods 47
  5.2.1 Experimental evaluation of the effect of density on passage 47
  5.2.2 Individual-based model 51
5.3 Results 53
  5.3.1 Experimental assessment of the effects of density on barrier passage 53
  5.3.2 Individual-based model 53
5.4. Discussion..55
  5.4.1 Effects of density on barrier passage 56
  5.4.2 Individual-based model 56
  5.4.3 The effect of a riverine barrier on crayfish dispersal.................................57
  5.4.4 Conclusion..58

Chapter 6: Personality-dependent passage behaviour of an aquatic invasive species at a barrier to dispersal...59

6.1 Introduction 59
6.2 Methods 62
  6.2.1 Crayfish collection and husbandry 62
  6.2.2 Personality characterisation 63
  6.2.3 Passage behaviour..65
  6.2.4 Ethical note...67
  6.2.5 Data analysis..68
6.3 Results 69
  6.3.1 Personality characterisation 69
  6.3.2 Passage behaviour..69
6.4 Discussion..72

Chapter 7: National-scale drivers of dispersal in a freshwater invasive species......77

7.1 Introduction 77
7.2 Methodology 79
  7.2.1 Model system 79
  7.2.2 Identifying distinct local invasions 79
  7.2.3 Calculating invasion rate 81
  7.2.4 Factors associated with invasion rate 81
7.3 Results 85
  7.3.1 Identifying distinct local invasions 85
  7.3.2 Calculating invasion rates 86
  7.3.3 Factors associated with invasion rate 86
7.4 Discussion..87
  7.4.1 Identifying distinct local invasions 87
  7.4.2 Calculating invasion rates 88
  7.4.3 Drivers of invasion rate..89
  7.4.4 Conclusion..91

Chapter 8: Optimising the installation of invasive species exclusion barriers under multiple conservation objectives 93

8.1 Introduction 93
8.2 Methodology 95

    8.2.1 IBM development 95
    8.2.2 Multi-criteria decision analysis 105
  8.3 Results 110
    8.3.1 IBM development 110
    8.3.2 Multi-criteria decision analysis 111
  8.4 Discussion 117
    8.4.1 IBM development 118
    8.4.2 Multi-criteria decision analysis 119
    8.4.3 Conclusions 121

Chapter 9: Thesis discussion 123

  9.1 Quantitative review of current literature 123
  9.2 Fundamental drivers of signal crayfish passage behaviour and dispersal 124
    9.2.1 Drivers of barrier passage behaviour 124
    9.2.2 Drivers of dispersal 126
  9.3 Long-term catchment-scale effectiveness of exclusion barriers 127
    9.3.1 Insights into long-term catchment-scale effectiveness of exclusion barriers 127
    9.3.2 Individual-based modelling approach 129
  9.4 Are barriers an effective management tool for freshwater invasive species? 130
    9.4.1 Effectiveness of exclusion barriers for signal crayfish 130
    9.4.2 Overall effectiveness of exclusion barriers 131
  9.5 Priorities for future work 133
  9.6 Conclusions 135
  9.7 Research outputs 135

Reference List 137

Appendix A: Supplementary information for Chapter 2 193

  A.1 Summary of studies included in the meta-analysis 193
  A.2 Diagnostic plots for meta-analysis 198
    A2.1 Diagnostic plots for introduction 198
    A2.2 Diagnostic plots for establishment 199
    A2.3 Diagnostic plots for spread 200

Appendix B: Supplementary information for Chapter 5 203

  B.1 Experimental evaluation of the effect of density on passage 203
    B.1.1 Morphological characteristics of experimental crayfish 203
    B.1.2 Details of experimental setup 203
  B.2 ODD description of crayfish dispersal IBM 205
    B.2.1 Purpose and patterns 205
    B.2.2 Entities, state variables and scales 205
    B.2.3 Process overview and scheduling 207
    B.2.4 Design concepts 207
    B.2.5 Initialisation 209
    B.2.6 Input data 210
    B.2.7 Submodels 210
  B.3 Additional information for model validation 215
  B.4 Impacts of a downstream barrier 216

Appendix C – Supplementary information for Chapter 6 217

  C.1 Repeatability of personality traits 217
  C.2 Boldness-activity syndrome 218
  C.3 Time to first attempt 218

Appendix D: Supplementary information for Chapter 7 219

  D.1 Keywords for image validation using Google Cloud Vision 219
    D.1.1 Boating 219

D.1.2 Angling 219

Appendix E: Supplementary information for Chapter 8 221

E.1 River Glaven segment map 221
E.2 Super-individual diagnostic plots 222
E.3 Flow scaling factor 223
E.4 Accessibility-weighted habitat availability calculations 224
E.5 Value functions 225
E.6 MCDA rankings 226
E.7 Forecast period sensitivity analysis 231
E.8 Weights sensitivity analysis 235

Table of Tables

Table 2.1 – The criteria for inclusion against which full texts were assessed. 22

Table 2.2 – The results of subgroup analysis to determine other factors which may have explained heterogeneity in effect size, showing the within-subgroup heterogeneity (Q), degrees of freedom (df) and significance (*p*). Dashes denote cases where only one category was present in the subgroup, meaning analysis was not possible..27

Table 5.1 – Key metrics used to assess crayfish movement behaviour when passing a model Crump weir at different densities...50

Table 6.1 – Metrics used to assess the behaviour of American signal crayfish at a model Crump weir installed in a recirculatory flume at the International Centre for Ecohydraulics Research Facility, University of Southampton Boldrewood Campus..67

Table 6.2 – Variables associated with the motivation of signal crayfish (n = 56) to pass an experimental weir. 71

Table 7.1 – Summary of metrics used to assess factors associated with local dispersal in American signal crayfish (*Pacifastacus leniusculus*) in England. 82

Table 8.1 – Criteria weights used in a sensitivity analysis to assess the robustness of a multi-criteria decision analysis aiming to identify containment solutions for American signal crayfish (*Pacifastacus leniusculus*). 109

Table 8.2 – Results of a multi-criteria decision analysis to determine to optimal combination of barrier modifications in the river Glaven catchment (Norfolk, UK), showing the 10 highest-ranked alternatives......................................112

Table 8.3 – The sensitivity of ranks obtained during a multi-criteria decision analysis aiming to identify a combination of barrier modifications that could limit the spread of American signal crayfish (*Pacifastacus leniusculus*) while minimising cost and impacts on native fishes, showing the ranks of the 10 originally best-performing alternatives under different weighting scenarios......117

Table 9.1 – Factors that should be considered prior to the installation of invasive exclusion barriers, including some examples of questions that should be addressed by conservation managers. 132

Table of Figures

Figure 1.1 – The unified framework for biological invasions, showing the stages of invasion (green), the barriers to moving between stages (dark blue), the management techniques that can be applied at each stage (light blue), and the terminology that can be applied throughout the process (red). Adapted from Blackburn *et al.* (2011)..2

Figure 1.2 – Pathways of introduction of freshwater non-native species (grey bars) and high-impact non-native species (white bars) in Europe. Data from Nunes *et al*. (2015)..7

Figure 2.1 – PRISMA literature search flow diagram showing the number of studies retained or excluded at each stage of the search. 23

Figure 2.2 – Overall effect size (Hedges' *g*) showing the effect of anthropogenic barriers on each stage of the invasion process. Error bars represent 95% confidence intervals (** = p < 0.01, *** = p < 0.001)...27

Figure 2.3 – Variation in summary effect sizes (Hedges' *g*) across different a) taxonomic groups, b) climatic regions, c) sample site locations relative to the barrier, and d) barrier heights...29

Figure 2.4 – Summary of biases in current research regarding the interaction between invasive species and river infrastructure, showing differences in the number of data points between: a) stages of the invasion process, b) taxonomic groups, c), geographic regions, d) barrier types, and e) barrier head drops. Bar colours denote the stage of the invasion process (black = introduction, grey = establishment, white = spread). 30

Figure 3.1 – Schematic of the thesis, showing the objectives, their links to the relevant results chapters, and the methodological approaches used in each chapter. 38

Figure 4.1 – a) American signal crayfish (*Pacifastacus leniusculus*) showing the characteristic pale 'signal' on the chelae. Image credit: Mark Philpott, published under a Creative Commons license. b) The distribution of the American signal crayfish in Europe, with black points representing areas with confirmed records. From Kouba *et al.* (2014). 39

Figure 5.1 – 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 of the experimental area. Grey circles indicate locations of measurements taken using an electromagnetic flow meter (Valeport Model 801; measurements averaged over 10 seconds). From left to right, white lines denote the downstream extent, crest and upstream extent of the weir. 48

Figure 5.2 – 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. 54

Figure 5.4 – 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. 55

Figure 5.3 – 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. 55

Figure 6.1 – Plan view of experimental arenas used to assess a) boldness and activity, and b) sociability in American signal crayfish (*Pacifastacus leniusculus*). . 63

Figure 6.2 – (a) Side view of the experimental area used to assess the behaviour of American signal crayfish at an artificial barrier, showing the model Crump weir (dark grey), PIT antennas (dashed lines), PIT antennas detection distances (light grey shaded area), and release location of the crayfish (cross). (b) Plan view flow velocity map of the experimental area (grey circles represent locations of flow velocity measurements). 66

Figure 6.3 - Relationships between the boldness of American signal crayfish and (a) probability of attempting to pass an experimental Crump weir, (b) the number of attempts, (c) the time to first attempt and (d) the maximum distance of ascent. Black lines show GLM predictions and grey shading denotes 95% confidence intervals. 70

Figure 6.4 – Relationship between the activity of American signal crayfish and the time to the first attempt. Black lines show GLM predictions and grey shading denotes 95% confidence intervals. 71

Figure 7.1 – The hierarchical clustering approach used to identify distinct local invasions of American signal crayfish (*Pacifastacus leniusculus*) in England, exemplified using the River Tamar Catchment. a) Dendrogram showing the relationships between individual records. Numbers at each branch terminal represent a single record. b) Records of signal crayfish overlayed on a map of the river network in the catchment. Different colours represent separate clusters...80

Figure 7.2 – An example of a distinct introduction of American signal crayfish (*Pacifastacus leniusculus*) in the River Tamar catchment (inset), identified using a hierarchical clustering approach. The grey shaded area denotes the 300 m buffer zone in which predictors of secondary spread were calculated. Blue points show records of signal crayfish, and the black line represents the river network. 82

Figure 7.3 – Sections of river in England (grey shaded area) which are currently occupied by American signal crayfish *(Pacifastacus leniusculus*; red lines), identified using a hierarchical clustering analysis of all publicly-available records.85

Figure 7.4 – Distribution of upstream and downstream invasion rates of American signal crayfish (*Pacifastacus leniusculus*) in English rivers...........................86

Figure 7.5 – Factors associated with the secondary spread of American signal crayfish (*Pacifastacus leniusculus*) in England, showing the relationships between a) boating density and upstream invasion rate, and b) water temperature and downstream invasion rate. Points denote distinct invasion events identified using a hierarchical clustering analysis of available records, solid lines show predictions obtained from a robust GLM, and dashed lines show the standard errors of the predictions. 87

Figure 8.2 – The workflow used to determine whether American signal crayfish (*Pacifastacus leniusculus*) can pass a riverine barrier. 100

Figure 8.3 – Predictions from first principles as to whether American signal crayfish (*Pacifastacus leniusculus*) can pass a flow-based barrier by walking or swimming (red), walking only (green), swimming only (blue), or are unable to pass (grey), showing a) predictions made using the original parameters proposed by Frings *et al*. (2013), and b) the updated parameters developed in this study. Solid lines show the maximum velocity against which crayfish can walk at different barrier slopes, and dashed lines show the maximum

flow velocity which crayfish can swim against. Black circles denote the original trials conducted by Frings *et al*., (2013), with crosses showing successful passages and circles showing trials with no passages. Red points show the results of additional, more recent studies (Kerr *et al*. 2021, Chapters 5 and 6) which were used to adjust the parameters. 101

Figure 8.4 – Modifications applied to a) sloped weirs, b) vertical weirs, c) stepped weirs, d) culverts, and e) fords (without vertical drops or steps) to limit the upstream movements of American signal crayfish (*Pacifastacus leniusculus*) in an individual-based model. Diagrams show existing structures (dark grey and black), the direction of water flow (white arrow), side plates extending downstream along the river banks (SP), overhanging lips (OL), plates at the crest of sloping weirs (CP), and new vertical barriers (NVB), with all modifications made of stainless steel. Modifications are based on Krieg *et al.* (2021) and Chucholl *et al.* (2022). 104

Figure 8.5 – Hierarchical decision tree used to inform a multi-criteria decision analysis aiming to quantify the trade-offs of management techniques used to manage the spread of American signal crayfish (*Pacifastacus leniusculus*). Numbers denote the weights applied to each criteria, as determined by swing weighting. 106

Figure 8.6– Predictions of an individual-based model regarding the spread of American signal crayfish (*Pacifastacus leniusculus*) in the River Glaven catchment (Norfolk, UK) over a 24 year period, showing a) the invaded area at the end of the simulation period (blue lines show invaded area, blue triangles show barriers), b) the total linear expansion rate (TLER) over time (dashed grey line = 20-day rolling average, solid black line = 365 day rolling average) c) the change in daily mean biomass over time (dashed grey line = 20-day rolling average, solid black line = 365 day rolling average, and d) the predicted time taken to pass the barrier at Letheringsett (Easting = 606204, Northing = 338685) compared to the known time from historic observations (error bars show standard deviation). 110

Figure 8.7 – Raw data from criteria assessments conducted as part of a multi-criteria decision analysis (MCDA) aiming to identify optimal containment techniques for American signal crayfish (*Pacifastacus leniusculus*), showing a) river length occupied by signal crayfish in 2033 as predicted by an individual-based model (points = means, error bars = 95% confidence intervals), b) accessibility-weighted habitat availability (AWHA) for native fishes (blue diamonds = European eel [*Anguilla anguilla*], orange triangles = brown trout [*Salmo trutta*], cyan circles = brook lamprey [*Lampetra*

planeri]), and c) the total cost associated with different combinations of barrier modifications. Barrier modifications are sorted by their rank in the final MCDA (left to right), starting with the optimal solution. 113

Figure 8.8 – Predictions from an individual-based model showing the performance of the optimal combination of barrier modifications to limit the spread of American signal crayfish in the river Glaven catchment (Norfolk, UK), while minimising costs and impacts on native fishes. The optimal combination was identified using multi-criteria decision analysis, and figures show: a) the total river length invaded over time in the optimal solution (orange line), compared to an alternative with no modifications (blue line), and b) signal crayfish range at the end of the 29-year model simulation (blue lines denote invaded area, blue triangles show unmodified barriers, orange triangles show modified barriers)..114

Figure 8.9 – The influence of uncertainty in individual-based model predictions on the results of a multi-criteria decision analysis aiming to identify optimal containment techniques for American signal crayfish (*Pacifastacus leniusculus*), showing the distribution of changes in rank after changing mean predictions to a) upper, and b) lower confidence intervals using a one-at-a-time approach..115

Figure 8.10 – The influence of forecast period on the results of a multi-criteria decision analysis comparing the performance of different combinations of barrier modifications against three criteria (ability to limit the spread of American signal crayfish [*Pacifastacus leniusculus*], impacts on native fishes, and cost). Figures show comparisons of the ranks obtained after 15-year forecasts with those obtained from a) 5-year and b) 10-year forecasts. Orange points show the 10 highest-ranked solutions from the 15-year forecasts. 115

Figure 8.11 – The influence of weights on the results of a multi-criteria decision analysis aiming to identify a combination of barrier modifications that effectively limited the spread of American signal crayfish (*Pacifastacus leniusculus*), while minimising the costs and impacts on native fishes. Figures show a comparison of the ranks obtained using the original weights with the ranks obtained under a variety of weighting scenarios (equal weights; each criteria assigned 60% of the overall weight with equal distribution of the remaining weight). Coefficients (r_s) were obtained from Spearman's rank tests. 116

Figure C3.1 – The relationship between a) boldness, and b) activity with the time taken for American signal crayfish (*Pacifastacus leniusculus*) to attempt to pass an experimental in-stream barrier. In these figures, individuals which did not attempt to pass the barrier within the experimental period have been removed. 218

List of Accompanying Materials

Daniels, J.A. 2023. Dataset in support of the publication 'The effects of anthropogenic in-stream structures on non-native species: a meta-analysis’. University of Southampton, doi: https://doi.org/10.5258/SOTON/D2693 [Dataset]

Daniels, J.A. 2023. Dataset for the journal paper 'River infrastructure and the spread of freshwater invasive species: inferences from an experimentally-parameterised individual-based model'. University of Southampton, doi: https://doi.org/10.5258/SOTON/D2552 [Dataset]

Daniels, J.A. 2022. Dataset for 'Personality-dependent passage behaviour of an aquatic invasive species at a barrier to dispersal'. University of Southampton, doi: https://doi.org/10.1016/j.anbehav.2022.07.005 [Dataset]

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Daniels, J.A. 2023. Dataset in support of the article 'Optimising the installation of invasive species exclusion barriers under multiple conservation objectives'. University of Southampton, doi: https://doi.org/10.5258/SOTON/D2691 [Dataset]

Research Thesis: Declaration of Authorship

Print name: Jack Daniels

Title of thesis: The effectiveness of anthropogenic in-stream barriers as a management strategy for non-native species

I declare that this thesis and the work presented in it are my own and has been generated by me as the result of my own original research.

I confirm that:

1. This work was done wholly or mainly while in candidature for a research degree at this University;
2. Where any part of this thesis has previously been submitted for a degree or any other qualification at this University or any other institution, this has been clearly stated;
3. Where I have consulted the published work of others, this is always clearly attributed;
4. Where I have quoted from the work of others, the source is always given. With the exception of such quotations, this thesis is entirely my own work;
5. I have acknowledged all main sources of help;
6. Where the thesis is based on work done by myself jointly with others, I have made clear exactly what was done by others and what I have contributed myself;
7. Parts of this work have been published as:
    - Chapter 6 - Daniels, J.A., Kemp, P.S. 2022. Personality-dependent passage behaviour of an aquatic invasive species at a barrier to dispersal. *Animal Behaviour*. 192. 63-74. https://doi.org/10.1016/j.anbehav.2022.07.005
    - Chapter 5 - 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*. 60:6. 999-1009. https://doi.org/10.1111/1365-2664.14387

Signature: Date: 23/05/24

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Definitions and Abbreviations

A. Referenced Nomenclature

A.1 Families

Aquatic snails (Tateidae)

Astacid crayfish (Astacidae)

Cambarid crayfish (Cambaridae)

Carp (Cyprinidae)

Cats (Felidae)

Cercopagidid water fleas (Cercopagididae)

Characids (Characidae)

Cottids (Cottidae)

Daphnid water fleas (Daphniidae)

Eels (Anguillidae)

Freshwater mussels (Dreissenidae)

Gammarids (Gammaridae)

Gobies (Gobiidae)

Higher termites (Termitidae)

Lamprey (Petromyzontidae)

Long-whiskered catfishes (Pimelodidae)

Mud crabs (Panopeidae)

Mussels (Mytilidae)

Neotropical spiny rats (Echimyidae)

Orb-weaver spiders (Araneidae)

Ovenbirds (Furnariidae)

Penaeid shrimps (Penaeidae)

Pike (Esocidae)

Poecelids (Poeciliidae)

Pondweeds (Potamogetonaceae)

Rodents (Cricetidae)

Salmon (Salmonidae)

Serrasalmids (Serrasalmidae)

Skinks (Scincidae)

Smelts (Osmeridae)

Snakeheads (Channidae)

Southern hemisphere crayfish (Parastacidae)

Squirrels (Sciuridae)

Starlings and Mynahs (Sturnidae)

Sunfishes (Centrarchidae)

Temperate basses (Moronidae)

Tits (Paridae)

True lizards (Lacertidae)

True toads (Bufonidae)

Water milfoils (Haloragaceae)

Water moulds (Leptolegniaceae)

Willowherbs (Onagraceae)

A.2 Species

American eel (*Anguilla rostrata*)

American signal crayfish (*Pacifastacus leniusculus*)

Angel de la Guarda deer mouse (*Peromyscus guardia*)

Asian carp (*Hypophthalmichthys* spp.)

Atlantic mud crab (*Panopeus herbstii*)

Atlantic salmon (*Salmo salar*)

Bighead goby (*Ponticola kessleri*)

Bitterling (*Rhodeus sericeus*)

Brook lamprey (*Lampetra planeri*)

Brook trout (*Salvelinus fontinalis*)

Brown trout (*Salmo trutta*)

Bullhead (*Cottus gobio*)

Cane toad (*Rhinella marina*)

Caramote prawn (*Melicertus kerathurus*)

Common carp (*Cyprinus carpio*)

Common lizard (*Lacerta vivipara*)

Common myna (*Acridotheres tristis*)

Common wall lizard (*Podarcis muralis*)

Conehead termite (*Nasutiternes corniger*)

Coypu (*Myocastor coypus*)

Crayfish plague (*Aphanomyces astaci*)

Curly pondweed (*Potamogeton crispus*)

Cutthroat trout (*Oncorhynchus clarkii pleuriticus*)

Delicate skink (*Lampropholis delicata*)

Domestic cat (*Felis catus*)

Dourado (*Salminus bralienses*)

Eastern Cape redfin minnow (*Pseudobarbus afer*)

Eurasian watermilfoil (*Myriophyllum spicatum*)

European eel (*Anguilla anguilla*)

Freshwater shrimp (*Gammarus fasciatus*)

Golden mussel (*Limnoperna fortunei*)

Great tit (*Parus major*)

Japanese tiger prawn (*Marsupenaeus japonicus*)

New Zealand mud snail (*Potamopyrgus antipodarum*)

Noble crayfish (*Astacus astacus*)

North American red squirrel (*Tamiasciurus hudsonicus*)

Northern pike (*Esox lucius*)

Northern snakehead (*Channa argus*)

Orb-weaving spider (*Cyrtophora citricola*)

Pacu (*Piaractus mesopotamicus*)

Pintado (*Pseudoplatystoma corruscans*)

Rainbow smelt (*Osmerus mordax*)

Rainbow trout (*Oncorhynchus mykiss*)

Red swamp crayfish (*Procambarus clarkii*)

Round goby (*Neogobius melanostomus*)

Rudd (*Scardinius erythrophthalmus*)

Rusty crayfish (*Faxonius rusticus*)

Sea lamprey (*Petromyzon marinus*)

Silver carp (*Hypophthalmichthys molitrix*)

Smallmouth bass (*Micropterus dolomieu*)

Spiny water flea (*Bythotrephes longimanus*)

Spinycheek crayfish (*Faxonius limosus*)

Thorn-tailed rayadito (*Aphrastura spinicauda*)

Topmouth gudgeon (*Pseudorasbora parva*)

Water flea (*Daphnia lumholtzi*)

Water primrose (*Ludwigia grandiflora*)

Western mosquitofish (*Gambusia affinis*)

White perch (*Morone americana*)

White-clawed crayfish (*Austropotamobius pallipes*)

Yabby (*Cherax destructor*)

Zebra mussel (*Dreissena polymorpha*)

B. Acronyms

AMBER	Adaptive Management of Barriers in European Rivers
API	Application programming interface
ART	Artificial refuge trap
AWHA	Accessibility-weighted habitat availability
CBD	Convention on Biological Diversity
CCTV	Closed-circuit television
CEE	Collaboration for Environmental Evidence
CIESIN	Center for International Earth Science Information Network
CL	Carapace length
CPU	Central processing unit
DOY	Day of the year
eDNA	Environmental deoxyribonucleic acid
EU	European Union
GLM	Generalised linear model
GLMM	Generalised linear mixed model
HDX	Half duplex
IBM	Individual-based model
IPM	Integrated pest management
IUCN	International Union for Conservation of Nature
LOR	Log odds ratio
MAM	Minimum adequate model
MCDA	Multi-criteria decision analysis
NBN	National Biodiversity Network
NRFA	National river flow archive
OAT	One-at-a-time
ODD	Overview, design concepts and details
OS	Ordnance survey
PC	Principal component
PICOS	Problem, Intervention, Control, Outcome, Study designs framework
PIT	Passive integrated transponder
PRISMA	Preferred Reporting Items for Systematic Reviews and Meta-Analyses
RAM	Random access memory
REML	Restricted maximum likelihood
SD	Standard deviation
SE	Standard error

TLER	Total linear expansion rate
VIF	Variance inflation factor
WCS	Wildlife Conservation Society

C. Notation

Notation	Unit	Description
n	Count	Sample size
df		Degrees of freedom
SD		Standard deviation
SE		Standard error
CI		95% confidence intervals
v		variance
p		p value, probability value
g		Hedge's g
S		Pooled standard deviation
J		Correction for small sample size
r		Correlation coefficient
X^2		Chi-squared statistic
z		z-value (derived Egger's test for publication bias)
Q		Total heterogeneity statistic
R_A		Adjusted repeatability
W	Metres (m)	Width
L	Metres (m)	Length
α	Degrees (°)	Barrier slope
μ		Coulomb friction factor
F_m	Newtons (N)	Muscular force
ρ	kg m^{-3}	Density
C_d		Drag coefficient
A	m^2	Frontal area
u	m s^{-1}	Flow velocity
V	m^3	Volume
m	g	Mass
G	m s^{-2}	Gravitational acceleration
s		Final score obtained from multi-criteria decision analysis
w		Weights used during multi-criteria decision analysis
WM	g	Wetted mass

DM	g	Dry mass
P		Probability of occurrence
MD	m	Movement distance
c		Correction factor
DDS		Density-dependent scaling factor
TDS		Temperature-dependent scaling factor
M		Probability of mortality
F	Number of eggs	Fecundity

D. General Terminology

Abiotic: Non-living (e.g., physical or chemical) features of the environment.

Acclimation: Process by which an organism adjusts to a change in its environment.

Animal personality: Intraspecific behavioural differences which are stable across time and context.

Anthropocene: Geological era during which human activities have caused disinct impacts on the environment.

Anthropogenic: Resulting from the influence of human beings.

Ark site: Isolated refuge areas used to protect native species.

Behavioural syndrome: Suite of correlated behavioural traits.

Benthic: Associated with or occurring on the bottom of a water body.

Biological control: The use of living organisms to control the population of an invasive species.

Carapace: Hard upper shell (in this thesis relating to crayfish).

Chela: Hinged, picer-like claw.

Chemical control: The use of chemicals (e.g., pesticides) to control the population of an invasive species.

Connectivity conundrum: Trade-off between increasing habitat connectivity for native species while limiting connectivity for invasive species.

Conservation: Preservation, protection, or restoration of natural environments to prevent species extinctions, enhance ecosystem services, and protect biological diversity.

Containment: Preventing the secondary range expansion of an invasive species.

Ecosystem engineer: A species that directly or indirectly modulates the availability of resources through their impacts on biotic or abiotic materials, leading to modification, maintenance, creation, or destruction of habitats.

Ecosystem services: The direct and indirect contributions of ecosystems to human wellbeing and quality of life.

Effect size: A value representing the strength of the relationship between variables.

Eradication: Removal of an entire population of an invasive species, including all propagules.

Established/naturalised species: A non-native species that has established a self-sustaining population outside of its native range.

Establishment: The process by which a non-native species forms a self-sustaining population within the introduced range.

Exclusion barrier: Anthropogenic infrastructure installed to prevent the dispersal of invasive species, typically in freshwater systems.

Fish pass: A structure designed to allow fish to pass an anthropogenic barrier to dispersal (e.g., a dam or weir).

Habitat: An area providing the resources and environmental conditions necessary for a species to survive or reproduce.

Habitat fragmentation: The subdivision of habitat into smaller and more isolated patches as a result of natural or anthropogenic processes.

Horizon scanning: The process of identifying species which may become invasive in the near future, and assessing their potential impacts.

Hydrochorous: Dispersed by the movement of water.

Impoundment: An area of elevated water levels caused by an anthropogenic structure (e.g., a dam or weir).

Individual-based modelling: Population and community modelling approach which conceptualises ecological systems as collections of unique and autonomous individuals.

Integrated pest management: Invasive species management approach which combines physical, chemical, biological, and cultural control methods.

Intentional fragmentation: The act of purposefully reducing habitat connectivity.

Introduced/casual species: A non-native species that has been introduced outside its native range, but has not established a self-sustaining population.

Introduction: The process by which a non-native species is released outside its native range.

Introduction pathway: Means and routes by which non-native species are introduced into new environments outside of their native range.

Invasion dynamics: Spatio-temporal variation of invasive species population size, density, and distribution.

Invasion front: The area occupied by an invasive species which is furthest from the initial point of introduction.

Invasion hub: An area containing an established population of non-native species which spreads into the surrounding environment.

Invasion process: The process by which a species becomes invasive, consistinf of four phases: 1) transport, 2) introduction, 3) establishment, and 4) spread.

Invasive species: A species that has established outside its native range due to anthropogenic activity, and is spreading to form multiple self-sustaining populations.

Isolation managament: The use of anthropogenic barriers to isolate an area of habitat within which native species are protected.

Lentic: Still fresh water.

Lotic: Flowing fresh water.

Mechanical control: The use of mechanical methods (e.g., trapping, physical removal) to control the population of an invasive species.

Mitigation: An action intended to reduce the negative impact of an anthropogenic disturbance.

Niche displacement: The process by which an invasive species overtakes an ecological niche that was previously occupied by a native species.

Non-native/alien species: Any organism that has been transported beyond its native range by anthropogenic activity.

Passive citizen science: The use of data generated by social media to derive ecological insights.

Prevention: Eliminating the introduction of non-native species into new habitats.

Publication bias: The failure to publish results based on the direction or strength of the study findings.

Range expansion: The spatial spread of a population into previously unoccupied regions.

Rheotaxis: Orientation relative to water currents.

River infrastructure: Any in-stream structure constructed by humans (e.g., dams, weirs, culverts, fords).

Selective fish passage: Solution to the connectivity conundrum which aims to allow movements by desirable species, while simultaneously blocking the movements of undesirable species.

Spread: The process by which a non-native species increases its range within the introduced region.

Transport: The process by which a non-native species is moved beyond its native range.

Vector: Means and routes by which non-native species are introduced into new environments outside of their native range.

Zoochorous: Dispersed by the movement of animals.

Chapter 1: Introduction

1.1 Invasive species

1.1.1 Background

Anthropogenic activity is now the dominant driver of environmental change, and the impacts on the global environment are so profound that the earth is moving into a new geological epoch: the Anthropocene (Crutzen, 2002; Steffen *et al.*, 2007; Lewis & Maslin, 2015). Global surface temperatures have risen by between 0.87 and 1.22 °C since 1850 as a result of human activity (Haustein *et al.*, 2017), and this has been accompanied by significant alterations to biogeochemical and hydrological cycles (Steffen *et al.*, 2011). Humans are also driving increasing levels of extinction and population decline, with current estimates suggesting that vertebrate extinction rates are up to 100 times greater than the background rate (Ceballos *et al.*, 2015). These rates of extinction are comparable with those in previous mass extinction events, leading some to suggest that a sixth mass extinction is currently underway (Barnosky *et al.*, 2011).

A key feature of the Anthropocene is the human-mediated movement of species beyond their natural range (Ricciardi, 2007). Fossil records have demonstrated that mass movement of species can occur under natural conditions (e.g., Vermeij, 1991; Webb, 1991), but the vast spatial-temporal scale of human-mediated invasions is unprecedented in the historical record (Ricciardi, 2007). Currently, there are nearly 17,000 non-native species recognised globally, including 7713 species of vascular plants, 5164 insects, 537 fishes, 494 molluscs, 424 birds, and 250 mammals (Seebens *et al.*, 2017). These non-native species are gradually replacing native biota, leading to a global homogenisation of flora and fauna (Olden *et al.*, 2004; Dornelas *et al.*, 2014). The extent of this homogenisation is likely to increase in the future, as increasing globalisation and climate change facilitate higher rates of introduction and establishment (Hellmann *et al.*, 2008; Seebens *et al.*, 2017).

1.1.2 Invasive species – process and definitions

Despite their prevalence, there is significant disagreement on the terminology used to describe species that occur outside their native range (Valéry *et al.*, 2008). However, Blackburn *et al.* (2011) and Richardson *et al.* (2010) provided clarity by defining the relevant terminology within the context of the invasion process. The process of biological invasion consists of four key phases: 1) transport beyond the native range through anthropogenic activity, 2) introduction into a new environment, 3) establishment of a viable population through several cycles of survival and reproduction, and 4) spread of invasives to new locations (Blackburn *et al.*, 2011; Fig. 1.1). To progress between stages a species must overcome a series of barriers, and an invasion can fail at any stage (Blackburn *et al.*, 2011). Any organism that has been transported by humans to an area outside its native range can be considered alien or non-native, regardless of whether it was transported intentionally (e.g., for agriculture, recreational or aesthetic reasons) or accidentally (e.g., in ballast water or on recreational equipment). A species that is introduced into the recipient ecosystem but is not capable of forming a self-sustaining population is referred to as casual or introduced. Conversely, species that are able to sustain self-replacing populations over several generations within the introduced range are referred to as naturalised or established. Finally, a species that has been through all four stages of the invasion process, including spreading to form multiple self-sustaining populations, is referred to as invasive.

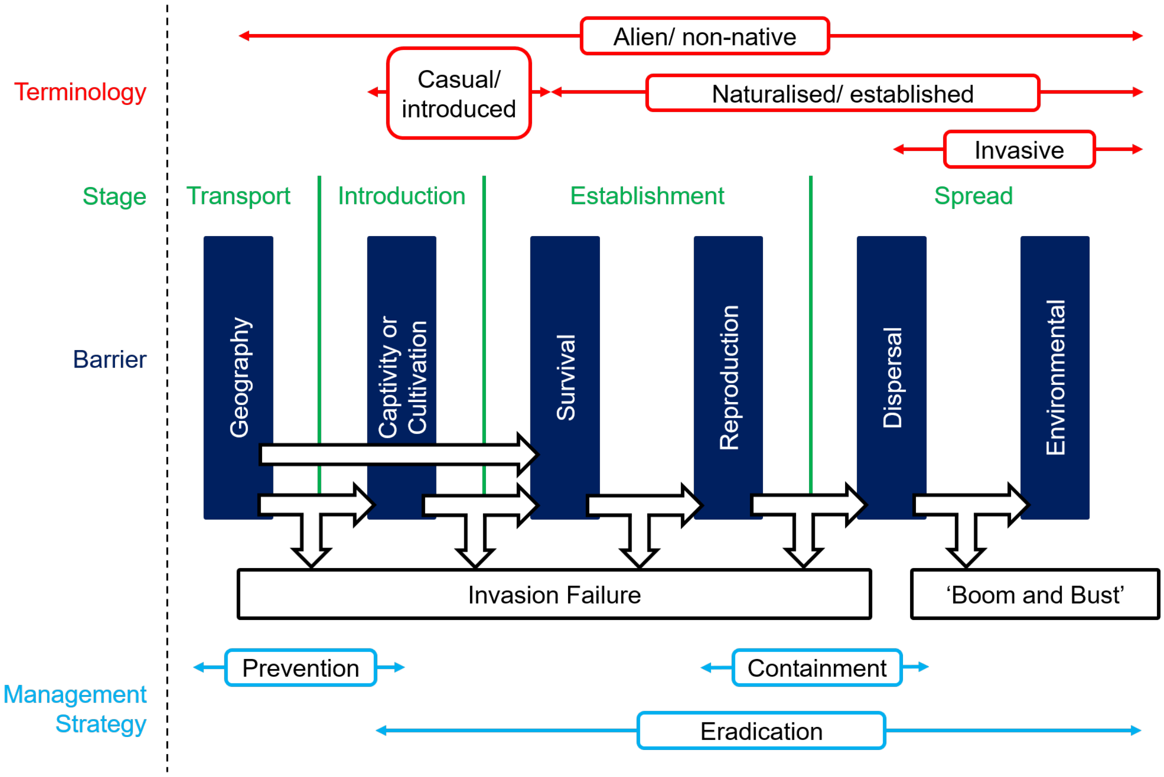

Figure 1.1 – The unified framework for biological invasions, showing the stages of invasion (green), the barriers to moving between stages (dark blue), the management techniques that can be applied at each stage (light blue), and the terminology that can be applied throughout the process (red). Adapted from Blackburn *et al.* (2011).

The definition of an invasive species proposed by both Blackburn *et al.* (2011) and Richardson *et al.* (2010) purposefully eschews any reference to the impact of the species in question, and is instead based on ecological and biogeographical concepts. Despite this, in a policy context, invasive species are commonly defined on the basis of their negative impacts. For example, the European Union (EU) defines an invasive species as one "…whose introduction or spread has been found to threaten or adversely impact upon biodiversity and related ecosystem services" (EU, 2014). Similarly, the International Union for the Conservation of Nature (IUCN, 2000) define an invasive species as a species which "… is an agent of change, and threatens native biological diversity". However, the impacts of non-native species can be manifested at any stage of the invasion process, and therefore this definition is difficult to reconcile with the framework proposed by Blackburn *et al.* (2011). For example, the introduction of a single cat (*Felis catus*) resulted in the extinction of the

Angel de la Guarda deer mouse (*Peromyscus guardia*) on Estanque Island in the Gulf of California (Vázquez-Domínguez *et al.*, 2004). This single individual had a significant impact on the recipient ecosystem and would thus be classified as invasive by the EU and IUCN, but did not undergo establishment or spread and therefore does not meet the biogeographical criteria for an invasive species. Further discrepancies between these definitions were highlighted by Ricciardi and Cohen (2007), who found that invasiveness (measured in terms of the rate of establishment and spread) does not predict impact across a wide variety of taxonomic groups. The impacts of non-native species often change over time and are heavily dependent on the characteristics of both the invader and the recipient ecosystem, meaning that definitions relating to impact are hard to apply consistently across different scenarios (Crooks & Soulé, 1999; Valéry *et al.*, 2008). Thus, from hereon in the term "invasive" refers to the ecological and biogeographic approach outlined above, and impactful non-native species are distinguished using the terms "damaging" and "high-impact" (for formal definitions of the terms used in this thesis, see Box 1.1).

1.1.3 Invasive species – impacts and management

1.1.3.1 Quantifying impacts

Non-native species can have significant ecological, evolutionary, and socioeconomic impacts on the recipient ecosystem at all stages of the invasion process (Mooney & Cleland, 2001; Pejchar & Mooney, 2009; Vilà *et al.*, 2010). However, high-impact invasive species form a small subset of those that are introduced, and the vast majority of non-native species have minimal impacts (Simberloff, 2011). Quantifying the proportion of non-native species that are impactful is challenging as thorough assessments are relatively rare (Simberloff, 2011), and the impacts of invasive species can change over time (Strayer *et al.*, 2006). However, the widely cited "tens rule" proposed by Williamson and Fitter (1996) suggests that only 10% of introduced species will establish successfully, and only 10% of established species will go on to become damaging invasive species. Indeed, only 11% of over 10,000 non-native species in Europe are known to cause a measurable ecological impact (Vilà *et al.*, 2010).

Even in situations where impacts are identified, quantifying the extent of the changes is often challenging (Simberloff *et al.*, 2013). Parker *et al.* (1999) provided a strong theoretical basis for assessing the magnitude of the impact associated with a non-native species, suggesting that overall impact is a product of the size of the invasive range, the average abundance within the native range, and the *per capita* effect. However, many impacts are subtle or occur in remote and inaccessible habitats, meaning that accurate quantification of these parameters is dependent on intensive study (Simberloff *et al.*, 2013). Further difficulties arise from the widespread classification of impacts as either positive or negative, as these classifications are often subjective and depend on the perspective of those assessing the impact (Pyšek *et al.*, 2012). For example, the Japanese tiger prawn

(*Marsupenaeus japonicus*) was highly prized by fishermen after its introduction to the Mediterranean, but led to the extirpation of a native prawn (*Melicertus kerathurus*) and was thus regarded as harmful by conservationists (Galil, 2007).

Box 1.1: Key definitions

Definitions adapted from Blackburn et al. (2011) and Richardson et al. (2010).

Alien/ non-native species: A species that is present in a region as a result of anthropogenic activity which has enabled fundamental biogeographical barriers to be overcome.

Casual/ introduced species: A non-native species that has not established a self-sustaining population in the recipient ecosystem.

Establishment: The process by which a non-native species undergoes several cycles of survival and reproduction within the invaded range, forming a self-sustaining population.

Introduction: The release of a species (i.e., inoculation of propagules) beyond its native range.

Invasion process: A four-stage process (transport, introduction, establishment, spread) by which a non-native species transitions to an invasive species.

Invasive species: A non-native species that has been through all four stages of the invasion process, including the formation of a self-sustaining population in the invaded range, and spread beyond the initial site of introduction.

Naturalised/ established species: A non-native species that survives and reproduces in the invaded region without (or in spite of) human intervention, and forms a self-sustaining population.

Spread: The process by which a non-native species expands its range within the invaded region.

Transport: The movement of a species beyond its native range as a result of human activity. This may occur as a result of direct movement by humans (i.e., human-mediated extra-range dispersal), but may also be a result of the removal of local

1.1.3.2 Ecological and socioeconomic impacts

Despite the challenges in evaluating the magnitude and direction of their impacts, non-native species are known to cause significant ecological changes in the recipient ecosystem (Ehrenfeld, 2010; Simberloff, 2011). High-impact invasive species often act as ecosystem engineers (Crooks, 2002), and can disrupt ecosystem processes such as nutrient cycling

(Vilà *et al.*, 2011) and fire regimes (Mandle *et al.*, 2011). Non-native species can also substantially modify the physical habitat (e.g., Bertness, 1984; Strayer *et al.*, 1999), and in some cases create entirely new habitats (e.g., Anderson *et al.*, 2006; Anderson & Rosemond, 2007). Furthermore, non-native species can directly impact native species through competitive exclusion, niche displacement, hybridisation, predation and disease transmission, and can lead to their extirpation and extinction (Mooney & Cleland, 2001; Kenis *et al.*, 2009). Indeed, the ecological impacts of non-native species are so severe that they have been implicated as a driving force in 33% of animal and 25% of plant extinctions since 1500 (Blackburn *et al.*, 2019).

Alongside the significant ecological implications, non-native species can have substantial socioeconomic impacts through the loss of ecosystem services and associated reductions in human wellbeing (Pejchar & Mooney, 2009). This loss of ecosystem services, coupled with damage to important industries (e.g., agriculture and forestry) and extensive management costs (e.g., for control, eradication and research), can lead to substantial economic losses (Diagne *et al.*, 2021). Indeed, between 1970 and 2017 the average annual costs associated with biological invasions globally was US$26.8 billion, although this figure is likely to be a substantial underestimation (Diagne *et al.*, 2021). Furthermore, the introduction of novel diseases and their associated vectors can lead to significant public health problems (e.g., Kramer *et al.*, 2007; Bataille *et al.*, 2009). Indeed, the global COVID-19 pandemic is in essence a biological invasion, although it is rarely considered in this context (Nuñez *et al.*, 2020).

1.1.3.3 Principles of invasive species management

Given their widespread and pervasive impacts, the management of impactful non-native species has been identified as a priority issue under the Convention on Biological Diversity (CBD), with all signatories agreeing to "…prevent the introduction of, control or eradicate those alien species which threaten ecosystems, habitats or species" (CBD, 1992). The CBD has reinforced this viewpoint in subsequent publications, with the most recent update recommending an even greater focus on non-native species management (CBD, 2018). Management strategies are commonly divided into three key approaches: 1) preventing introduction into the new environment, 2) detecting and eradicating the non-native species, and 3) limiting the extent of the impacts through containment and mitigation (CBD, 2002). The CBD (2002) suggests that these approaches should be treated hierarchically, with prevention the preferred method of management. If prevention is not possible then early detection and eradication is a priority, followed by containment and mitigation if this is unsuccessful. Although not explicitly recognised by the CBD, these strategies are inherently linked to the invasion process (Fig. 1.1; Blackburn *et al.*, 2011), as prevention explicitly aims to stop the transport and introduction of non-native species, eradication is more likely to succeed prior to establishment (Simberloff, 2009; Caffrey *et al.*, 2014), mitigation is applied to those species which have successfully established, and containment focuses on preventing spread.

1.1.4 Aquatic invasive species

1.1.4.1 Vulnerability of freshwaters to invasion

Freshwater ecosystems are particularly vulnerable to invasion due to a number of unregulated sources of invasive species (e.g., aquarium release, ballast water, boat hulls and aquaculture; Moorhouse & MacDonald, 2015). Furthermore, the impacts of invasive species are more severe in freshwater than terrestrial ecosystems, as hydrological and biotic isolation leads to higher levels of endemism and a greater risk of extinction (Moorhouse & MacDonald, 2015). Indeed, a recent meta-analysis demonstrated that non-native species caused a strong decrease in the abundance and diversity of native aquatic communities (Gallardo *et al.*, 2016). Consequently, invasive species have been listed as a key threat to freshwater biodiversity in a number of reviews (Dudgeon *et al.*, 2006; Strayer & Dudgeon, 2010; Reid *et al.*, 2019), although a lack of effective management techniques means that invasive species still persist at high levels in many freshwater ecosystems. For example, the Laurentian Great Lakes support over 180 invasive species, with a new species discovered approximately every 28 weeks (Ricciardi, 2006; United States Geological Survey, 2019). Similarly, 11.3% of macroinvertebrate species richness in the River Rhine is composed of invasive species, with invasion fronts advancing at a maximum of 137-461 km per year (Leuven *et al.*, 2009). In the UK, more than 120 non-native species have become established in freshwater systems, accounting for 24% of fish, 12% of plant, 54% of amphibian and 88% of decapod crustacean species richness (Keller *et al.*, 2009). The River Thames alone supports approximately 100 non-native species, 53% of which have become established in the past 30 years (Jackson & Grey, 2013).

1.1.4.2 Managing aquatic invasive species

Given the vulnerability of freshwaters to invasion, preventing the introduction of non-native species is particularly important (Nunes *et al.*, 2015). This approach is largely dependent on the identification and management of introduction pathways, as this allows the introduction of specific and targeted legislation (CBD, 1992; EU, 2014; DEFRA, 2015). In Europe, the main pathways of freshwater invasive species introduction are releases and escapes from the aquaculture and aquarium trades, followed by stowaways transported by the shipping industry (Nunes *et al.*, 2015; Fig. 1.2). These pathways are increasingly subjected to legislation, with EU Council Regulation 1143/2014 mandating that invasive species cannot be kept, bred, transported, sold or released unless strict permit conditions are met (EU, 2014). Similarly, the International Maritime Organisation's Ballast Water Treaty (International Maritime Organization, 2017) demands that all ships must implement a ballast water management plan designed to prevent the transport of aquatic non-native species. Alongside pathway management, the use of horizon scanning techniques, whereby a systematic approach is used to prioritise the risk posed by potentially new non-native species that are not currently established in the region, is seen as a vital component for preventing the introduction of non-native species (CBD, 1992; EU, 2014; DEFRA, 2015). This approach allows potentially high-impact species to be identified and managed prior to their introduction, and is known to provide net economic benefits (Keller *et al.*, 2007). A recent horizon scanning exercise identified 6 freshwater species (Northern snakehead [*Channa argus*], golden mussel [*Limnoperna fortunei*], rusty crayfish [*Faxonius rusticus*], white perch [*Morone americana*], a freshwater shrimp [*Gammarus fasciatus*], and a water flea [*Daphnia lumholtzi*]) that were likely to have a significant impact on biodiversity and ecosystem services in the European Union within the next 10 years (Roy *et al.*, 2019).

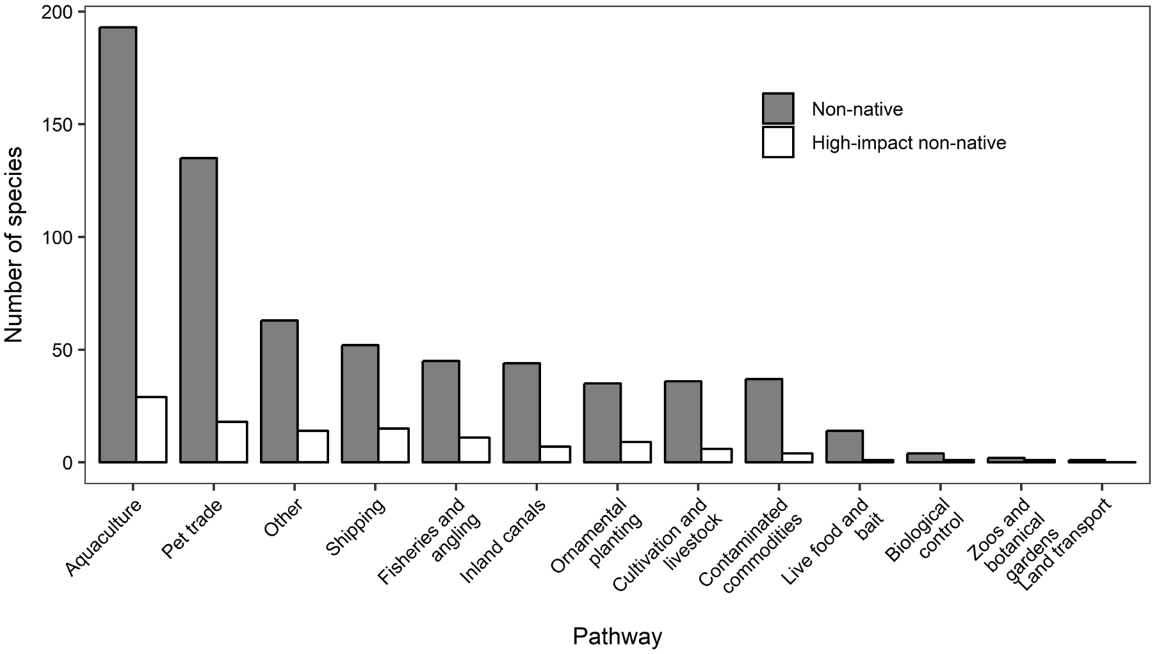

Figure 1.2 – Pathways of introduction of freshwater non-native species (grey bars) and high-impact non-native species (white bars) in Europe. Data from Nunes *et al*. (2015).

In cases where prevention has failed and non-native species have been introduced into the new environment, the primary management aim is to eradicate the novel population (CBD, 1992). A number of approaches have been attempted to eradicate aquatic non-native species, including chemical treatment (e.g., Britton & Brazier, 2006; Sandodden, 2018), manual removal (e.g., Tiberti *et al.*, 2019), mechanical control (e.g., Hoffmann *et al.*, 2013), overharvest (e.g., Syslo *et al.*, 2011; Gaeta *et al.*, 2015), and biological control (e.g., Koenig *et al.*, 2015; Musseau *et al.*, 2015). However, eradication is often viewed as controversial due to the potential non-target effects, low probability of success, and high economic costs (e.g., Myers *et al.*, 2000; Simberloff, 2002). Furthermore, there is substantial variation in the success of eradication programs for freshwater non-native species, and effectiveness can be limited by habitat complexity, species-specific factors, and the properties of the waterbody (Rytwinski *et al.*, 2018). Nonetheless, there have been a number of high-profile eradications, including localised eradications of topmouth gudgeon (*Pseudorasbora parva*;

Britton & Brazier, 2006) and water primrose (*Ludwigia grandiflora*; Renals, 2017) in the UK. Successful eradication programs are dependent on a number of factors, including the early detection of the species, the provision of sufficient resources, widespread support from both the public and relevant agencies, and the characteristics of the species itself (Mack *et al.*, 2000). Among these factors, perhaps the best predictor of eradication success is early detection and rapid response (Simberloff, 2009; Leuven *et al.*, 2017). A number of novel techniques such as eDNA, remote sensing, and citizen science are increasingly being used for early detection of freshwater non-native species, and the development of these techniques is likely to facilitate the development of more effective eradication programs (Larson *et al.*, 2020).

In cases where eradication is not possible, mitigation measures may be used to suppress the impact of the non-native species and allow the continued provision of ecosystem services (Gozlan *et al.*, 2010). Mitigation measures often utilise techniques similar to those used for eradication (e.g., physical removal, chemical treatment, and biological control), but explicitly recognise that the probability of eradication is low (Gozlan *et al.*, 2010; Britton *et al.*, 2011). For example, the eradication of non-native rudd (*Scardinius erythrophthalmus*) in a series of lakes in New Zealand was not possible due to potential non-target effects on native species, but populations were suppressed using gill netting (Neilson *et al.*, 2004). Similarly, an extensive hand weeding program was used to successfully control, but not eradicate, non-native water primrose in the River Leda, Germany (Hussner *et al.*, 2016). It is also possible to combine mitigation measures with habitat restoration, as demonstrated in the Murray River, Australia, where the addition of large woody debris (a common strategy in river restoration; e.g., Thompson *et al.*, 2018) led to a decreased abundance of non-native carp *(Cyprinus carpio*; Nicol *et al.*, 2004). However, the effectiveness of mitigation approaches is highly variable, and is dependent on continued and costly long-term efforts (Gozlan *et al.*, 2010; Rytwinski *et al.*, 2018). Indeed, in some cases the costs of long-term mitigation may exceed the high initial costs of eradication (Simberloff *et al.*, 2013). For example, the cost of a single year of control for invasive coypus (*Myocastor coypus*) in Italy would cost more than twice as much as the successful eradication program utilised in Great Britain (Panzacchi *et al.*, 2007).

Despite significant recent advances in prevention, eradication, and mitigation, there are still a significant number of high-impact invasive species present in freshwater systems (see section 1.1.4.1). For these species, preventing or slowing secondary range expansion (i.e., containment) is vital, as this may present the only method of limiting their impacts (Vander Zanden & Olden, 2008; Gozlan *et al.*, 2010; Britton *et al.*, 2011). Containment can be achieved through the introduction of biosecurity programs such as the *Check Clean Dry* campaign, which aims to limit the spread of non-native species through the promotion of good biosecurity practices among recreational water users in the UK (Great Britain Non-Native Species Secretariat, 2010). Similarly, much of the legislation designed to prevent the introduction of non-native species may also serve to limit secondary spread (e.g., EU, 2014). Alternatively, a reduction in secondary spread may be achieved by targeting satellite populations with a high dispersal potential (Gozlan *et al.*, 2010). This approach was utilised for the management of topmouth gudgeon in the UK, whereby populations that established in highly connected lakes were prioritised for eradication, and approximately 280 km of river were protected from their dispersal (Britton *et al.*, 2008).

1.2 River infrastructure

1.2.1 Prevalence and uses of river infrastructure

The world's rivers have been extensively modified through the construction of river infrastructure (e.g., dams, weirs, and culverts), with only 37% of rivers longer than 1000 km remaining uninterrupted along their entire length (Grill *et al.*, 2019). These structures vary substantially in size, ranging from the "mega-dams" constructed for hydropower generation on the world's greatest rivers [e.g., the Three Gorges dam on China's Yangtze river (Wu *et al.*, 2004), the Belo Monte dam in the Brazilian Amazon (Jiang *et al.*, 2018), and Ethiopia's Grand Renaissance dam on the Blue Nile River (Eldardiry & Hossain, 2021)] to the vast network of low-head structures present in rivers throughout Europe (Belletti *et al.*, 2020). The numbers and locations of large dams (typically over 10-15 m high) have been studied extensively, with global databases containing between 6,800 and 58,000 records (Lehner *et al.*, 2011; International Commission on Large Dams, 2020; Mulligan *et al.*, 2020). However, recent studies examining the prevalence of smaller structures have suggested that they may be orders of magnitude more abundant than large dams (Jones *et al.*, 2019; Belletti *et al.*, 2020). Indeed, in Europe alone it is estimated that at least 1.2 million individual structures are present, equating to an average of one structure in every 1.35 km of river (Belletti *et al.*, 2020).

The functions of river infrastructure are highly varied, and include: storing water for domestic and industrial use (i.e., abstraction), raising water levels for irrigation, controlling the direction and magnitude of flow (e.g., for flood management), facilitating navigation of rivers (e.g., locks), allowing measurement of flow conditions (e.g., gauging weirs), and generating electricity (Kemp, 2015). Additionally, impounded areas created by river infrastructure are often used for recreational activities such as angling (Rolfe & Prayaga, 2007) and boating (Johnson *et al.*, 2008), and can support profitable aquaculture schemes (Welcomme & Bartley, 1998). In some cases, river infrastructure can also attract substantial numbers of tourists; the Hoover Dam on the Colorado River, USA, is visited by approximately 7 million people each year (National Parks Service, 2018). The demand for many of these services (particularly potable water and renewable energy from hydropower) is likely to continue to increase in the future as the human population continues to grow rapidly (United Nations, 2019). Indeed, over 3,700 additional large hydropower plants have been planned globally

(Zarfl *et al.*, 2015), as well as more than 10,000 small hydropower plants (Couto & Olden, 2018).

1.2.2 Impacts of river infrastructure

The construction of river infrastructure causes fundamental changes to freshwater ecosystems (extensively reviewed in Kemp, 2015), leading to its classification as a primary threat to freshwater biodiversity in several key reviews (Dudgeon *et al.*, 2006; Strayer & Dudgeon, 2010; Reid *et al.*, 2019). Upstream of impoundments, the shift from lotic to lentic conditions can cause changes in temperature, chemical composition, and dissolved oxygen levels (Winton *et al.*, 2019), often reducing the suitability of the habitat for native river-dwelling species (e.g., Winston *et al.*, 1991). Changes in temperature (e.g., Cai *et al.*, 2018) and physico-chemical conditions (e.g., Ling *et al.*, 2016) are also observed downstream of impoundments, where the volume and variation of flow is substantially reduced (Graf, 2006). River infrastructure can also reduce the longitudinal, lateral, and vertical transport of nutrients and sediment, leading to disruptions of natural biogeochemical cycles (Ward & Stanford, 1995).

Perhaps one of the most extensively studied impacts of river infrastructure is the fragmentation of river habitats (Grill *et al.*, 2015; Grill *et al.*, 2019). In-stream structures act as a barrier to longitudinal movements of aquatic organisms, preventing access to important habitat and delaying critical migrations (Sheer & Steel, 2006; Marschall *et al.*, 2011). For example, in the Parana basin, Brazil, over 145 large dams have been constructed, impounding a total area of 16,700 km^2 (Agostinho *et al.*, 2008). While there have been numerous changes to the local fish assemblages, the most pronounced has been the decline of species dependent on long-distance migrations (Agostinho *et al.*, 2008). Numerous migratory species, including dourado (*Salminus brasilienses*), pintado (*Pseudoplatystoma corruscans*), and pacu (*Piaractus mesopotamicus*), have disappeared from impounded areas, with significant impacts on commercial and artisanal fisheries (Agostinho *et al.*, 2008). Similar patterns have been observed in the Willamette and Lower Columbia River basins, where 1491 barriers block 14,391 km of streams and rivers, leading to declines and even extirpations of migratory salmonid populations (Sheer & Steel, 2006). Although effects on migratory species are most prominent, a recent meta-analysis suggested that dams affect entire fish communities, causing declines in both richness and diversity (Turgeon *et al.*, 2019). These effects are not limited to large dams; low-head barriers (Porto *et al.*, 1999; Jones *et al.*, 2021a) and culverts (Makrakis *et al.*, 2012) are also known to substantially reduce longitudinal movements of fishes.

Although research is strongly biased towards fish populations, it is possible that habitat fragmentation by river infrastructure can impact the dispersal ability of other important freshwater groups. For example, reservoirs can trap the hydrochorous propagules of macrophytes, reducing the abundance and richness of downstream plant communities

(Andersson *et al.*, 2000; Merritt & Wohl, 2006). Furthermore, fish can act as important vectors for the upstream dispersal of macrophytes (Pollux, 2011; VonBank *et al.*, 2018), and barriers to their migration can therefore disrupt macrophyte dispersal and population structure (Jones *et al.*, 2020). Similarly, macroinvertebrates that depend on downstream drift for dispersal can become trapped in slow-flowing pools such as those generated by impoundments (Lancaster *et al.*, 1996; Bond *et al.*, 2000). Indeed, Brooks *et al.* (2018) found that a 2.7 m high weir reduced downstream dispersal by 68 – 98%, and Sondermann *et al.* (2015) found that in-stream barriers reduced the habitat accessible to macroinvertebrates by 18-39%.

1.2.3 Mitigation of river infrastructure

A wide variety of national and international legislation has been implemented to limit or mitigate the impacts of river infrastructure on native flora and fauna. This legislation commonly focuses on mitigating the impacts of river infrastructure on fish migration through the construction of fish passes (structures primarily designed to facilitate upstream movement of fishes), bypasses (structures designed to provide an alternative route for downstream migrations, avoiding in-stream infrastructure), and screens (structures placed over intakes to prevent fishes entering infrastructure) (Kemp, 2015). Such legislation is commonplace throughout the world, with notable examples in the USA (e.g., the Fish and Wildlife Coordination Act 1934, the Clean Water Act 1972, the Endangered Species Act 1973), the UK (e.g., the Water Resources Act 1991, The Salmon [fish passes and screens] [Scotland] Regulations 1994, the Eels [England and Wales] Regulations 2009), China (Fisheries Law of the People's Republic of China 1986, Water Law of the People's Republic of China 1988), and Brazil (IBAMA Normative Instruction N° 146, 2007). Legislation specifically addressing other ecological and physico-chemical impacts of river infrastructure is substantially less common, although these impacts can be covered by broader water quality legislation. For example, the European Union's Water Framework Directive (WFD) requires member states to achieve good quantitative and qualitative status of all water bodies, with assessments incorporating hydrological conditions, biological quality, and physico-chemical conditions, as well as measures of habitat connectivity for fish migrations (EU, 2000).

Numerous types of fish passes have been designed with the aim of improving upstream passage of fishes. Improvements to fish passage have been reported for traditional fish ladders (e.g., Gowans *et al.*, 1999; Gutfreund *et al.*, 2018), Denil fishways (e.g., Bunt *et al.*, 1999; Mallen-Cooper & Stuart, 2007), and nature-like fishways (e.g., Steffensen *et al.*, 2013; Landsman *et al.*, 2018). Similarly, low-cost modifications retrofitted to low-head structures (e.g., studded tiles and cylindrical bristle clusters) can improve passage by increasing water depth and flow heterogeneity (Vowles *et al.*, 2017; Montali-Ashworth *et al.*, 2020). However, despite some notable successes, meta-analyses have demonstrated that the efficacy of fish passes is often low and highly species-specific (Bunt *et al.*, 2012; Noonan *et al.*, 2012; Bunt *et al.*, 2016; Hershey, 2021). Indeed, Kemp (2016) suggested that the negative impacts of river infrastructure cannot be effectively mitigated through the provision of fish passes, and that over-emphasis of well-designed and effective fish passes has impeded wider acceptance of this viewpoint.

Given the limitations of current fish passage technologies, it has been suggested that the physical removal of river infrastructure is the only method of effectively restoring river connectivity (Birnie-Gauvin *et al.*, 2017a; Sun *et al.*, 2022). Alongside restoration of connectivity, infrastructure removal re-establishes natural hydrological conditions, improves nutrient and sediment transport, and enhances the physical habitat (Bednarek, 2001). Numerous studies have demonstrated that these changes can dramatically enhance fish populations, with notable examples from China (Ding *et al.*, 2019a), the USA (Catalano *et al.*, 2007; Burroughs *et al.*, 2010), and Northern Europe (Fjeldstad *et al.*, 2012; Sun *et al.*, 2022). In Denmark, the density of young of year brown trout (*Salmo trutta*) upstream of the Vilholt hydropower dam was over 200 times greater after the dam was removed, and the density of large trout (>14 cm) doubled (Birnie-Gauvin *et al.*, 2017b). To date, at least 3869 dams have been removed globally, but a growing body of evidence regarding the potential ecological benefits is driving an exponential increase in removals (Ding *et al.*, 2019b). Despite this, questions remain regarding the effects on other important groups of aquatic organisms (e.g., phytoplankton, zooplankton, algae, macrophytes, and macroinvertebrates), and the impacts of removal in systems which are already degraded through pollution or biological invasions (Tullos *et al.*, 2016; Ding *et al.*, 2019b).

1.3 Invasive species and river infrastructure

1.3.1 River infrastructure as a management technique

A growing body of work suggests that the reduced lateral and longitudinal connectivity induced by river infrastructure may act as a barrier to the spread of invasive species (Rahel, 2013; Tummers & Lucas, 2019; Jones *et al.*, 2021b). This idea initially took the form of "isolation management" strategies, whereby native species of conservation concern are isolated upstream of custom-built migration barriers (Novinger & Rahel, 2003; Fausch *et al.*, 2009). This technique was used to protect native populations of cutthroat trout (*Oncorhynchus clarki pleuriticus*) from non-native brook trout (*Salvelinus fontinalis*) and rainbow trout (*Oncorhynchus mykiss*) in the Western United States, although only short-term benefits were observed (Novinger & Rahel, 2003). Isolation management has since been generalised to form the concept of "intentional fragmentation", which emphasises the importance of maintaining or enhancing habitat fragmentation in situations where the negative impacts of non-native species may outweigh the benefits of increased connectivity (Rahel, 2013). Similarly, Rahel and McLaughlin (2018) introduced the term "selective fragmentation", which highlights the need to maintain river connectivity for desirable species, while preventing or reducing the passage of undesirable species. Isolation management, intentional fragmentation, and selective fragmentation all make use of "exclusion barriers", which are any structures that prevent the passage of non-native species (Jones *et al.*, 2021b).

Four approaches can be used to reduce river connectivity for invasive species containment: 1) utilising existing natural barriers, 2) eliminating human-induced connectivity (e.g., through closing canals), 3) exploiting anthropogenic barriers constructed for other purposes (e.g., dams and culverts), and 4) constructing barriers explicitly designed to prevent the spread of non-native species (Rahel, 2013). Natural barriers can limit the spread of non-native species at a variety of spatial scales (Rahel, 2007). For example, endangered Eastern Cape redfin minnow (*Pseudobarbus afer*) in the Swartkops River, South Africa, largely persist above waterfalls which act as barriers to non-native predators (Ellender *et al.*, 2011). Similarly, subsurface flows through boulder fields prevent the spread of northern pike (*Esox lucius*; Spens *et al.*, 2007). However, approaches using natural barriers are largely opportunistic, and thus cannot be applied flexibly to different scenarios. Eliminating human-induced connectivity is also challenging, as connectivity between water bodies often brings substantial economic benefits (Fairlie, 1898; Gibbs, 1978; Marinov *et al.*, 1997; Kenawy, 2016; Pagano *et al.*, 2016). Thus, in many cases the use of existing or purpose-built exclusion barriers presents the best option for implementing intentional fragmentation. While these are commonly considered together (e.g., Jones *et al.*, 2021b), there are important conceptual differences, namely that pre-existing barriers are generally optimised for other purposes (e.g., hydropower, abstraction, navigation etc.), whereas purpose-built barriers can be optimised specifically to reduce the spread of invasive species. Additionally, existing barriers are already present at high densities throughout river systems globally (e.g., Jones *et al.*, 2019; Belletti *et al.*, 2020), whereas purpose-built barriers remain relatively uncommon. These differences affect the situations in which these barriers may be most effective; existing barriers are likely to have greater effects on large-scale invasion dynamics (e.g., overall invasion rate) but are less likely to completely block the spread of non-native species, whereas purpose-built barriers are likely to block more individuals but can only be utilised at relatively small spatial scales (e.g., protecting a reach of river that contains a species of high conservation value).

Physical exclusion barriers such as dams, weirs and culverts have been used to successfully limit the spread of numerous non-native species (Jones *et al.*, 2021b). The height of these barriers, coupled with localised increases in water velocity, shear stress, and turbulence, can prevent passage by swimming, climbing or jumping (Rahel & McLaughlin, 2018). For example, the upstream movement of non-native salmonids can be limited by rock filled gabions (brown trout and rainbow trout; Avenetti *et al.*, 2006), culverts (brook trout; Thompson & Rahel, 1998), and low-head dams (brown trout and rainbow trout; Porto *et al.*, 1999). At a larger spatial scale, a network of over 1000 barriers (of which 77 have been purpose-built) prevent non-native sea lamprey (*Petromyzon marinus*) accessing spawning habitat in the American Great Lakes, and are critical to the viability of the control program (Zielinski *et al.*, 2019). Physical barriers have also been successfully used to limit the spread of high-impact decapod crustaceans, including American signal crayfish (*Pacifastacus leniusculus*; Rosewarne *et al.*, 2013), and red swamp crayfish (*Procambarus clarkii*; Kerby *et al.*, 2005; Manenti *et al.*, 2014). Such physical barriers are often already widespread in aquatic environments, and thus present an important opportunity for within-catchment management (Rahel & McLaughlin, 2018; Jones *et al.*, 2019). Indeed, a recent quantitative review found that physical barriers are the most commonly used and effective form of exclusion barrier (Jones *et al.*, 2021b)

Non-physical (i.e., sensory and physiological) exclusion barriers are increasingly being used for non-native species management as, unlike physical barriers, they do not disrupt natural hydrological and sediment regimes (Jones *et al.*, 2021b). Perhaps the most widely used of these are electric barriers, which have been used to guide and deter species such as common carp (Bajer *et al.*, 2018), sea lamprey (Miehls *et al.*, 2017a), and spinycheek crayfish (*Faxonius limosus*; Benejam *et al.*, 2015). Other notable examples of sensory barriers for non-native species include the use of acoustics to guide silver carp (*Hypophthalmichthys molitrix*; Vetter *et al.*, 2015), bubble curtains to deter common carp (Zielinski & Sorensen, 2015), and a multi-modal system incorporating acoustics, bubble curtains and strobe lights to deter sea lamprey (Miehls *et al.*, 2017b). However, implementing sensory barriers under field conditions is challenging as they rarely block all individuals, and depend on uninterrupted operation (Zielinski & Sorensen, 2015; Jones *et al.*, 2021b). Physiological barriers such as elevated carbon dioxide concentrations (e.g., Cupp *et al.*, 2018), and chemical barriers such as copper-based substrates (e.g., Hoyer & Myrick, 2012) have also been used to limit the spread of non-native species. However, non-physical barriers are significantly more costly and complex to implement than physical barriers, and considerable further research is necessary prior to their widespread implementation (Rahel & McLaughlin, 2018). Conversely, physical exclusion barriers are relatively cheap and easy to implement (Rahel & McLaughlin, 2018), and are already widely used in non-native species management plans (Jones *et al.*, 2021b). Given their broad applicability, the focus of this thesis is on physical barriers to the dispersal of aquatic non-native species, although further research is recommended to increase the efficacy of non-physical exclusion barriers.

1.3.2 Limitations of management using river infrastructure

The installation or maintenance of exclusion barriers to prevent the spread of invasive species directly contradicts efforts to remove or mitigate barriers to increase connectivity for native fauna (Rahel & McLaughlin, 2018). Indeed, physical exclusion barriers typically isolate upstream populations (e.g., Novinger & Rahel, 2003), although rigorous tests regarding the impacts on native species are rare (Jones *et al.*, 2021b). This contradiction is referred to as the "connectivity conundrum" (Zielinski *et al.*, 2020), and may be resolved through the development of selective fish passage technologies, which prevent passage by invasive species without impacting the movements of native species (Rahel & McLaughlin, 2018). To date, selective fish passage systems have typically exploited differences in characteristics such as maximum swimming speed (Hoover *et al.*, 2017; Starrs *et al.*, 2017), maximum jumping height (Holthe *et al.*, 2005), and body morphology (Hillyard *et al.*, 2010), although modern technologies such as artificial intelligence may facilitate selective removal of invasive fishes at exclusion barriers in the future (Eickholt *et al.*, 2020). However, selective fish passes are often ineffective, particularly when all life stages and flow conditions are considered, and substantial development is required prior to widespread implementation (Rahel & McLaughlin, 2018; Jones *et al.*, 2021b). Exclusion barriers are therefore a useful management technique in areas where containment of invasive species is a high priority, although the trade-offs between invasive species containment and the impacts on native fauna must be carefully considered.

While there are numerous notable examples of successful physical exclusion barriers, it is important to note that these successes generally only occur in relatively limited circumstances. In particular, it is likely that exclusion barriers can only limit local dispersal (i.e., expansion into adjacent habitat through diffusive processes), rather than long distance dispersal (i.e., establishment of new populations outside the invasion core) (Shigesada *et al.*, 1995). Local dispersal is dependent on active movements which can be blocked by exclusion barriers, whereas long distance movements are typically driven by vectors such as recreational activities (Anderson *et al.*, 2014; Peoples & Midway, 2018), water transfers (Gallardo & Aldridge, 2018) and zoochory (Reynolds *et al.*, 2015), which are unlikely to be limited by the presence of exclusion barriers. Additionally, many aquatic organisms undergo life stages which facilitate downstream dispersal through passive drifting (Brittain & Eikeland, 1988; Johnston *et al.*, 1995; Johansson *et al.*, 1996), meaning that physical barriers are generally only effective against upstream movements. The restriction to local dispersal, coupled with limited effectiveness against downstream movements, means that exclusion barriers are only likely to be effective against non-native species that actively disperse upstream. While this description does include several major groups of invasives (e.g., salmonids and decapod crustaceans), it is important to acknowledge that exclusion barriers are unlikely to be the 'silver bullet' for containment of freshwater non-native species.

The use of exclusion barriers to limit the spread of non-native species may present trade-offs with other stages of the invasion process (Tummers & Lucas, 2019; Barnett & Adams, 2021; Jones *et al.*, 2021b). For example, non-native species may be more likely to be introduced to impoundments, as these areas are commonly used for activities such as angling, boating, and aquaculture (Quist *et al.*, 2005; Johnson *et al.*, 2008), which are known pathways of non-native species introduction (Nunes *et al.*, 2015). Indeed, impoundments created by river infrastructure can be up to 300 times more likely to contain non-native species than comparable natural lakes (Johnson *et al.*, 2008), and recent meta-analyses have demonstrated that the proportion (Liew *et al.*, 2016) and diversity (Turgeon *et al.*, 2019) of non-native fishes are higher in regions with large dams. Similarly, disturbed habitat created by altered hydrological conditions may facilitate the establishment of viable populations through changes in resource availability and reduced competitive ability of native species (Shea & Chesson, 2002). Effective management decisions require an understanding of the nature and magnitude of impacts experienced during the different stages of invasion, but there is currently no fully quantitative consideration of the effects on establishment or spread. Given the potential trade-off between the impacts of river infrastructure at different stages of the invasion process, a sound quantification of costs and benefits is essential.

Alongside the fundamental limitations of exclusion barriers previously described, a recent quantitative literature review identified a number of weaknesses in the current evidence base (Jones *et al.*, 2021b). The global review incorporated physical and non-physical exclusion barriers, and only incorporated structures that were built specifically to control invasive species. Overall, Jones *et al.* (2021b) found that 86% of studies focused on fish, particularly sea lamprey and “Asian carp” (*Hypophthalmichthys* spp.). Studies were also biased towards North America (66%) and Europe (10%), with only three studies (3%) identified across Asia, Africa and South America. Although 86% of studies reported that the exclusion barrier could successfully block the movements of >70% of the target species, current research is limited by poor study design (only 5% of studies used a robust before-after-control-impact design), short-term monitoring efforts (only 13% of studies continued monitoring after five years) and a failure to consider the catchment-scale network of river infrastructure within which exclusion barriers are placed. The meta-analysis presented in Chapter 2 builds on this review by quantitatively assessing the current literature, including barriers not built specifically to limit the spread of invasive species, and assessing the effects of in-stream infrastructure on the introduction and establishment of invasive species, as well as their spread.

1.4 Preliminary aims and objectives

The overall aim of this thesis was to:

> Investigate the effectiveness of anthropogenic in-stream infrastructure as a management technique for invasive species.

To achieve this aim, an initial objective was developed to identify areas for further research, before adopting the set of finalised aims and objectives provided in Chapter 3. The initial objective was to:

1. Quantitatively review current literature to determine the influence of in-stream infrastructure on invasive species at each stage of the invasion process and to identify research trends, biases, and knowledge gaps.

Chapter 2: The effects of anthropogenic in-stream structures on non-native species: a meta-analysis.

Abstract:

River infrastructure and non-native species are widely recognised as key threats to global freshwater biodiversity. These stressors commonly co-occur, and understanding their interactions is essential for effective management. This study aimed to determine how river infrastructure influenced the success of invasion by aquatic non-native species. A global meta-analysis was conducted to determine the overall effect of river infrastructure on the success of non-native species at each stage of the invasion process, and to identify the consistency of these effects across taxonomic groups, climatic regions, sample site locations, and infrastructure heights. The presence of river infrastructure had a strong, positive effect on the introduction and establishment of non-native species. No effect was observed on the spread of non-native species, although this may have resulted from a lack of high-quality studies. The magnitude and direction of effects were similar upstream and downstream of infrastructure, and were unaffected by structure height. Similarly, the overall effect sizes did not differ between taxonomic groups (fish, macroinvertebrates and plants) or climatic regions (tropical, subtropical, and temperate) at any stage of the invasion process. However, studies were strongly biased towards the effects of large dams on the introduction and establishment of non-native fishes in temperate regions, which may limit the generalisability of these results. These results demonstrate that river infrastructure may increase the success of non-native species, and emphasise the importance of targeted management interventions in regulated areas. Further studies of the long-term, catchment-scale effects of river infrastructure on the spread of invasive species is recommended as a key focus for future research.

2.1 Introduction

Freshwater ecosystems are considered to be the most degraded and threatened of all (Dudgeon *et al.*, 2006), with river engineering widely recognised as a primary threat to freshwater biodiversity (Dudgeon *et al.*, 2006; Strayer & Dudgeon, 2010; Reid *et al.*, 2019). River systems have been extensively modified at a variety of spatial scales through the installation of infrastructure such as dams, weirs, and culverts (Grill *et al.*, 2015; Kemp, 2015). These structures degrade and fragment essential habitats (Fuller *et al.*, 2015), obstruct critical migrations (Sheer & Steel, 2006), and reduce the lateral and longitudinal transport of nutrients and sediments (Ward & Stanford, 1995), with significant impacts on native fauna (e.g., Liermann *et al.*, 2012; Linares *et al.*, 2018) and flora (e.g., Jansson *et al.*, 2000). River development is currently accelerating on a global scale, with at least 3700 large dams either planned or currently under construction (Zarfl *et al.*, 2015), meaning these impacts are likely to increase in the future.

Alongside the negative impacts on native flora and fauna, anthropogenic river infrastructure also affects non-native species, although the nature of this relationship remains uncertain. River infrastructure can limit the spread of non-native species (Rahel, 2013; Jones *et al.*, 2021b), and its installation for this purpose has helped reduce the movement of fish [e.g., sea lamprey, *Petromyzon marinus*, Zielinski *et al.* (2019); brook trout, *Salvelinus fontinalis*, Novinger and Rahel (2003); and common carp, *Cyprinus carpio* Bulow *et al.* (1988)] and other aquatic biota [e.g., red swamp crayfish, *Procambarus clarkii*, Dana *et al.* (2011)]. Furthermore, there is increasing concern that fish passage structures designed to increase longitudinal connectivity for native species may unintentionally facilitate the spread of non-native species (McLaughlin *et al.*, 2013). However, impoundments created by river infrastructure can be up to 300 times more likely to contain non-native species than comparable natural lakes (Johnson *et al.*, 2008), and frequently support higher densities of non-natives (Alexandre & Almeida, 2010; Jellyman & Harding, 2012). Additionally, in the Rio Paraná basin, Brazil, the construction of the Itaipu dam flooded a large natural barrier, allowing 33 species to move beyond their native range and into the upper basin (Júnior *et al.*, 2009). Recent meta-analyses have also demonstrated that the proportion (Liew *et al.*, 2016) and diversity (Turgeon *et al.*, 2019) of non-native fishes are higher in temperate regions with large dams. Consideration of this uncertainty is vital for effective management (Tummers & Lucas, 2019), although current advice frequently advocates the use of infrastructure as a control mechanism (Fausch *et al.*, 2009; Rahel, 2013).

Invasion by non-native species typically follows a series of phases: 1) transport beyond the native range through anthropogenic activity, 2) introduction to a new environment, 3) establishment of a viable population through several cycles of survival and reproduction, and 4) spread to new locations (Blackburn *et al.*, 2011). During the initial stages of invasion, the increased accessibility of impounded areas for boating and recreational activities (Johnson *et al.*, 2008) is likely to favour the transport and subsequent introduction of a greater number of individuals from a wider variety of species (Havel *et al.*, 2005). Similarly, disturbed habitat created by altered hydrological conditions may facilitate the establishment of viable populations through changes in resource availability and reduced competitive ability of native species (Shea & Chesson, 2002). In contrast, river infrastructure can act as a barrier to the longitudinal spread of non-native species, and therefore may limit further spread (Rahel, 2013).

Given the potential trade-off between the impacts of river infrastructure at different stages of the invasion process, a sound quantification of costs and benefits is necessary for effective management decisions. This requires an understanding of the nature and magnitude of impacts experienced during the different phases of invasion, but there is currently no fully quantitative consideration of the effects on establishment or spread. Furthermore, previous quantitative syntheses relating to introduction have been limited to the impacts of large dams on non-native fishes present in upstream impoundments (Liew *et al.*, 2016; Turgeon *et al.*, 2019), despite the prevalence of smaller structures (Belletti *et al.*, 2020), the high taxonomic diversity of non-native species (e.g., Jackson & Grey, 2013), and significant downstream impacts of river infrastructure (Brandt, 2000; Granzotti *et al.*, 2018). These reviews have also identified a paucity of studies in tropical and sub-tropical regions, and further information is needed as these regions are likely to be hotspots of future river development (Zarfl *et al.*, 2015).

In this study, a meta-analysis including a wide variety of taxonomic groups, climatic regions, and infrastructure types was conducted to determine how river infrastructure influences the success of invasion by aquatic non-native species. To achieve this, three main objectives were addressed: 1) to determine the overall effect of river infrastructure on aquatic non-native species at each stage of the invasion process, 2) for each invasion stage, to identify variation in the magnitude of the overall effect between different: a) taxonomic groups, b) climatic regions, c) locations relative to the structure, and d) infrastructure heights, and 3) to identify biases in the current literature and areas for future research.

2.2 Methods

2.2.1 Search protocol

Before commencing the meta-analysis, a review protocol was established in line with the PRISMA protocol (Moher *et al.*, 2009) and guidance published by the Collaboration for Environmental Evidence (Collaboration for Environmental Evidence, 2018). At this stage, the populations, interventions, comparators, outcomes, and study designs that would be eligible in this meta-analysis were clearly defined using the PICOS framework (Thomas *et al.*, 2019a; Table 2.1).

To identify relevant sources, three academic databases (Web of Science, Scopus, and Aquatic Sciences and Fisheries Abstracts) were searched using the Boolean search string "*(invasive OR non-native OR alien OR introduced OR exotic) AND (freshwater OR aquatic OR lake OR river OR pond OR stream OR reservoir OR canal) AND (barrier OR dam OR weir OR culvert OR fragmentation OR impoundment)*". Additionally, the first 100 results of a Google scholar search with the same search string and the bibliographies of 11 relevant reviews were screened (Stanley & Doyle, 2003; Rahel, 2007, 2013; Liew *et al.*, 2016; Tullos *et al.*, 2016; Garcia *et al.*, 2018; Rahel & McLaughlin, 2018; Francis *et al.*, 2019; Tummers & Lucas, 2019; Turgeon *et al.*, 2019; Jones *et al.*, 2021b). All searches were conducted during November 2019 and utilised the private browsing feature of Google Chrome to prevent user-specific results. Searches and results were restricted to English language only, but no restrictions were placed on publication year.

Table 2.1 – The criteria for inclusion against which full texts were assessed.

Category	Criteria for Inclusion
Population	Any freshwater species recognised as non-native in the study and contained in the Global Register of Introduced and Invasive Species (Pagad *et al.*, 2018). Terminology is often inconsistent within the field of invasion science (Richardson *et al.*, 2000), so invasive and non-native species were treated as one group, henceforth referred to as non-native.
Intervention	The treatment area of the study must include at least one form of anthropogenic in-stream structure (e.g., dams, weirs and culverts). Natural barriers (see Rahel, 2007) and behavioural barriers (e.g., Swink, 1999; Zielinski & Sorensen, 2015) were not considered in this study.
Comparator	The study utilised a relevant control site that was not influenced by any anthropogenic infrastructure.
Outcomes	The relevant outcomes depended on the stage of the invasion process to which the study relates. For introduction, relevant outcomes were propagule pressure and species diversity; for establishment, any measure of abundance was classed as a relevant outcome; and for spread the outcomes of interest were dispersal rates and passage success rates. The outcomes need to be reported as either 1) raw data, 2) summary data for treatment and control sites, 3) exact p values accompanied by sample size or degrees of freedom, or 4) a graphical form of any of these data sources.
Study Design	Any study design that incorporated both a treatment and control site was eligible for conclusion.

2.2.2 Screening and data collection

Initial literature searches returned 5518 articles after duplicates were removed, resulting in a final database of 217 full texts (Fig. 2.1). Each of these full texts was assessed against the PICOS framework shown in Table 2.1 to determine their eligibility for inclusion.

During the screening phase, the invasion stage that each full text related to was classified based on the metrics used. Distinguishing between transport and introduction is challenging as the first evidence of transport is often the observation of free-living individuals outside their native range (Blackburn *et al.*, 2016). Therefore, these stages were combined into a single metric (henceforth introduction) and any study that measured either the number of individuals introduced (i.e., propagule pressure) or the number of species introduced (i.e., diversity) was classified as related to introduction. For a study to be classified as related to establishment, it was required to include a metric that reflected differences in the rates of survival or reproduction (e.g., recruitment), or differences in population size (e.g., abundance, number of sites with non-native species). Finally, any study that reported an explicit measure of infrastructure passage or invasion rate was classified as being related to spread.

A number of other variables were recorded alongside the data required to calculate effect sizes, including the geographic location of the study (latitude and longitude), the climatic region (tropical, subtropical or temperate), the metric used, the study design, the location of the sample site (upstream/downstream from the structure or not differentiated), the taxonomic group studied (mammal, fish, macroinvertebrate, plant or algae), the height of the structure, and the duration of the study. In cases where results were presented graphically, relevant information was extracted using imageJ (Rasband, 2018). Where sufficient data was reported, effect sizes were calculated individually for different species, sampling locations and invasion stages, resulting in a total of 103 measures of effect size (introduction n = 29, establishment n = 68, spread n = 6) from 45 studies (a summary of the included studies is provided in Appendix A.1).

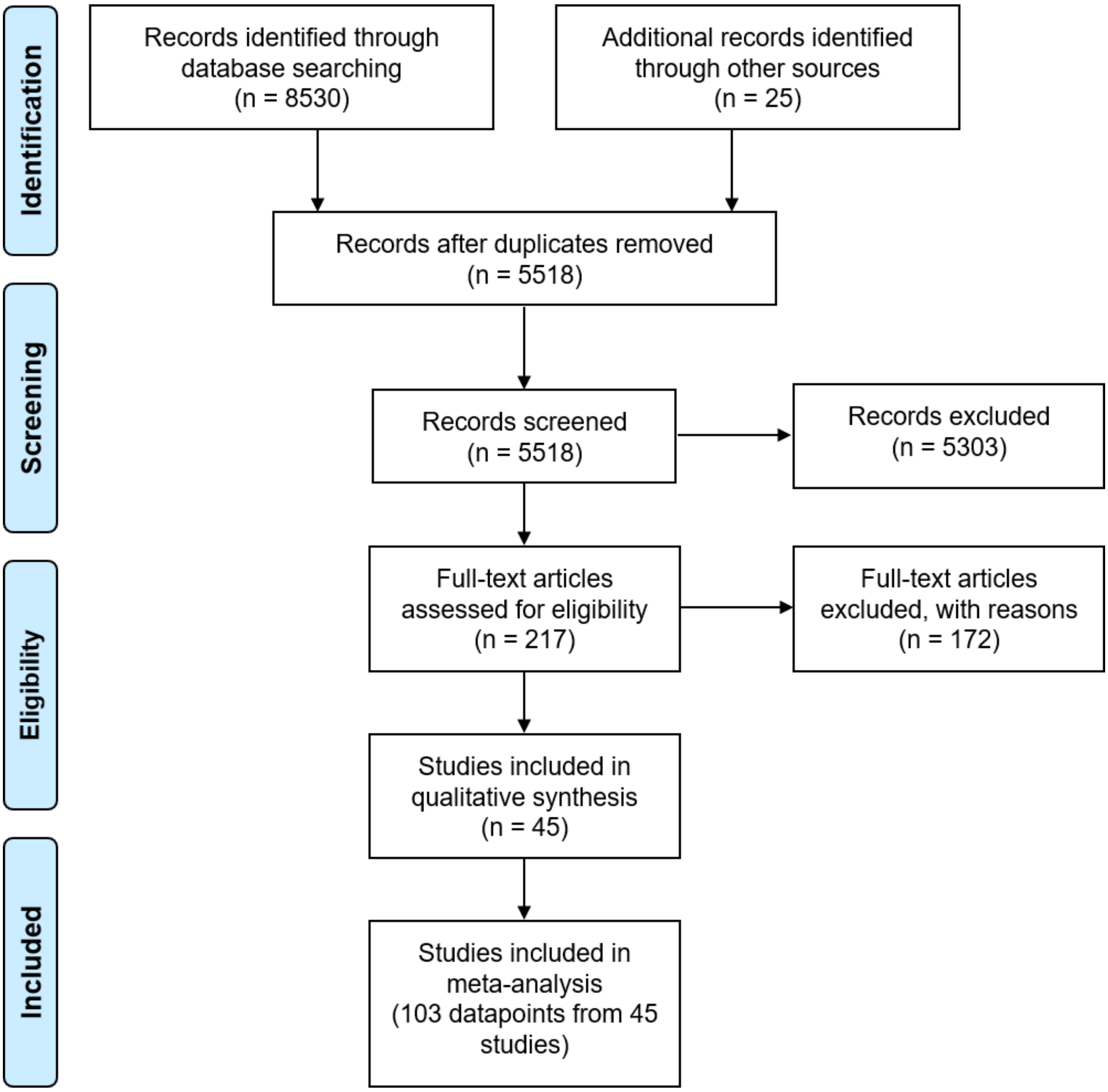

Figure 2.1 – PRISMA literature search flow diagram showing the number of studies retained or excluded at each stage of the search.

2.2.3 Effect size calculation

For each data point, Hedges' *g*, a measure of standardised mean difference corrected for small sample size, was calculated (Hedges & Olkin, 1985). The magnitude of *g* in this study was interpreted following Cohen (1988), with 0.2 representing a small effect, 0.5 a medium effect, 0.8 a large effect, and any effect size greater that 1.0 considered very large. In this study, a positive effect indicates that the river infrastructure increased the success of the invader at that stage of the process, whereas a negative effect indicates that invasion success was reduced.

The methodology used to calculate Hedges' *g* varied based on whether the study reported mean values, contingency tables, or correlation coefficients. For studies where mean values were compared (n datapoints = 66) between areas where in-stream structures were present (*sp*) and regions where structures were absent (*sa*), Hedges' *g* was calculated using the formula:

$$g = \frac{\bar{X}_{sp} - \bar{X}_{sa}}{S} J$$

where *S* is the pooled standard deviation and *J* is the correction for small sample sizes, calculated as:

$$J = 1 - \frac{3}{4(n_{sp} + n_{sa} - 2) - 1}$$

The variance of *g* was calculated as:

$$v_g = \left(\frac{n_{sp} + n_{sa}}{n_{sp} n_{sa}} + \frac{g^2}{2(n_{sp} + n_{sa})} \right) J^2$$

In cases where data was reported in the form of 2 x 2 contingency tables (n datapoints = 33), *g* was derived by calculating the log odds ratio (LOR) then converting to *g* using the formula:

$$g = \left(\ln\left(\frac{\mathrm{AD}}{\mathrm{BC}}\right) \times \frac{\sqrt{3}}{\pi} \right) J$$

where A = the number of occurrences observed where in-stream structures were present, B = the number of non-occurrences where structures were present, C = the number of occurrences observed where structures were absent, and D = the number of non-occurrences observed where structures were absent (Borenstein *et al.*, 2009). In cases where zeroes were present in the contingency table, a Haldane-Anscombe correction was applied, whereby 0.5 is added to each value (Haldane, 1940; Anscombe, 1956). The variance of *g* derived from LOR was calculated as:

$$v_g = \left(\left(\frac{1}{\mathrm{A}} + \frac{1}{\mathrm{B}} + \frac{1}{\mathrm{C}} + \frac{1}{\mathrm{D}}\right) \times \frac{3}{\pi^2}\right) J^2$$

In cases where data was reported in the form of correlation coefficients (n datapoints = 4), *g* was calculated by converting the correlation coefficient (*r*) to Fisher's Z and then to *g* using the formula:

$$g = \left(\frac{2 \times \left(0.5 \times \ln\left(\frac{1+r}{1-r}\right)\right)}{\sqrt{1 - \left(0.5 \times \ln\left(\frac{1+r}{1-r}\right)\right)^2}}\right) J$$

with variance:

$$v_g = \left(\frac{{}^{4}/_{n-3}}{\left(1 - \left(0.5 \times \ln\left(\frac{1+r}{1-r}\right)\right)^2\right)^3}\right) J^2$$

2.2.4 Data analysis

2.2.4.1 Overall effects by invasion stage

To calculate the overall effect size for each invasion stage, random-effects models were fitted using the restricted maximum likelihood (REML) approach. To account for both within- and between-study variability, a random effect with sub-study nested within study was incorporated in the model. Additionally, the total heterogeneity statistic (Q) was calculated to determine whether heterogeneity of effect sizes for each invasion stage was greater than would be expected through sampling error alone.

To identify the presence of publication bias, Egger's test for funnel plot asymmetry was conducted for introduction and establishment by incorporating standard error as a predictor variable in the random effects model (Egger *et al.*, 1997). This approach was not possible for spread, as statistical tests for funnel plot asymmetry have insufficient power where less than 10 data points are available (Sterne & Egger, 2005; Sterne *et al.*, 2011). Additionally, a visual assessment of funnel plots (standard error against effect size) was conducted for each invasion stage (see Appendix A.2).

Publication bias is a pervasive problem in ecological meta-analyses (Nakagawa & Santos, 2012; Koricheva & Gurevitch, 2014), and can lead to overestimation of summary effect sizes due to an overrepresentation of small studies with large effect sizes and high variance (Sterne *et al.*, 2000). Consequently, it is important to report unbiased overall effects, but common methods such as the trim and fill (Duval & Tweedie, 2000) have not yet been generalised for multi-level data structures, as present in the current meta-analysis. Therefore, in cases where publication bias was detected, studies were removed sequentially in descending order of variance, until funnel plots and Egger's test showed no evidence for publication bias. Summary effect sizes were then recomputed using the previously described random effects models, and an overall estimate unaffected by publication bias was obtained.

2.2.4.2 Variation in overall effects

A relatively low number of studies reported all of the information necessary for subgroup analysis (introduction n datapoints = 15, establishment n datapoints = 49, spread n datapoints = 6). This meant it was not possible to construct complex multivariate meta-regression models, as the low number of observations per variable would likely have led to overfitting (Sterne *et al.*, 2001). Therefore, for each categorical subgroup (taxonomic group, sample site location, and climatic region), individual random effects models were created for each category (provided that more than one data point was available), and the coefficients were compared using a Wald test to identify differences between categories. For structure height, a simple meta-regression model incorporating structure height as a fixed effect, and sub-study nested within study as a random effect, was constructed to identify its relationship with effect size. Bonferroni corrections were applied to all significance tests to account for multiple testing.

2.3 Results

2.3.1 Overall effects by invasion stage

The presence of anthropogenic in-stream structures had a large positive effect on both introduction ($g = 1.30$, $p < 0.001$, Fig. 2.2) and establishment ($g = 0.83$, $p < 0.001$, Fig. 2.2). Conversely, in-stream structures had a negative effect on spread, although this was not significantly different from zero ($g = -0.54$, $p = 0.230$, Fig. 2.2). For all invasion stages, the overall heterogeneity was greater than expected through sampling error alone, suggesting that the true effect size differed between studies (introduction $Q = 243.22$, $p < 0.001$; establishment $Q = 720.19$, $p < 0.001$; spread $Q = 38.43$, $p < 0.001$).

Publication bias was detected for both introduction ($z = 4.733$, $p < 0.001$) and establishment ($z = 2.252$, $p = 0.024$). Sequential removal of studies with high variance led to the exclusion of 5 datapoints for introduction and 7 datapoints for establishment, and these modified datasets showed no evidence of publication bias (introduction: $z = 1.437$, $p = 0.150$; establishment $z = 0.484$, $p = 0.628$). Recomputed summary effect sizes were smaller than those calculated from the full dataset, but remained statistically different from zero (introduction: $g = 0.80$, $p = 0.002$; establishment: $g = 0.59$, $p < 0.001$).

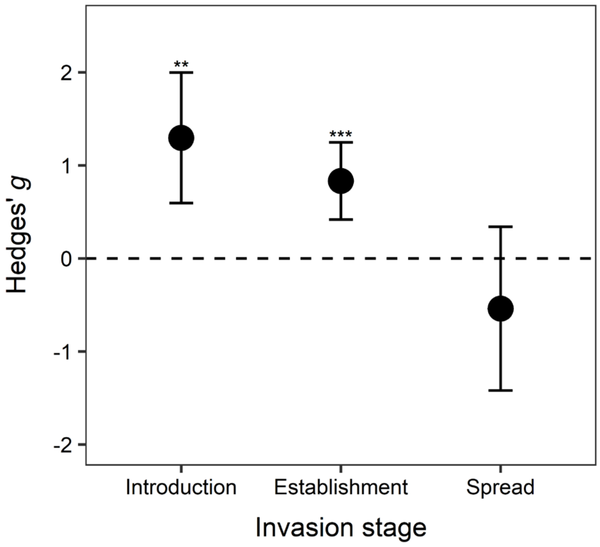

Figure 2.2 – Overall effect size (Hedges' *g*) showing the effect of anthropogenic barriers on each stage of the invasion process. Error bars represent 95% confidence intervals (** = $p < 0.01$, *** = $p < 0.001$).

2.3.2 Variation in overall effects

Effect sizes were consistent between different taxonomic groups (Fig. 2.3a), climatic regions (Fig. 2.3b), sample site locations (Fig. 2.3c), and structure heights (Fig. 2.3d) at all stages of the invasion process (Table 2.2).

Table 2.2 – The results of subgroup analysis to determine other factors which may have explained heterogeneity in effect size, showing the within-subgroup heterogeneity (Q), degrees of freedom (df) and significance (*p*). Dashes denote cases where only one category was present in the subgroup, meaning analysis was not possible.

	Introduction			Establishment			Spread		
	Q	df	*p*	Q	df	*p*	Q	df	*p*
Taxonomic group	1.48	2	0.476	6.12	2	0.047	0.34	1	0.56
Climate	5.96	2	0.051	1.8	2	0.407	-	-	-
Sample site location	0.68	2	0.71	1.97	2	0.373	0.61	1	0.434
Structure height	1.12	1	0.291	0.21	1	0.648	0.09	1	0.77

2.3.3 Biases in current research

Studies relating to the effects of river infrastructure on the spread of invasive species were underrepresented compared to studies of introduction and establishment (introduction = 28.2%, establishment = 66%, spread = 5.8%; Fig. 2.4a)). Studies of introduction and establishment were overwhelmingly focused on fish (introduction = 82.8%, establishment =

86.8%), although studies relating to spread were distributed evenly between fish and decapod crustaceans (Fig. 2.4b). Current research efforts are concentrated in Europe (32.4%) and North America (43.7%), leading to a substantial overrepresentation of studies conducted in temperate regions (82.5%). Indeed, only 4.9%, and 12.6% of studies were conducted in tropical and subtropical regions, respectively, and no research from polar regions was included (Fig. 2.4c). Dams were the most common infrastructure type at all stages of the invasion process (introduction = 89.7%, establishment = 89.7%, spread = 50%; Fig. 2.4d), with a particular focus on large dams. Indeed, of the studies that reported head drop, 89.7% focused on structures greater than 2 m in height (Fig. 2.4e).

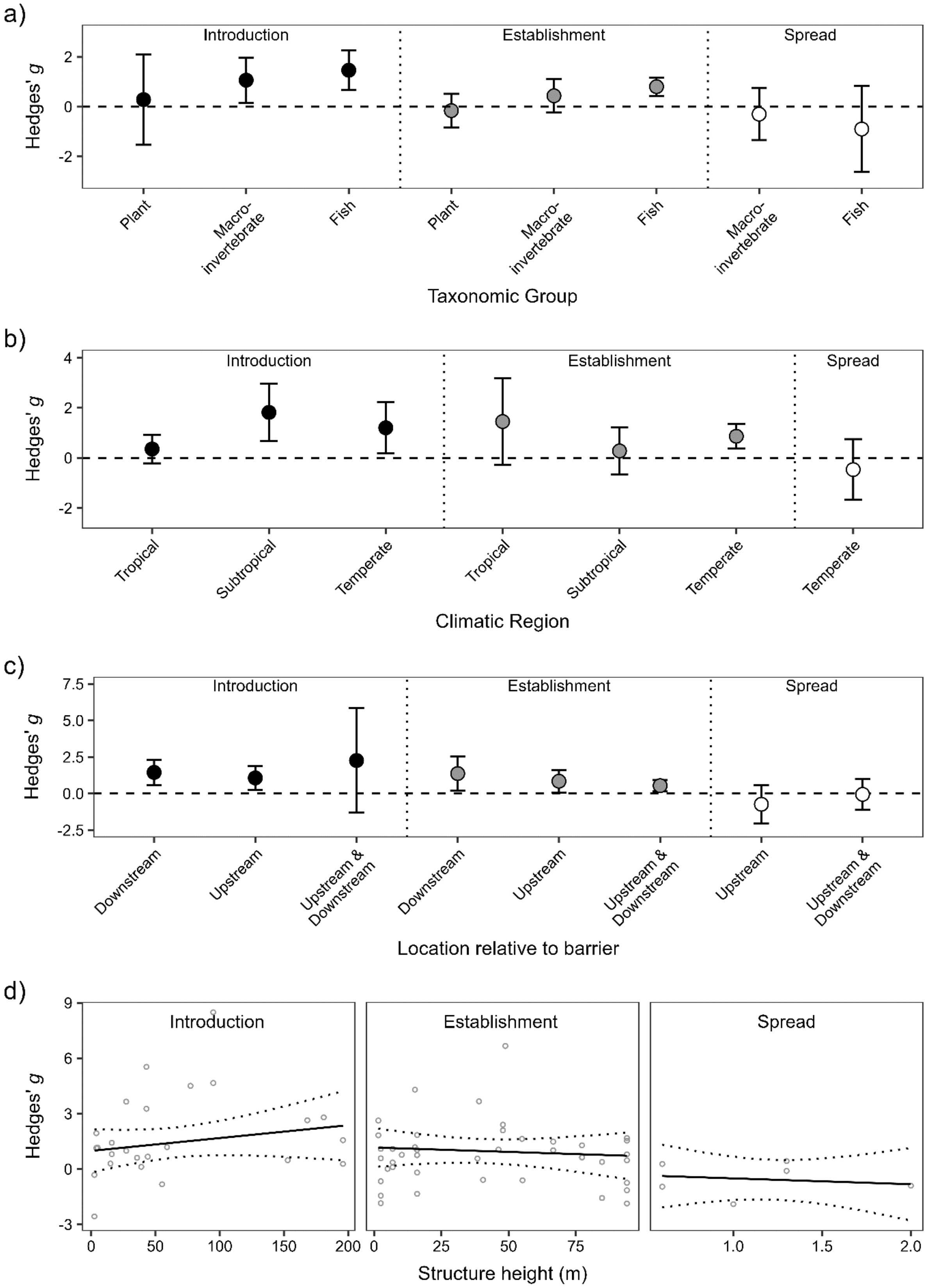

Figure 2.3 – Variation in summary effect sizes (Hedges' *g*) across different a) taxonomic groups, b) climatic regions, c) sample site locations relative to the barrier, and d) barrier heights.

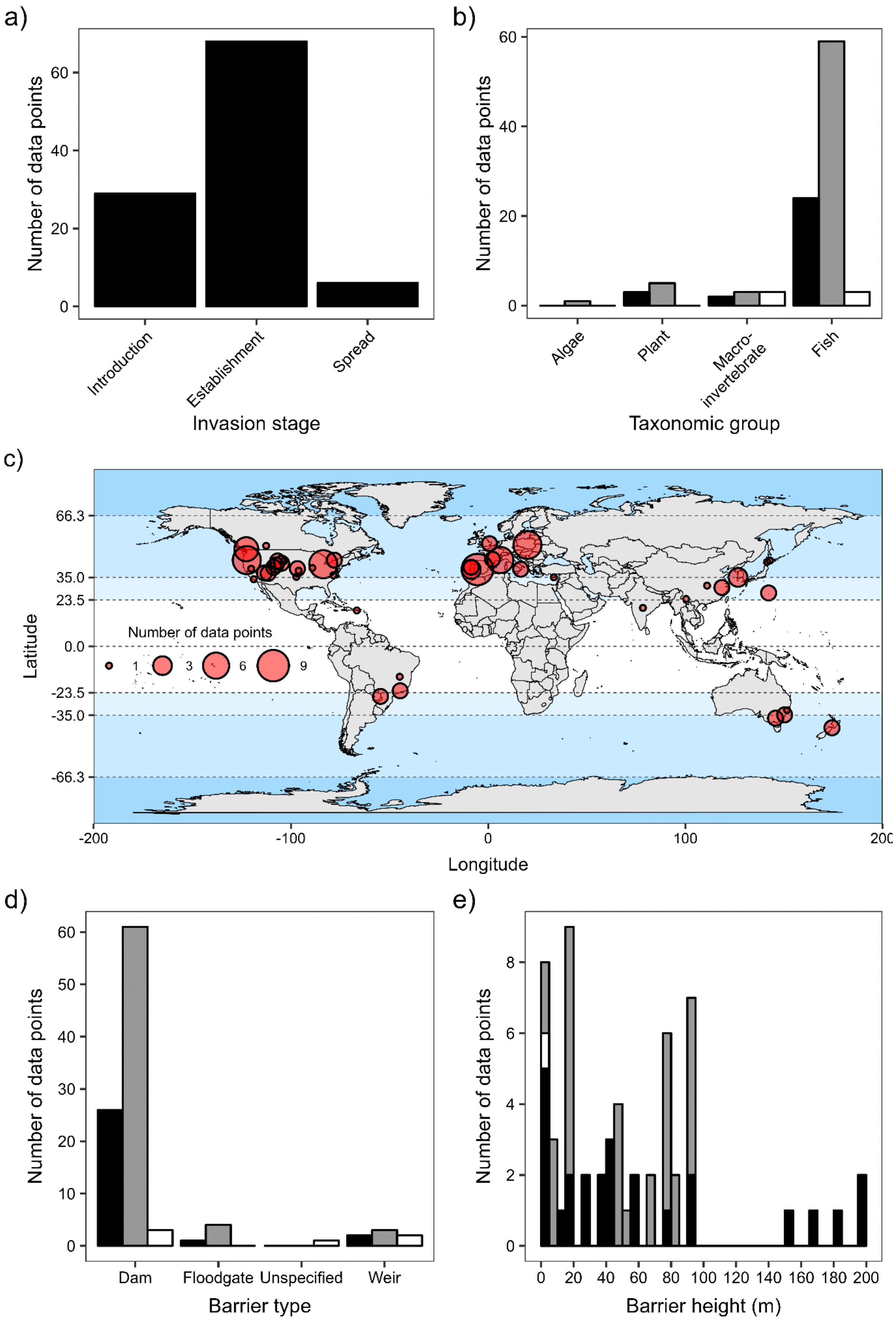

Figure 2.4 – Summary of biases in current research regarding the interaction between invasive species and river infrastructure, showing differences in the number of data points between: a) stages of the invasion process, b) taxonomic groups, c), geographic regions, d) barrier types, and e) barrier head drops. Bar colours denote the stage of the invasion process (black = introduction, grey = establishment, white = spread).

2.4 Discussion

Understanding the effects of anthropogenic in-stream infrastructure at each stage of the invasion process is vital for informed management decisions. This study utilised meta-analytic techniques to quantitatively summarise current literature, and provides strong evidence that in-stream infrastructure facilitates the introduction and establishment of non-native species, but does not affect their spread. Effect sizes did not vary between different taxonomic groups, climatic regions, sample site locations or infrastructure heights. However, included studies showed numerous biases, with large dams, non-native fishes, and temperate regions strongly overrepresented. Further studies are needed to elucidate the impacts of river infrastructure on the spread of invasive species, particularly over large spatio-temporal scales.

2.4.1 Overall effects by invasion stage

The results of this meta-analysis demonstrate that a greater number of non-native species are introduced in areas with anthropogenic in-stream structures than in unregulated areas. Two previous meta-analyses have identified a similar pattern, with both suggesting that the number of non-native fish species is greater in impounded areas (Liew *et al.*, 2016; Turgeon *et al.*, 2019). This may be driven by the increased accessibility of impounded areas for recreational activities such as angling and boating (Quist *et al.*, 2005; Johnson *et al.*, 2008), which are known to act as transport vectors for a wide variety of taxonomic groups, including fish (e.g., round goby [*Neogobius melanostomus*] and bighead goby [*Ponticola kessleri*]; Hirsch *et al.*, 2016), bivalves (e.g., zebra mussel [*Dreissena polymorpha*]; Buchan & Padilla, 1999), and plants (e.g., Eurasian watermilfoil [*Myriophyllum spicatum*] and curly pondweed [*Potamogeton crispus*]; Bruckerhoff *et al.*, 2015). Angling is also associated with intensive fish stocking (e.g., Garcia *et al.*, 2018), which may also contribute to the observed increases in introductions.

River infrastructure also facilitates the establishment of non-native species, likely as a result of high levels of habitat disturbance (Havel *et al.*, 2005). The presence of in-stream infrastructure leads to profound changes in upstream physical habitat, with free-flowing areas replaced by deeper, lentic habitats (Ward & Stanford, 1995). Reaches downstream of impoundments are also subjected to significant hydrological changes, and generally experience a smaller and less variable discharge than unregulated areas (Poff *et al.*, 1997). Disturbed habitats, such as those created by in-stream infrastructure, are particularly susceptible to invasion due to changes in resource availability and reduced resilience of the native community (Elton, 1958). These changes provide resource opportunities, whereby non-native species are able to exploit the newly available resources to enhance their survival and reproduction (Shea & Chesson, 2002).

The identification of areas with anthropogenic infrastructure as hotspots for introduction and establishment may have significant management implications. These results suggest that areas with in-stream structures may act as "invasion hubs", where non-native species are able to form viable populations before dispersing into new regions (Muirhead & Macisaac, 2005). Specific and targeted interventions in invasion hubs are often highly effective (Moody & Mack, 1988; Letnic *et al.*, 2015), meaning that in-stream structures should be considered important management targets. Additionally, non-native species management is most effective in the early stages of the invasion process (Simberloff, 2009), meaning that areas with high levels of introductions (such as areas with anthropogenic infrastructure) require large-scale monitoring efforts.

Although a number of studies have argued that in-stream infrastructure may be an effective containment strategy (e.g., Rahel, 2013; Krieg & Zenker, 2020), the results of this study suggest that these structures do not affect the spread of invasive species. This may reflect the lack of a true effect, as a recent review suggested that barriers only blocked 100% of the population in 36% of cases (Jones *et al.*, 2021b). Indeed, recent studies utilising eDNA have reported that in-stream infrastructure has no effect on the spread of non-native species (Ikeda *et al.*, 2019; Robinson *et al.*, 2019). Alternatively, this may be a result of the relatively small number of data points (n = 6), which is in turn a result of generally inadequate study design. Of the 41 full-texts classified as being related to spread, 19 were excluded due to the lack of a sufficient control site, including a number of papers that are widely cited as support for management using intentional fragmentation (e.g., Avenetti *et al.*, 2006; Dana *et al.*, 2011). The use of a control site unaffected by in-stream barriers is vital for robust statistical conclusions, and future studies relating river infrastructure to the spread of non-native species should ensure that an appropriate study design is used (e.g., Porto *et al.*, 1999).

2.4.2 Variation in overall effects

The magnitude of the overall effect did not differ between taxonomic groups at any stage of the invasion process, suggesting that the effects of river infrastructure are consistent between non-native fishes, macroinvertebrates, and plants. This finding supports the work of Johnson *et al.* (2008), who found that impoundments in the Laurentian Great Lakes were more likely to be invaded by plants (e.g., Eurasian watermilfoil), macroinvertebrates (e.g., spiny water flea [*Bythotrephes longimanus*], and rusty crayfish [*Faxonius rusticus*]) and fish (rainbow smelt [*Osmerus mordax*]) than comparable natural lakes. Although this finding could be influenced by strong biases towards studies of non-native fishes (see section 2.4.3), these results highlight the importance of considering a wide variety of taxonomic groups when assessing the impacts of river infrastructure on non-native species.

The results of this study also suggested that effect sizes are consistent across climatic regions. However, this finding contrasts with two previous reviews which suggested that the diversity (Turgeon *et al.*, 2019) and growth rate (Rypel, 2014) of freshwater non-native species vary along climatic gradients. Thomaz *et al.* (2015) also suggested that tropical regions may be more resilient to invasion than temperate regions due to their higher native biodiversity. These discrepancies could result from the strong biases towards studies conducted in temperate regions (see section 2.4.3), and further work in tropical and subtropical regions is essential to understand global patterns affecting the interaction between river infrastructure and non-native species.

The overall effect size did not differ between studies conducted upstream and downstream of in-stream infrastructure. Previous reviews have focussed on non-native species in impoundments upstream of anthropogenic infrastructure (Havel *et al.*, 2005; Liew *et al.*, 2016; Turgeon *et al.*, 2019), but this meta-analysis suggests that the effects will be equally as severe in downstream reaches. This was initially predicted by Havel *et al.* (2005) who suggested that reservoirs could support source populations of non-natives for downstream regions, but this study provides the first summative evidence.

Subgroup analysis also demonstrated that the size of in-stream infrastructure did not modify the overall effect size. Infrastructure size strongly influences the magnitude of the associated environmental change (Poff & Hart, 2002), meaning the observed homogeneity of effect sizes is unexpected. However, this demonstrates that even small structures have the potential to facilitate the introduction and establishment of non-native species, highlighting the importance of considering invasion risk in ecological assessments prior to construction of all river infrastructure.

2.4.3 Biases in current research

Currently, studies regarding the influence of river infrastructure on the spread of non-native species are substantially underrepresented compared to studies of introduction and establishment. This may be a result of the metrics used to assess the impacts of river infrastructure at each stage of the invasion process, as diversity (used as a proxy for introduction) and abundance (used as a proxy for establishment) are commonly collected as part of routine monitoring studies. Reporting of this monitoring data facilitates assessments of the impact of river infrastructure on non-native species, with some comparisons taking place over long time periods (e.g., Hoagstrom *et al.* (2007) compared fish assemblages from 1892 to those in 2004 to assess the impacts of the construction of Angostura dam in 1949). In contrast, studies aiming to quantify the impact on spread are relatively new (research relating to exclusion barriers began to accelerate in the late 1990s; Jones *et al.* (2021b)), and barrier passage cannot be inferred from historic monitoring data.

The studies included in this review are strongly biased towards non-native fishes, reflecting the well-recognised bias towards charismatic vertebrate species in conservation science (Di Marco *et al.*, 2017). Indeed, fishes are typically the focus of freshwater conservation efforts due to their socioeconomic value, contribution to ecosystem services, and importance as keystone species (Geist, 2015). However, freshwater non-native species are taxonomically diverse; of 96 non-native species identified in the River Thames catchment, UK, only 15 were fish (Jackson & Grey, 2013). Furthermore, over 440 non-native plants are known to occur in European freshwaters (Lambdon *et al.*, 2008), and 45 non-native macroinvertebrates are known to occur in the River Rhine alone (Leuven *et al.*, 2009). The identification of this strong taxonomic bias highlights the need to extend current research to a wider variety of taxonomic groups.

The strong bias towards temperate regions (particularly those in North America and Europe) observed in this study also reflects pervasive and well-recognised biases in current literature (Pyšek *et al.*, 2008; Thomsen *et al.*, 2014). Temperate regions are already heavily impounded (e.g., Graf, 1993; Jones *et al.*, 2019), and the effects of in-stream infrastructure are widely studied (see Liew *et al.*, 2016; Turgeon *et al.*, 2019). However, the future construction of in-stream infrastructure is likely to be focused in tropical and subtropical regions, with particularly high levels of development in the emerging economies of south-east Asia, South America, and Africa (Zarfl *et al.*, 2015). Understanding the interaction between river infrastructure and non-native species in these regions is essential for sustainable development, and is therefore recommended as a focus for future research. While it is likely that the observed geographic bias does reflect global differences in publication rates (Nuñez *et al.*, 2021), it is important to note that studies included in this meta-analysis were restricted to those published in English, meaning this review may not have provided a comprehensive assessment of the available literature (Zenni *et al.*, 2023). Future syntheses should therefore endeavour to include multi-lingual literature searches, either through global collaboration or the use of modern translation software (Zenni *et al.*, 2023).

Biases towards large dams are also common in studies of river infrastructure (e.g., Grill *et al.*, 2019; Mulligan *et al.*, 2020), although these structures typically represent a small fraction of all instream infrastructure (Belletti *et al.*, 2020). Indeed, recent estimates suggest that assessments based solely on large dams would disregard 99.6% of the river infrastructure present in Great Britain (Jones *et al.*, 2019). Despite the limited assessments, there is evidence to suggest that small structures (<2 m head drop), which account for 68% of the river infrastructure present in Europe (Belletti *et al.*, 2020), can have substantial effects on the establishment (e.g., Beatty *et al.*, 2009) and spread (e.g., Rosewarne *et al.*, 2013) of non-native species, although no included studies assessed the impact of small structures on introduction. Given the prevalence of these structures in modern rivers, further assessments of their impacts on non-native species is essential.

2.4.4 Priorities for future research

Given that the impacts of river infrastructure on the introduction and establishment of non-native species are comparatively well understood, further studies regarding the impacts on spread are essential. Such research is particularly important due to the increasing interest in installing infrastructure as a containment strategy; 81% of studies relating to exclusion barriers have been published since 2005, and their use is being extended to a wider variety of habitats and species (Jones *et al.*, 2021b). However, it is vital that these studies use robust experimental designs. Both this study and the recent review conducted by Jones *et al.* (2021b) identified that the majority of studies aiming to assess the effectiveness of exclusion barriers failed to include a control site, which increases the probability of missing or misinterpreting the effects of the barrier. Future assessments of exclusion barrier effectiveness should therefore aim to include at least an appropriate control site, although before-after-control-impact (BACI) designs are preferential due to their increased statistical power and greater accuracy in detecting true effects (Christie *et al.*, 2019).

Studies regarding the effect of river infrastructure on the spread of invasive species are also currently hindered by temporal (i.e., short monitoring periods) and spatial (i.e., assessments of a single barrier) limitations. Of the three included studies in this meta-analysis, the longest monitoring period was two years (Rosewarne *et al.*, 2013), and Jones *et al.* (2021b) found that 87% of studies monitored exclusion barrier effectiveness for ≤5 years. These studies may not accurately reflect the effectiveness of barriers when used for long periods under field conditions, as flooding (Rahel, 2013), barrier damage (Hasegawa, 2017), and even algal growth on the barrier surface (Frings *et al.*, 2013) may all reduce the effectiveness of barriers over time. Similarly, the vast majority of studies regarding exclusion barrier effectiveness focus on assessing passage success at individual structures (e.g., Porto *et al.*, 1999; Krieg *et al.*, 2021) and rarely consider the additive effects of multiple barriers (but see Zielinski *et al.*, 2019). In reality, modern river systems are heavily fragmented by a multitude of structures (Belletti *et al.*, 2020), and this catchment-scale network of barriers may provide a useful tool for managing within-catchment invasions (Jones *et al.*, 2021b). Careful consideration of the landscape context and long-term effectiveness is therefore essential for the effective implementation of invasive species exclusion barriers.

Due to the close association with the field of fish passage (Silva *et al.*, 2018), research aiming to assess the effectiveness of exclusion typically focuses on quantifying passage success (i.e., the number of individuals that can successfully pass the barrier). However, the current focus on this metric has prevented considerations of the wider impacts on invasion dynamics (e.g., invasion rate, population size, biomass), even though this information may be particularly informative for the effective use of exclusion barriers. For example, understanding the impacts of exclusion barriers on population size and biomass could improve the ability of integrated pest management strategies to suppress the overall population, as removal could be targeted where non-native species accumulate downstream of barriers. Alternatively, the installation of exclusion barriers may exert a strong selection pressure for individuals with high dispersal tendency (Silva *et al.*, 2018), leading to faster invasion rates once the barrier is passed. The importance of invasion dynamics is currently underappreciated, but could prove vital for understanding the long-term catchment-scale effectiveness of exclusion barriers.

2.4.5 Conclusion

River infrastructure and non-native species are widely recognised as major threats to global freshwater biodiversity, yet the interactions between these stressors are rarely considered. This study used a meta-analytical approach to assess the influence of river infrastructure on the success of non-native species at each stage of the invasion process, and to identify priority areas for future research. Studies are currently biased towards non-native fishes, temperate regions, and large dams, and further work is required to assess the impacts of river infrastructure using a wider variety of infrastructure types, taxonomic groups and climatic regions. However, current research indicates that river infrastructure facilitates the introduction and establishment of invasive species, likely as a result of increased accessibility and habitat disturbance, respectively. Current research regarding the impact of river infrastructure on the spread of non-native species is insufficient, and there is an urgent need for further research assessing the long-term, catchment-scale effects of exclusion barriers on invasion dynamics.

Chapter 3: Thesis aims and objectives

3.1 Aims and objectives

As stated in section 1.4, the overall aim of this thesis is to investigate the effectiveness of anthropogenic in-stream infrastructure as a management technique for invasive species. To meet this aim, an initial objective was formulated: 1) to determine the influence of in-stream infrastructure on invasive species at each stage of the invasion process and to identify research trends, biases, and knowledge gaps. The meta-analysis undertaken to address this objective highlighted that there was a strong need to assess the long-term, catchment-scale effects of exclusion barriers on the spread of invasive species, with a particular focus regarding the impacts on invasion dynamics. Individual-based modelling was deemed the most appropriate methodology to address this need (see Chapter 4), and the American signal crayfish (*Pacifastacus leniusculus*; Chapter 4) was identified as an appropriate model species for which to formulate an individual-based model (IBM). However, some information regarding the underlying drivers of dispersal and barrier passage behaviour (as required to parameterise an IBM) was unavailable in the literature. Therefore, the remainder of the thesis is structured around two additional primary objectives: 2) to provide insight into fundamental drivers of signal crayfish barrier passage behaviour and dispersal, and 3) to assess the long-term, catchment-scale effectiveness of exclusion barriers as a method of limiting signal crayfish spread.

These primary objectives were further subdivided into the following secondary objectives:

2a) Determine the influence of signal crayfish population density on barrier passage behaviour.

2b) Assess the relationship between signal crayfish personality and barrier passage behaviour.

2c) Identify external drivers of signal crayfish invasion rate over large spatio-temporal scales.

3a) Determine the impacts of exclusion barriers on invasion dynamics over large spatio-temporal scales.

3b) Quantify the catchment-scale trade-offs between exclusion barriers, native fish migration and installation costs.

3.2 Thesis structure

An overview of the study species and individual-based modelling techniques that underpin the remainder of this thesis are provided in Chapter 4. Objectives 2a and 3a are addressed in Chapter 5, which combines experimental results generated by the PhD candidate with the results of an IBM originally developed by Dr James Kerr. To expand this IBM to real river systems with diverse barrier networks, additional information about crayfish personality (objective 2b) and external drivers of dispersal (objective 2c) was required, and the results of experimental and spatial modelling studies to assess these factors are described in Chapters 6 and 7, respectively. Finally, objectives 3a and 3b are addressed in Chapter 8, which substantially develops the original IBM to facilitate its application to a full river catchment, and quantitatively assesses the catchment-scale trade-offs associated with exclusion barrier installation. A schematic showing the objectives and their links to each chapter is provided in Figure 3.1.

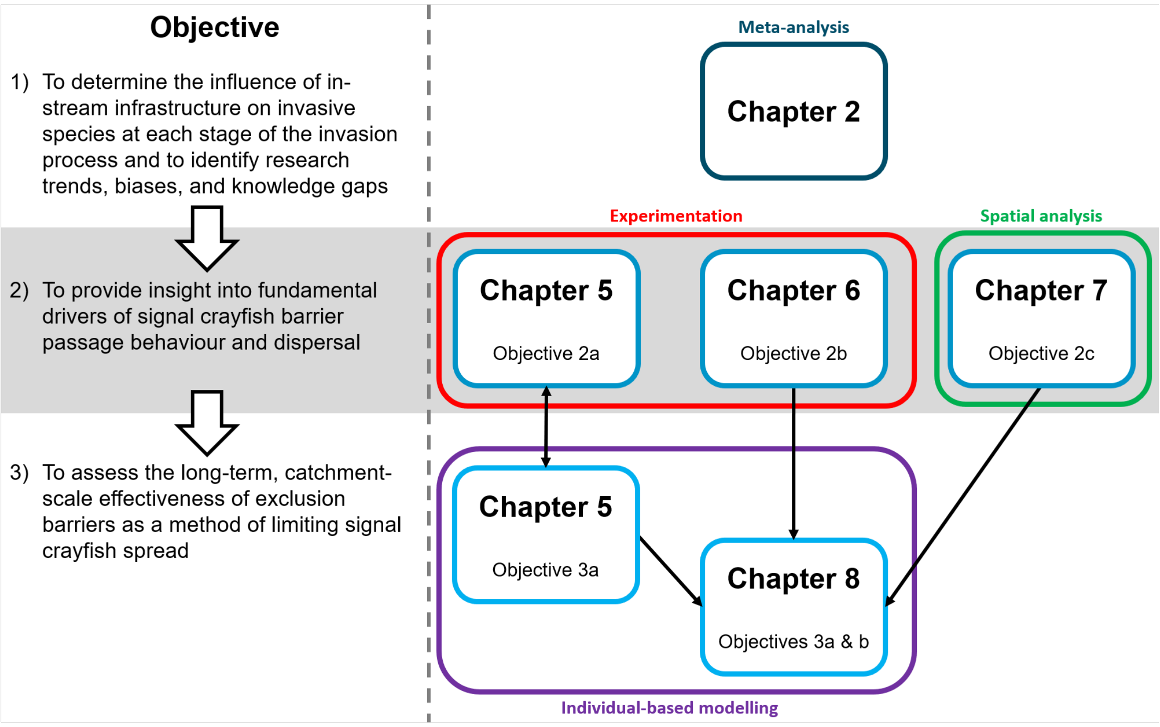

Figure 3.1 – Schematic of the thesis, showing the objectives, their links to the relevant results chapters, and the methodological approaches used in each chapter.

Chapter 4: Study species and methodology

4.1 American signal crayfish

In Europe, freshwater crayfish are one of the most prevalent and widespread groups of freshwater invasive species, with at least 10 species established across 37 different countries (Kouba *et al.*, 2014). The most widespread of these species is the American signal crayfish (*Pacifastacus leniusculus*; Fig. 4.1a), which was initially introduced to Sweden in 1959 to boost crayfish stocks (Svärdson, 1965). Since their introduction, signal crayfish have spread rapidly throughout Europe through a combination of unintended transport, intentional stocking, and active dispersal (Souty-Grosset *et al.*, 2006), and are now established in 29 countries across the continent (Kouba *et al.*, 2014; Fig. 4.1b). Signal crayfish have also become established in Japan, having spread rapidly across the country after initial introductions for aquaculture between 1926 and 1930 (Usio *et al.*, 2007; Usio *et al.*, 2016).

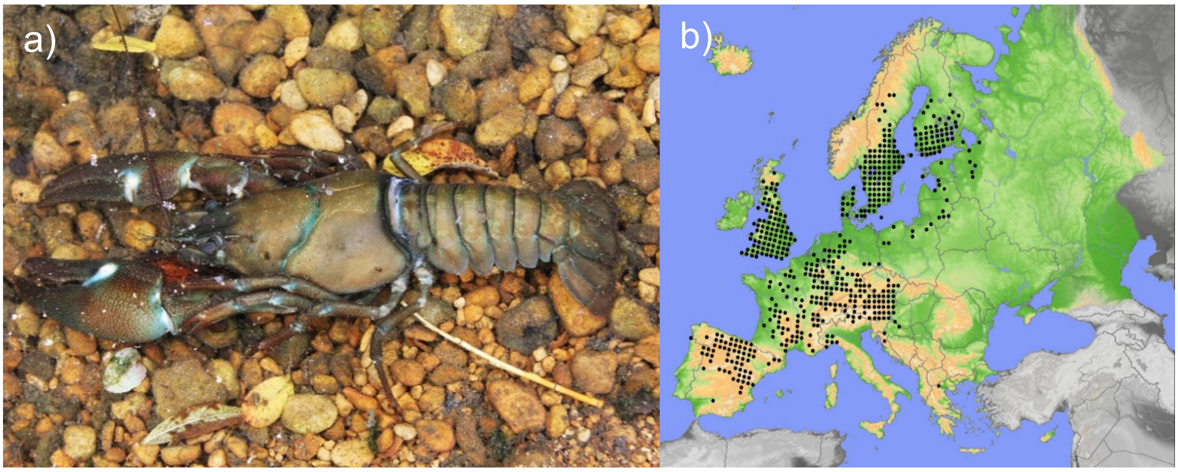

Figure 4.1 – a) American signal crayfish (*Pacifastacus leniusculus*) showing the characteristic pale 'signal' on the chelae. Image credit: Mark Philpott, published under a Creative Commons license. b) The distribution of the American signal crayfish in Europe, with black points representing areas with confirmed records. From Kouba *et al.* (2014).

Once established within a catchment, signal crayfish populations expand rapidly. For example, after their introduction to the Karana River, Croatia, in 2012, signal crayfish moved upstream at a rate of 2.23 km year^{-1} and downstream at a rate of 2.84 km year^{-1}, invading 18.7% of the watercourse over a five year period (Hudina *et al.*, 2017). Similarly, high upstream (0.5 – 4.0 km year^{-1}) and downstream (1.9 – 7.0 km year^{-1}) dispersal rates have been reported in Carinthia, Austria (Weinländer & Füreder, 2009), and high downstream dispersal rates (1.2 km year^{-1}) have been observed in the River Wharfe, UK (Peay & Rogers, 1999). This rapid range expansion is largely driven by the ability of individual crayfish to make active movements in both upstream and downstream directions (Bubb *et al.*, 2004). Bubb *et al.* (2004) radio tagged 64 signal crayfish and monitored their movements over several months. At the population level, average distances moved by crayfish were low (13.5 m upstream and 15.0 m downstream), but individual level analysis revealed high intraspecific variation, with some individuals moving as far as 283 m upstream and 417 m downstream. Bubb *et al.* (2006a) found similar results using passive integrated transponder (PIT) telemetry, with most individuals remaining close to the release site, and some moving as far as 345 m. Long distance dispersal by some individuals have also been observed in the River Maçãs, Portugal, where one individual was found to have moved 461 m in 12 hours (Anastácio *et al.*, 2015). Signal crayfish also have a strong climbing ability (Peay & Dunn, 2014) and are known to undergo terrestrial dispersal (Marques *et al.*, 2015; Thomas *et al.*, 2019b), further aiding their rapid range expansion.

The implications of signal crayfish introductions are overwhelmingly negative (Holdich *et al.*, 2014). Native crayfish species are rapidly extirpated by the crayfish plague (*Aphanomyces astaci*; Alderman *et al.*, 1990) and competitive exclusion from refuges (Dunn *et al.*, 2009). Invasion by signal crayfish also affects ecologically and economically important fish species through competitive displacement (e.g., juvenile Atlantic salmon [*Salmo salar*], Griffiths *et al.*, 2004; bullhead [*Cottus gobio*], Bubb *et al.*, 2009) and direct predation (Edmonds *et al.*, 2011), leading to reduced diversity and abundance of fish communities (Galib *et al.*, 2021). This reduction of diversity and abundance also extends to macroinvertebrates (Crawford *et al.*, 2006; Galib *et al.*, 2021), subsequently reducing the reliability of macroinvertebrate indicators (Mathers *et al.*, 2016). Furthermore, burrowing behaviour leads to higher levels of turbidity and fine sediment deposition (Harvey *et al.*, 2014), as well as higher levels of bank erosion and instability (Faller *et al.*, 2016). These impacts culminate in a reduction of supporting, regulating and cultural ecosystem services (Lodge *et al.*, 2012), and significant economic costs (Oreska & Aldridge, 2011; Cuthbert *et al.*, 2021b).

Given the substantial negative impacts of signal crayfish, effective management techniques are of critical importance. A wide variety of techniques have been employed to control signal crayfish populations, but efficacy is often low and successful eradication is rare (Gherardi *et al.*, 2011; Manfrin *et al.*, 2019). Physical removal using traps is the most common management technique for signal crayfish, but intensive and sustained efforts are necessary to exert significant control over invasive populations (Moorhouse & MacDonald, 2011a, b). Furthermore, a recent study utilising a novel ‘triple drawdown’ methodology demonstrated that 97.7% of the crayfish population was too small to be caught using traditional baited traps, meaning that trapping is unlikely to be an effective method of signal crayfish control (Chadwick *et al.*, 2021). This issue has partially been addressed throught the use of Artificial Refuge Traps (ARTs) which can capture a greater proportion of small individuals, but ARTs are not currently widely used, and further work is required to optimise their application (Green *et al.*, 2018). Treatments such as biological control (Freeman *et al.*, 2010), biocides (Peay *et al.*, 2019) and electrocution (Peay *et al.*, 2015) have also been proposed, but significant non-target effects prevent their widespread application (Manfrin *et al.*, 2019). Emerging technologies such as sexual attractants, establishment of monosex populations, silencing of key hormones, sterile male release, and oral delivery of autocidal neuropeptides may increase the likelihood of invasive crayfish eradication, although these techniques are unlikely to be available for widespread use in the near future (Manfrin *et al.*, 2019).

The limited success of previous eradication attempts means that containment of signal crayfish is a management priority, and there is evidence to suggest that river infrastructure may be able to limit upstream movements (Krieg & Zenker, 2020). For example, Rosewarne *et al.* (2013) demonstrated that the number of upstream passages of signal crayfish at a low-head gauging weir was 45% lower than the number of upstream passages in an unmodified control reach. In a laboratory study, Frings *et al.* (2013) found that some signal crayfish were unable to pass relatively small barriers (maximum height of 0.26 m), even at relatively low velocities (<1.0 m s^{-1}). Kerr *et al.* (2021) also found that low flow velocities (0.74 m s^{-1}) at the crest of a model crump weir allowed only 10-16% of crayfish to pass. Similar observations have also been described anecdotally, with (Peay, 2001) observing that two small weirs (<1 m head height) acted as a temporary barrier to signal crayfish in the River Rother, UK. Exclusion barriers built specifically to contain signal crayfish remain uncommon (but see Clyde River Foundation, 2011; Krieg *et al.*, 2021), but recent research has demonstrated that modifications to existing barriers may provide a cost-effective method of containment. For example, Krieg *et al.* (2021) found that adding overhanging lips at the barrier crest, as well as steel plates to the barrier face and river banks, could prevent upstream passage by signal crayfish. Similarly, Chucholl *et al.* (2022) found that raising culverts and adding an overhanging lip to the downstream entrance successfully limited the spread of signal crayfish through the upper reaches of the river Bottwar, Germany.

Observations of signal crayfish dispersal being limited by exclusion barriers have led some to propose that barrier installation may be an effective management strategy (Stebbing *et al.*, 2014; Manfrin *et al.*, 2019; Krieg & Zenker, 2020). Indeed, UK government advice on the development of ‘ark’ sites (isolated areas where new populations of native crayfish can be established and protected) suggests that in-stream barriers may be sufficient to slow or stop the upstream invasion of signal crayfish into protected reaches (Peay *et al.*, 2009b; Nightingale *et al.*, 2017). However, recent studies using environmental DNA suggest that in-stream barriers have not limited the spread of signal crayfish in either the UK or Japan (Ikeda *et al.*, 2019; Robinson *et al.*, 2019). Additionally, signal crayfish can disperse over land upon encountering obstacles (Marques *et al.*, 2015; Thomas *et al.*, 2019b), meaning there is concern that the effectiveness of exclusion barriers may be limited (Peay, 2001). Furthermore, algal build up (Frings *et al.*, 2013) and periods of low flow (Chucholl *et al.*, 2022) can reduce the effectiveness of barriers to signal crayfish, meaning their long-term efficacy remains unknown.

The high impact and broad geographic range of signal crayfish, coupled with strong applied interest in the use of barriers as a management technique, means that this species is an ideal model to address the questions posed in this thesis. Additionally, the long history of research regarding American signal crayfish has generated a detailed understanding regarding many aspects of their biology, meaning the development of an individual-based model (IBM) is feasible for this species. Indeed, the development of IBM requires a large quantity of detailed data, meaning this technique cannot be applied to all species (see section 4.2). For signal crayfish, detailed information is available on population dynamics (e.g., Guan & Wiles, 1999; Hudina *et al.*, 2012; Almeida *et al.*, 2013), reproduction (e.g., Guan & Wiles, 1999), mortality (e.g., Momot, 1984; Houghton *et al.*, 2017), and movement (e.g., Bubb *et al.*, 2002; Bubb *et al.*, 2004, 2006a, b; Moorhouse & MacDonald, 2011b; Wutz & Geist, 2013; Johnson *et al.*, 2014; Anastácio *et al.*, 2015). This data provided much of the information needed to develop an IBM for signal crayfish, but some aspects of their behaviour (particularly relating to barrier passage) remained unclear. Therefore, additional experimentation (Chapters 5 and 6) and computational modelling (Chapter 7) has been conducted throughout this thesis to provide the detail required for IBM parameterisation.

4.2 Individual-based modelling

Individual-based modelling is a population and community modelling approach which conceptualises ecological systems as collections of unique and autonomous individuals (Grimm & Railsback, 2005). Each individual is assigned any number of state variables (e.g., morphological traits, behavioural traits, spatial location), which vary according to behaviours (e.g., growth, reproduction, movement) derived from ecological theory (DeAngelis & Grimm, 2014). Unlike traditional population models which are governed by factors such as birth and death rates (i.e., top-down approaches), individual-based models (IBMs) take a bottom-up approach whereby emergent population-level behaviours arise from interactions between individuals with each other and their environment (DeAngelis & Grimm, 2014). IBMs can incorporate any number of individual-level mechanisms, facilitating the simulation of highly complex interactions that cannot be captured using population-level techniques (Grimm & Railsback, 2005). Furthermore, the ability of IBMs to incorporate detailed spatial information means they are particularly useful for addressing pragmatic questions regarding the effectiveness of different management strategies (Grimm, 1999). However, IBMs are computationally intensive and require detailed information to parameterise the state variables and define the behavioural rules, which may limit their use in certain circumstances (DeAngelis & Diaz, 2019).

IBMs are particularly useful for studying detailed invasion dynamics (Thompson *et al.*, 2021), meaning this approach has been used to simulate the spread of a variety of invasive species, including conehead termites (*Nasutiternes corniger*; Tonini *et al.* (2014)), common wall lizards (*Podarcis muralis*; Williams *et al.* (2021)), round gobies (*Neogobius melanostomus*; Samson *et al.* (2017)), and bitterling (*Rhodeus sericeus*; Dominguez Almela *et al.* (2020)). IBMs have also proven particularly useful for assessing the effectiveness of management interventions for invasive species (Thompson *et al.*, 2021). For example, Day *et al.* (2018) tested the effectiveness of electrofishing and exclusion barriers for management of eastern brook trout (*Salvelinus fontinalis*) in the North-Western USA, and found that long-term population suppression was only possible through sustained management efforts. Similarly, Messager and Olden (2018) used an IBM to assess whether trapping could limit the spread of rusty crayfish (*Faxonius rusticus*) in the John Day River basin (Oregon, USA), and found that rapid management intervention was essential to protect critical salmonid spawning habitat.

The ability of IBMs to simulate invasion dynamics over large spatio-temporal scales, as well as predict the impacts of management interventions, means they are ideally suited to address the objectives of this thesis. In Chapter 5, an IBM that can accurately predict the spread of American signal crayfish was developed and used to test the impacts of a simple in-stream barrier in a virtual river system. This IBM was based on the detailed information regarding signal crayfish biology available in the literature (see section 4.1), as well as additional experimentation (Chapters 5 and 6) and computational modelling (Chapter 7). In Chapter 8, the initial IBM is developed further to include a substantially more detailed barrier passage module, and is applied to a case study system in the River Glaven catchment, Norfolk, UK. The predictions of the IBM are combined with information on costs and potential non-target effects to develop recommendations for signal crayfish management in the catchment.

Chapter 5: River infrastructure and the spread of freshwater invasive species: inferences from an experimentally-parameterised individual-based model

N.B. This chapter is presented as a modified version of the published manuscript (Daniels et al., 2023). The IBM described was developed by Dr Jim Kerr, and all experimental work and writing was led by the PhD candidate.

Abstract:

1. 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.

5.1 Introduction

Invasive species are among the greatest threats to global biodiversity (Olden *et al.*, 2004; Blackburn *et al.*, 2019). 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., Rahel, 2013; Jones *et al.*, 2021b). 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., Rahel, 2013; Jones *et al.*, 2021b).

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: Kerby *et al.*, 2005; Dana *et al.*, 2011). 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 population-level 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.

5.2 Materials and methods

5.2.1 Experimental evaluation of the effect of density on passage

5.2.1.1 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 hours, 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 1000 litre indoor holding tanks at an average temperature of 17.8°C (range = 16.6 - 19.1°C). The maximum stocking density of crayfish was 25 individuals m^{-2}, and tanks contained an excess of refugia (PC pipes with diameter from 40-150 mm) to minimise aggressive interactions. Crayfish were held on a 12:12h light:dark photoperiod cycle, and were fed with an excess of commercially available fish food each day.

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 HDX 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 (Appendix B Table B1.1).

5.2.1.2 Experimental setup

A model Crump weir (length = 2380 mm, width = 60 mm, height = 340 mm) constructed of 18 mm thick plywood was installed in an indoor recirculating flume (length = 16 m, width = 0.6 m, depth = 0.8 m) at the University of Southampton Boldrewood Innovation Campus

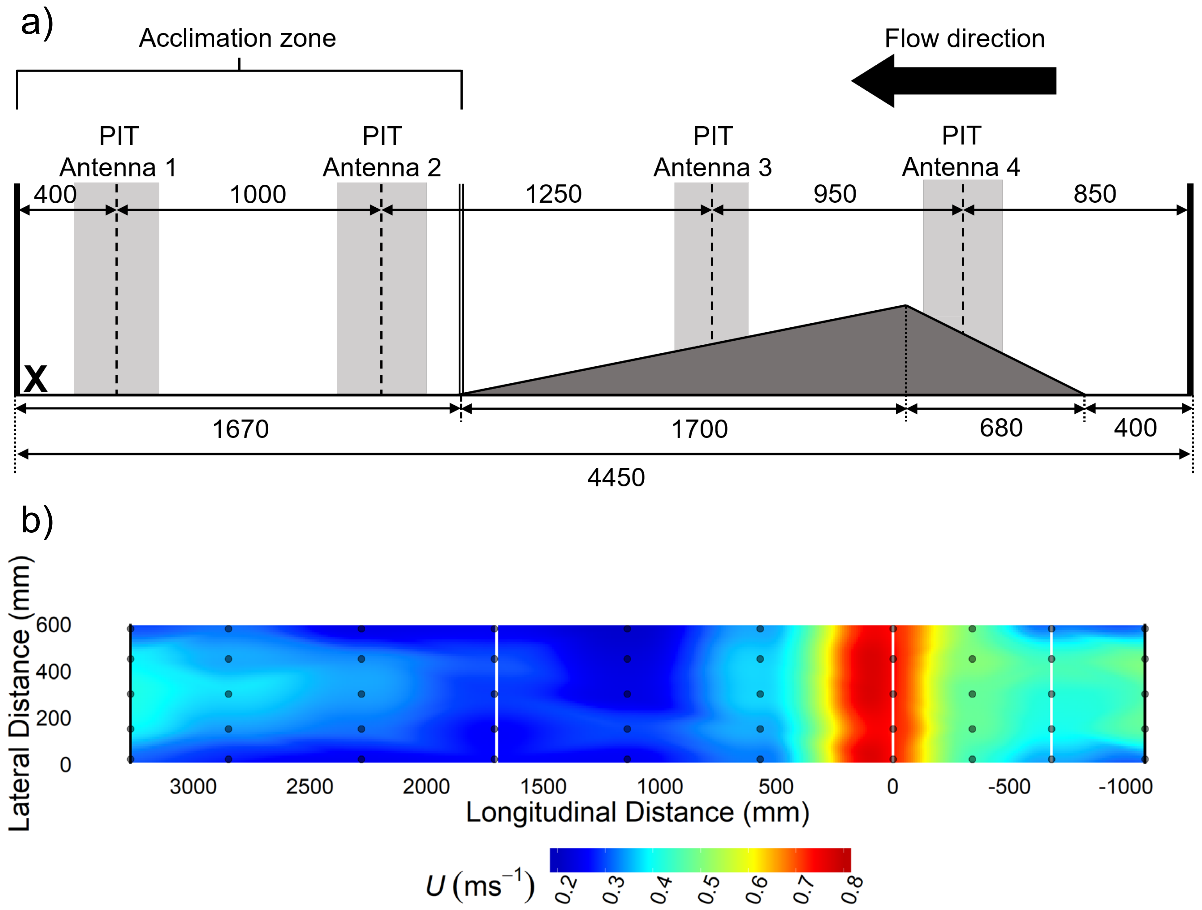

Figure 5.1 – a) Side view of a recirculatory flume used in an experiment to determine influence of crayfish density on upstream passage at a model Crump weir (dark grey). Location of PIT antennas (dashed lines) and their detection distance (light grey shaded area), removable screen (double line) and release location of the crayfish (cross) are depicted. b) Plan view of recirculatory flume illustrating flow velocities of the experimental area. Grey circles indicate locations of measurements taken using an electromagnetic flow meter (Valeport Model 801; measurements averaged over 10 seconds). From left to right, white lines denote the downstream extent, crest and upstream extent of the weir.

(Fig. 5.1). A removable screen was placed at the foot of the weir to create a 1 m^2 "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 (Fig. 5.1a). Each antenna formed a loop encompassing the entire water column, meaning crayfish were record when walking or swimming through. 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.

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^{-1}; Kerr *et al.*, 2021 found that 14% of crayfish passed crest velocities of 0.74 ms^{-1}). However, the crayfish used here were sourced from the same population as Kerr *et al.* (2021), and therefore the experimental setup (Fig. 5.1a) and flow conditions (Fig. 5.1b) were chosen to replicate this study. A full description of the experimental setup is available in Appendix B1.2.

5.2.1.3 Experimental procedure

Four density treatments (1, 5, 10, and 20 crayfish m^{-2}), were selected for use in this experiment. The density of signal crayfish in the wild is highly variable, with estimates ranging from 0.8-110 individuals per m-2 (Appendix B Table B1.2). Although very high densities of signal crayfish have been recorded, a relatively small proportion of individuals are adult crayfish with a carapace length greater than 35 mm, as used in this study (Chadwick *et al.*, 2021). As a result, the densities used here may be higher than those observed for adult crayfish in natural conditions. However, in-stream barriers are known to act as bottlenecks for dispersal, meaning high densities of individuals can accumulate downstream. As a result, information on barrier passage behaviour at higher densities than observed in non-impounded river sections is useful.

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 20 L 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 (Fig. 5.1a) and acclimatised for 30 minutes. On removing the screen, the crayfish could access the experimental area for one hour before the trial was terminated. Individual crayfish movements during the acclimation period and experimental trial were recorded using a combination of PIT telemetry and video. Each crayfish was used once only. Flume water temperature (mean = 20.7°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).

5.2.1.4 Ethical Note

All animal holding protocols and experimental procedures were sanctioned by the University of Southampton Animal Welfare Ethical Review Board (ERGO ID: 51963). Crayfish were captured and transported under licence from the Environment Agency (EP-EW094-L-209/16097/01 and EP/EW002-I-426/16416/02), and were dispatched humanely at the conclusion of the study by freezing at -14°C.

5.2.1.5 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 5.1). 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 30 s were treated as individual detections.

Table 5.1 – Key metrics used to assess crayfish movement behaviour 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.

5.2.1.6 Data analysis

Generalised linear models (GLMs) with a binomial error structure and a "logit" link function were used to investigate the influence of 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).

5.2.2 Individual-based model

5.2.2.1 Model Overview

A full description of the model following the updated Overview, Design concepts and Details (ODD) reporting format (Grimm *et al.*, 2020) is provided in Appendix B.2. 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 [g m^{-2}]), and 100 m 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 Appendix B.2) and the experiment described in section 5.2.1. 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. See Appendix B Section B.2.7.1.
2) **Population calculations**. Crayfish density and biomass were calculated for each 10 m river section. See Appendix B Section B.2.7.2.
3) **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. See Appendix B Section B.2.7.3.
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 5.3.1), density-dependent barrier passage was not implemented. See Appendix B Section B.2.7.4.

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 seven years of age. See Appendix B Section B.2.7.5.
6) **Reproduction**. Females became gravid during the breeding season (late September to early October) if they were sexually mature (CL > 39 mm) and there was an adult male in the same 100 m breeding area. Eggs were released after an incubation period of 223 days, with the number of eggs calculated as a function of carapace length. See Appendix B Section B.2.7.6.
7) **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. See Appendix B Section B.2.7.7.

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 2 hours 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).

5.2.2.3 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 (Sibley, 2000; Bubb *et al.*, 2005; Peay *et al.*, 2009a; Bernardo *et al.*, 2011; Hudina *et al.*, 2013; Hudina *et al.*, 2017; Appendix B Table B3.1). 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.

5.2.2.4. 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% CIs.

5.3 Results

5.3.1 Experimental assessment of the effects of density on barrier passage

Density did not influence any of the passage metrics. The *Proportion of attempts* (mean [±SD] = 0.70 [± 0.34]; z = -0.481, *p* = 0.631; Fig. 5.2a), *Proportion of passes* (mean [±SD] = 0.37, [± 0.32]; z = -0.493, *p* = 0.622; Fig. 5.2b), *Time to first attempt* (mean [±SD] = 855 [± 836] s; z = 0.006, *p* = 0.995; Fig. 5.2c) and *Time to first pass* (mean [±SD] = 1393 [± 956] s; z = -0.173, *p* = 0.863; Fig. 5.2d) were not affected by density.

5.3.2 Individual-based model

5.3.2.1 Model validation

For the base model (no barrier), the yearly rate of longitudinal expansion gradually increased after introduction and plateaued at approximately 1.42 km year^{-1} and 2.14 km year^{-1} in the upstream and downstream directions, respectively, after 8.5 years (TLER: 3.56 km year^{-1}) (Fig. 5.3a). Temperature-dependent dispersal resulted in annual fluctuations in invasion rate, with the maximum and minimum observed in the summer (upstream = 2.64 km year^{-1}, downstream = 3.98 km year^{-1}) and winter (upstream = 0.02 km year^{-1}, downstream = 0.02 km year^{-1}), respectively (Fig. 5.3a).

The average invasion rates predicted by the model (0 - 10.4 years: upstream = 0.73; downstream = 1.07; TLER = 1.83 km year^{-1}) were within the 95% CIs of the mean rates (upstream: 0.98; downstream: 1.54; TLER: 2.70 km year^{-1}) reported in the literature (Fig. 5.3b, Appendix B Table B3.1), indicating that the model was appropriate.

5.3.2.2 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 km year^{-1} to 0.52 km year^{-1} over a period of approximately 12 months (Fig. 5.4a). The invasion rate recovered to pre-barrier levels after 6.5 years (<1% difference for more than seven 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 (Fig. 5.4b).

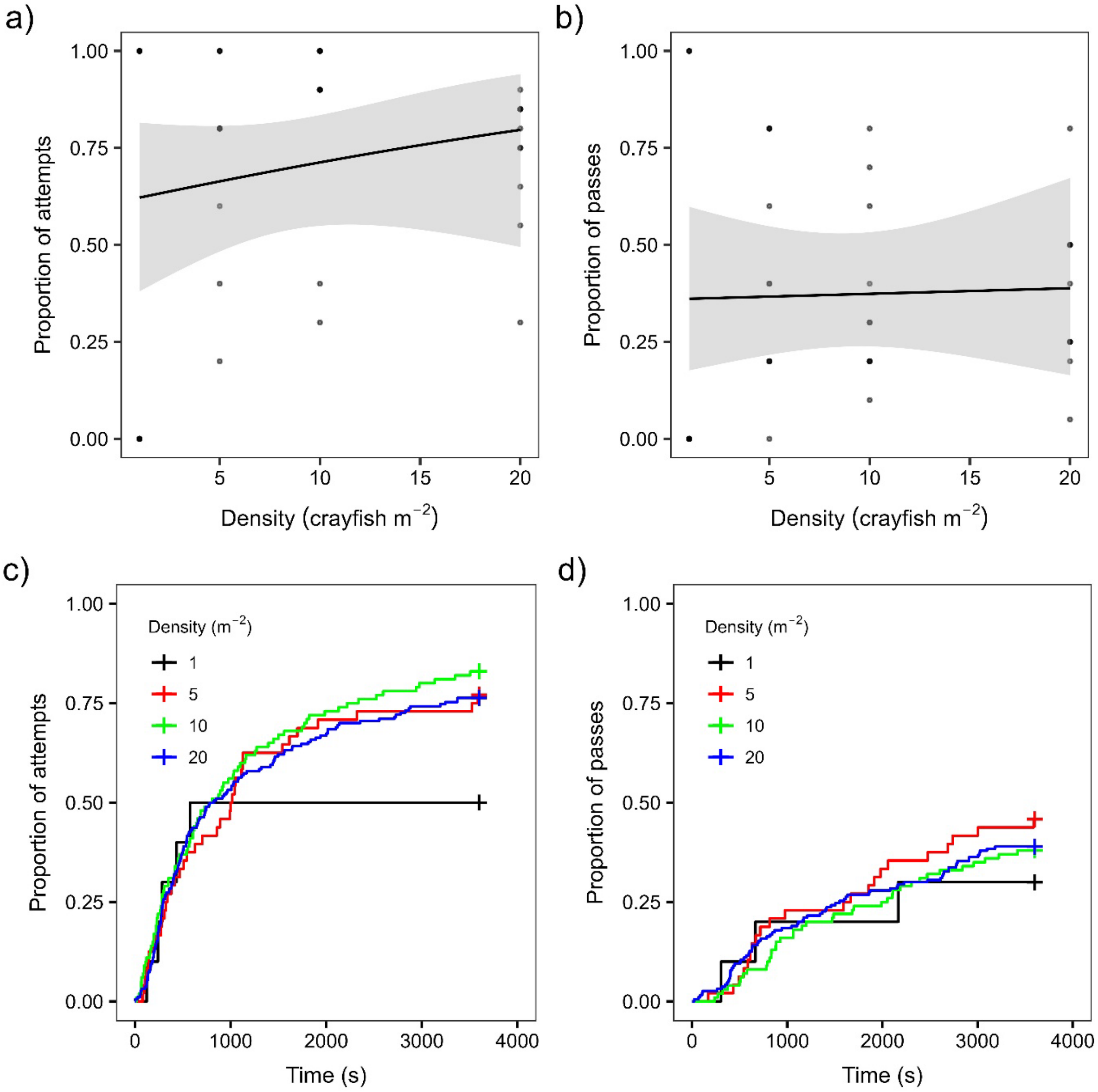

Figure 5.2 – The proportion of American signal crayfish that a) attempted to pass, and b) successfully passed a model Crump weir at different densities (points represent results from individual experimental trials, black line denotes model predictions and grey shading represents 95% confidence intervals), and the cumulative proportion of individuals over time that c) attempted to pass, and d) successfully passed a model Crump weir at different densities.

Crayfish first reached the barrier 10 km downstream of the release point after approximately 10.1 years but it had no effect on the invasion rate or location of the downstream invasion front (Appendix B Fig. B4.1).

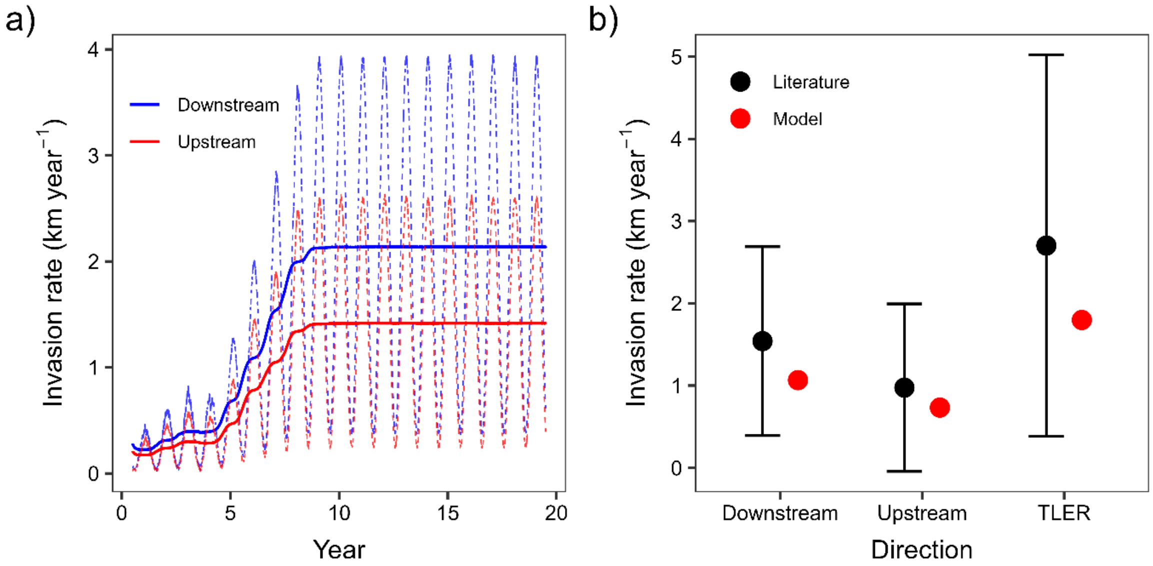

Figure 5.3 – a) Changes in invasion rate predicted by the individual-based model over a 20-year period (solid lines denote 365 day smoothed average, and dashed lines denote 20 day smoothed averages), b) Mean (circles) and 95% confidence intervals (error bars) upstream, downstream, and total linear expansion rates (TLER) of signal crayfish populations as reported in the literature and predicted by the individual-based model.

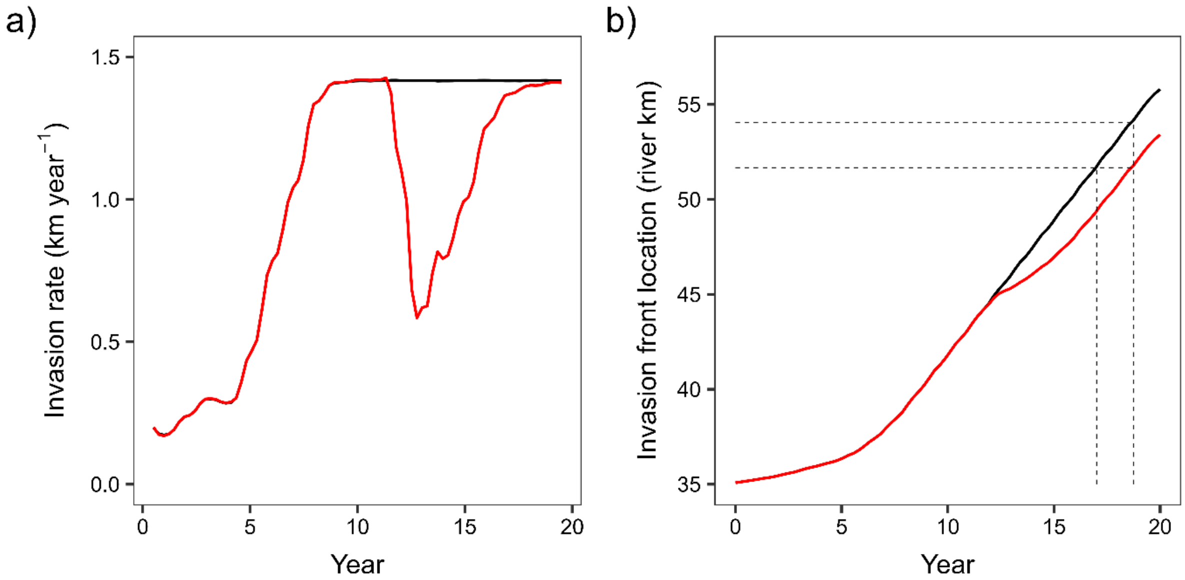

Figure 5.4 – Predictions of the individual-based population dispersal model for the no barrier control (black lines) and upstream barrier (red lines) scenarios, showing: a) differences in invasion rate, and b) shift in location of the invasion front over time.

5.4. Discussion

Riverine barriers are increasingly used to control aquatic invasive species (Jones *et al.*, 2021b), 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.

5.4.1 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. The relationship between personality and barrier passage in signal crayfish is explored further in Chapter 6, where it is found that bolder crayfish are more motivated to pass in-stream barriers. 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.

5.4.2 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 three years (upstream = 0.22 km year^{-1}, downstream = 0.29 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).

5.4.3 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.*, 2021b). 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., Stuart *et al.*, 2006; Kerr *et al.*, 2021).

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). Similarly, in Chapter 8, the IBM is applied to the River Glaven in Norfolk, and used to identify a catchment-scale combination of barriers that can limit the spread of signal crayfish with minimal effects on native species. However, the value of IBMs to inform IPM depends on high-quality 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, long-term 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.

5.4.4 Conclusion

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 installing 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 catchment-scale IPM strategies using the IBM.

Chapter 6: Personality-dependent passage behaviour of an aquatic invasive species at a barrier to dispersal.

N.B. This chapter is presented as a modified version of the published manuscript (Daniels & Kemp, 2022).

Abstract:

Intraspecific variation in personality traits is increasingly recognised as an important determinant of invasion success and is associated with the dispersal ability of several invasive species. However, previous studies have focussed on the dispersal of invasive species through continuous habitats, despite the high levels of anthropogenic fragmentation in modern environments. This study investigated how personality influences the behaviour of aquatic invasive species at an anthropogenic barrier to dispersal, using the passage behaviour of American signal crayfish (*Pacifastacus leniusculus*) at an experimental Crump weir as a model system. Personality was characterised by determining the repeatability of boldness, activity and sociability, with correlations between traits indicating behavioural syndromes, while passage behaviour was quantified as motivation and subsequent ability to pass the weir. Boldness and activity were repeatable and positively correlated, indicating a boldness-activity syndrome. However, sociability was not repeatable and was therefore not classified as a personality trait, potentially as a result of the confounding effects of social hierarchy formation. Bolder individuals tended to be more motivated to pass the weir, although motivation was not related to activity. Few individuals passed the weir, and personality was not related to passage success. This study evidences the presence of behavioural syndromes in signal crayfish and demonstrates that personality can influence the motivation of invasive species to expand their range in a fragmented habitat. Although no relationship with passage success was observed, the higher levels of motivation in bold individuals may lead to differential passage success in natural situations where the time to attempt passage is not constrained by experimental conditions.

6.1 Introduction

Human translocation of species beyond their native range is a defining feature of the Anthropocene (Ricciardi, 2007). Invasive species have profound impacts on native ecosystem functioning, resulting in substantial biodiversity losses (Vilà *et al.*, 2011; Simberloff *et al.*, 2013; Blackburn *et al.*, 2019), degradation of ecosystem services (Vilà *et al.*, 2010; Vilà & Hulme, 2017), and associated socio-economic impacts (Diagne *et al.*, 2021). With the rise of globalisation in recent decades, there has been a rapid increase in the rate of invasion and spread of non-native species within recipient ecosystems (Seebens *et al.*, 2017; Seebens *et al.*, 2021). This has been further exacerbated by shifts in climate, both through the elimination of thermal barriers to invasion (e.g., Chown *et al.*, 2012; Vilizzi *et al.*, 2021), and the emergence of new pathways for introduction and spread (e.g., Miller & Ruiz, 2014).

Understanding the species-level traits associated with invasiveness has been a primary focus in invasion science, with attributes such as high dispersal rates, rapid reproduction, and broad physiological tolerance among the key predictors of success (e.g., Liao *et al.*, 2021; Quell *et al.*, 2021). Furthermore, intraspecific variation is increasingly recognised as an important driver of invasion dynamics, with particular attention focussed on variation in personality traits (e.g., boldness, sociability, activity, aggression and exploration), and associated behavioural syndromes (i.e., correlations between these traits) (Chapple *et al.*, 2012; Juette *et al.*, 2014; Rehage *et al.*, 2016). Personality, defined as individual differences in behaviours that are stable over time and context (Sih *et al.*, 2004), can impact success at any stage of the invasion process (Juette *et al.*, 2014; Rehage *et al.*, 2016; Brand *et al.*, 2021), as traits that maximise the probability of being introduced outside the native range may also promote successful establishment and spread within the recipient ecosystem (Chapple *et al.*, 2012). These traits are also likely to influence interactions with native species and habitats, and thus may play an important role in determining the intensity of ecological impacts (Juette *et al.*, 2014).

Intraspecific variation in personality traits can influence dispersal tendency in a wide variety of taxa [e.g., great tits, *Parus major* (Dingemanse *et al.*, 2003); common lizards, *Lacerta vivipara* (Cote & Clobert, 2007); North American red squirrels, *Tamiasciurus hudsonicus* (Cooper *et al.*, 2017); mud crabs, *Panopeus herbstii* (Belgrad & Griffen, 2018); and thorn-tailed rayaditos, *Aphrastura spinicauda* (Botero-Delgadillo *et al.*, 2020)], suggesting a strong influence on the spread of invasive species (Cote *et al.*, 2010a; Sih *et al.*, 2012; Rehage *et al.*, 2016). Indeed, sociability [e.g., negative relationship for western mosquitofish, *Gambusia affinis* (Cote *et al.*, 2010b)], aggression [e.g., positive relationship for delicate skinks, *Lampropholis delicata* (Michelangeli *et al.*, 2017)] activity [e.g., positive relationship for round gobies, *Neogobius melanostomus* (Thorlacius *et al.*, 2015)], and certain behavioural syndromes [e.g., boldness-exploration-climbing syndrome in signal crayfish, *Pacifastacus leniusculus* (Galib *et al.*, 2022)] are important predictors of invasive dispersal. Furthermore, several studies have demonstrated that behavioural traits vary along the invasion gradient, with individuals at the invasion front showing higher levels of boldness and exploratory behaviour (Myles-Gonzalez *et al.*, 2015; Gruber *et al.*, 2017), and lower levels of aggression (Hudina *et al.*, 2015).

Previous studies exploring the influence of personality on dispersal in invasive species have focused on continuous, uninterrupted environments (e.g., Cote *et al.*, 2010b), but modern habitats are often heavily fragmented by anthropogenic barriers to animal movement [e.g., roads (Shepard *et al.*, 2008), fences (Ito *et al.*, 2013), deforested areas (Feeley & Rehm, 2012), and river infrastructure (Jones *et al.*, 2019)]. These barriers can have considerable impacts on native species by preventing access to critical habitat (Sheer & Steel, 2006), increasing levels of human-wildlife conflict (e.g., vehicle collisions; Hill *et al.*, 2019), and reducing gene flow between populations (Dixon *et al.*, 2007). For this reason, considerable effort is directed at removing such barriers (O'Connor *et al.*, 2015), or at least mitigating for their adverse effects (Silva *et al.*, 2018; Denneboom *et al.*, 2021). However, there is also increasing recognition that barriers to movement may be both ecologically and economically beneficial if they slow or block the secondary spread of invasive species (Hermoso *et al.*, 2015). For example, fences have been used in New Zealand and Australia to exclude introduced mammalian predators from areas of habitat that are important for native and reintroduced species (Clapperton & Matthews, 1996; Short & Turner, 2000; Moseby & O'Donnell, 2003). Similarly, common river infrastructure such as dams, weirs and culverts (Belletti *et al.*, 2020), can act as a barrier to the spread of invasive species (e.g., Kerby *et al.*, 2005), and in some cases are constructed specifically for this purpose (i.e., exclusion barriers; Jones *et al.*, 2021b). This trade-off between mitigating the impacts of habitat fragmentation while using discontinuity as a means of invasive species control is described as the “Connectivity Conundrum” (Zielinski *et al.*, 2020). The potential for barriers to exclude invasive species may be influenced by personality, with higher levels of boldness and activity, and low levels of sociability, being potential indicators of a greater probability of successful passage (Hirsch *et al.*, 2017). However, despite the use of exclusion barriers in invasive species management, understanding of how personality influences barrier passage behaviour remains limited. This information is important for accurate predictions of the spread of invasive species in fragmented habitats, and for effective implementation of exclusion barriers as a management technique (Hirsch *et al.*, 2017).

This study investigated how personality influences the behaviour and ability of an aquatic invasive species to overcome an impediment to movement. Using the American signal crayfish as a model, we investigated the role of personality on passage behaviour at a gauging weir, a low-head partial barrier that is a common feature in anthropogenically fragmented fluvial landscapes. Signal crayfish are the most widespread invasive crayfish in Europe (Kouba *et al.*, 2014), and their introduction has an overwhelmingly negative impact on native biodiversity (Crawford *et al.*, 2006; Dunn *et al.*, 2009; Edmonds *et al.*, 2011) and hydromorphology (Harvey *et al.*, 2014; Faller *et al.*, 2016). Repeatable personality traits, including boldness, activity, and foraging voracity, have previously been observed in signal crayfish (Taylor, 2016; Galib *et al.*, 2022). Additionally, recent research has demonstrated that behavioural syndromes (namely activity-distance moved and boldness-exploration climbing syndromes) influence the dispersal of signal crayfish in continuous habitats (Galib *et al.*, 2022). Exclusion barriers limit the movement of invasive crayfish *in situ* (Rosewarne *et al.*, 2013) and in laboratory conditions (Frings *et al.*, 2013; Kerr *et al.*, 2021), and their intentional use is likely to be an important tool in integrated pest management strategies

(Krieg & Zenker, 2020). However, the factors that drive barrier passage behaviour remain unclear. Indeed, the results of Chapter 4 suggest that passage behaviour is not driven by density, and evidence for sex- and size-dependent passage is inconsistent (Frings *et al.*, 2013; Rosewarne *et al.*, 2013). Understanding the mechanisms that underpin barrier passage behaviour of signal crayfish is vital for effective management.

To understand the relationship between personality and barrier passage behaviour, we characterised the personality of signal crayfish by: 1) quantifying the repeatability of boldness (latency to emerge from refuge after simulated danger), activity (distance moved in an open field environment) and sociability (tendency to gravitate towards conspecifics), and 2) identifying the presence of behavioural syndromes based on correlations between personality traits. Thereafter, we determined how personality influenced the behaviour of signal crayfish at a low-head weir by quantifying: 1) motivation and 2) passage success under experimental conditions. Following the theoretical predictions proposed by Hirsch *et al.* (2017), we expected that bolder, more active, and less sociable individuals would exhibit higher levels of motivation, and therefore an increased likelihood of successful barrier passage. Bolder individuals may be more likely to interact with novel environments such as the barrier, and boldness is known to be associated with a greater dispersal tendency (Galib *et al.*, 2022). Similarly, Thorlacius *et al.* (2015) demonstrated that activity is an important predictor of dispersal, and the greater dispersal potential of more active individuals is likely to lead to increased interaction with the barrier, and a higher probability of passage success. Less sociable individuals are known to disperse greater distances (Cote *et al.*, 2010b), and in this case may be more motivated to pass the barrier to move into an area with a low density of conspecifics.

6.2 Methods

6.2.1 Crayfish collection and husbandry

Signal crayfish (n = 90) were collected from the River Barle, Somerset (51°10’67.3” N, 3°65’77.7” W), between the 11th of August and 1st of September 2020 using a combination of artificial refuge traps (ARTs) and hand surveying. ART catches tend to be less sex and size-biased than traditional baited traps (Green *et al.*, 2018) and ARTs have been used seasonally to control signal crayfish populations on the River Barle since 2015. Hand surveys were conducted in an upstream direction, focusing on areas of low flow (glides or pools), by overturning cobbles and small boulders and searching the exposed area for crayfish. Once captured, crayfish were held in cooled transportation tanks with water from the source site, before being transported to the International Centre for Ecohydraulics Research Facility, University of Southampton Boldrewood Campus. On arrival in the laboratory, each crayfish was weighed, and the carapace and chela length recorded. The sex of each crayfish was ascertained, after which each individual was marked with three unique identifiers to enable them to be tracked during the study: 1) number written on the carapace using an oil-based permanent marker (as described in Ramalho *et al.*, 2010); 2) pattern punctured in the uropods using a needle (as described in Guan, 1997); and 3) a passive integrated transponder (PIT) tag attached to the carapace using cyanoacrylate glue (as in Kerr *et al.*, 2021). Crayfish were then held for at least 24 hours prior to use in behavioural assays. To reduce the risk of aggressive interactions crayfish were separated by sex and held together in two 1000 litre holding tanks (aerated and filtered with 75% weekly water change) with an excess of shelters (PVC pipes) at a mean temperature of 16.1°C (SD = 1.4).

6.2.2 Personality characterisation

Between the 14th of August and 8th of September 2020, crayfish were subjected to three different behavioural assays designed to quantify individual boldness, activity and sociability. To assess the repeatability of these behaviours, each crayfish was tested twice (as in Cote *et al.* (2010b) and Taylor (2016)), with a minimum of 24 hours between assays of the same type. Boldness and activity assays were conducted consecutively, and were not conducted within 24 hours of the separate sociability tests. Assays were conducted overnight (19:00 – 06:00) in glass tanks (650 mm long, 180 mm wide, 290 mm high) containing water from the holding tanks (Fig. 6.1) that was changed between each test. To prevent visual disturbance during the trials, the arena was surrounded by black plastic sheeting and crayfish were observed remotely using infrared security cameras.

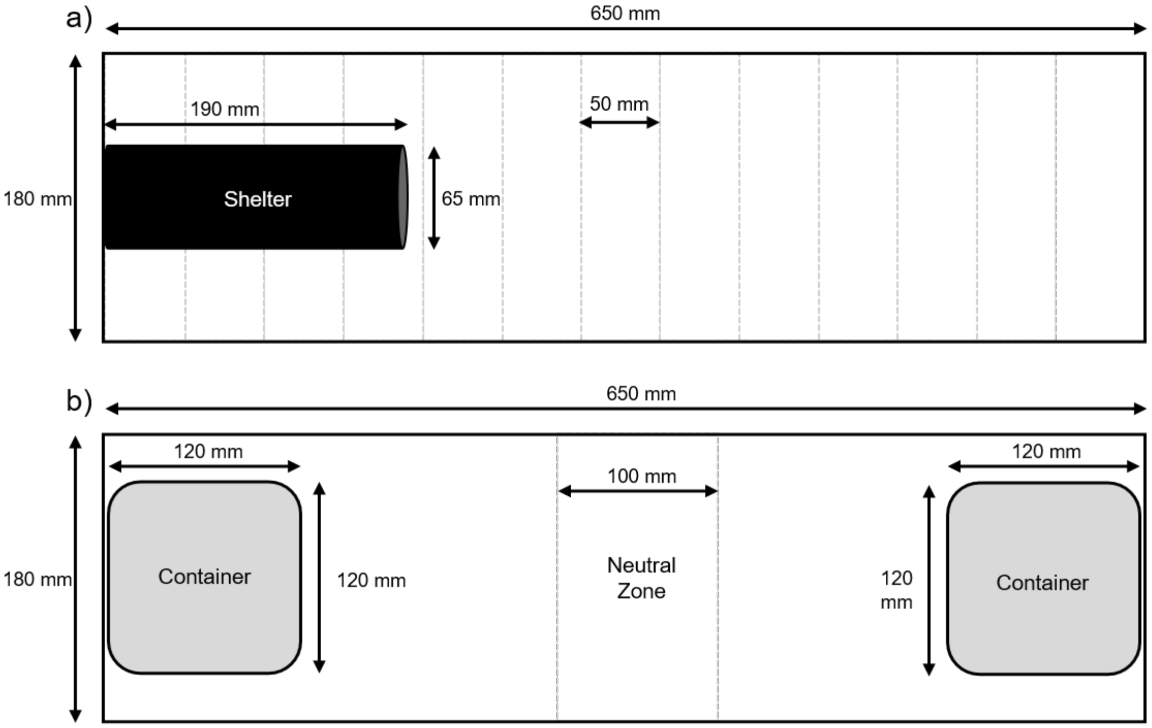

Figure 6.1 – Plan view of experimental arenas used to assess a) boldness and activity, and b) sociability in American signal crayfish (*Pacifastacus leniusculus*).

As crayfish behaviour is known to change both pre- and post-moult (Chang, 1995; Bacqué-Cazenave *et al.*, 2019), any individual tested within one week of moulting was excluded from further testing and analysis. Crayfish that moulted early in the experiment (n = 8) were separated from the main population for at least one week or until the carapace had completely hardened, at which point they were returned to the main population and subjected to the behavioural assays as described. Thirty-four individuals moulted during the experiment, resulting in a final sample size of 56 individuals (25 males and 31 females; mean±SD, mass = 14.98±4.49g, carapace length = 36.52 ±3.36 mm, chela length = 27.45±4.71 mm).

6.2.2.1 Boldness

Crayfish were placed in a submerged shelter (PVC pipe with diameter 65 mm) positioned at one end of the experimental arena (Fig. 6.1a). The open end of the shelter was sealed using a piece of 12 mm thick plywood, secured by a bucket containing several large rocks. The individual was allowed to acclimate for five minutes, after which the seal was removed by lifting the plywood and the bucket vertically. A stimulus simulating danger was presented immediately after unsealing the shelter by rattling a pair of stainless steel tongs (length = 360 mm) against the open end (opposite sides of the shelter hit five times each in quick succession). Boldness was measured as the time taken for the entire carapace to emerge from the shelter (s), with shorter latencies reflecting higher levels of boldness.

6.2.2.2 Activity

Activity was measured using an open-field test, whereby crayfish were allowed to move freely throughout the arena for 15 minutes once they had emerged from the shelter in the boldness assay. The arena was divided laterally into 50 mm sections (Fig. 6.1a), and activity was recorded as the number of times the individual moved between sections. A single movement between sections was recorded each time the joint of the carapace and the abdomen fully crossed a line on the base of the arena. It is possible that this measure of activity may have been influenced by exploratory behaviour, as crayfish were tested in a novel environment (Réale *et al.*, 2007). However, Perals *et al.* (2017) demonstrated that activity is not correlated with exploratory behaviours in open-field tests, and numerous studies have successfully measured activity using this approach (Cote *et al.*, 2010b; Taylor, 2016; Hirsch *et al.*, 2017), suggesting this measure accurately reflects activity.

6.2.2.3 Sociability

Crayfish sociability was assessed using the methods established by Taylor (2016). The focal crayfish was placed in the centre of the experimental arena and held in an upturned PVC pipe. A companion crayfish was then placed into a perforated plastic container (120 mm long, 120 mm wide, 150 mm high) at one end of the arena, and a rock of similar shape and size was placed in an identical container at the opposite end (Fig. 6.1b). Companions were randomly selected from the group of individuals that matched the sex and length (carapace length within 10%) of the focal individual, as both factors are known to influence the likelihood of antagonistic interactions (Sippel *et al.*, 1995; Ahvenharju & Ruohonen, 2007). Given that personality traits should be consistent over time and context (Sih *et al.*, 2004), the order in which crayfish experienced the trials (i.e., either as a companion or focal first) was not controlled. The location of the companion and rock relative to the focal individual were randomised between trials. After a five-minute acclimation period, the focal individual was released and allowed to move freely through the experimental arena for 10 minutes. A 100 mm neutral zone was established in the centre of the tank, and the time spent on each side of the neutral zone was recorded during the trial. Sociability was then calculated as log(time spent with companion crayfish / time spent with rock).

6.2.3 Passage behaviour

6.2.3.1 Experimental setup and procedure

To assess crayfish passage behaviour, a model Crump weir (2.38 m long, 0.60 m wide, 0.34 m high) was installed in a recirculating flume (16 m long, 0.60 m wide, 0.80 m high) at the International Centre for Ecohydraulics Research Facility, University of Southampton Boldrewood Campus (Fig. 6.2a). A Crump weir was selected as an example of a low-head structure commonly installed in the UK to gauge river flow (National River Flow Archive, 2022) and known to impede the movement of native aquatic species (Russon *et al.*, 2011; Vowles *et al.*, 2015). The experimental area was delineated by screens placed 1m upstream and downstream of the leading edge and foot of the weir, respectively. The base of the flume was covered with gravel to provide a semi-natural substrate to a depth of approximately 25 mm.

Flow velocity at the weir crest (mean = 0.68 m s^{-1}; Fig. 6.2b) was maintained at a constant discharge of 0.071 m^3 s^{-1}, and a sloped overshot weir at the downstream end of the flume was used to flood the weir and maintain a water depth of 570 mm throughout the flume. These conditions resembled those presented in a previous experiment that observed partial barrier passage of crayfish (Kerr *et al.*, 2021). Flow velocity was measured 25 mm above the substrate at 95 locations in the experimental area using an electromagnetic flowmeter (Valeport Model 801; measurements averaged over 10 seconds).

The movements of crayfish within the experimental area were monitored using four PIT antennas (two coils of 2.5 mm^2 stranded copper wire) positioned laterally in the flume (Fig. 6.2a). Each antenna was connected to a detection system consisting of four external tuning units (Oregon RFID) and a single multi-antenna half duplex (HDX) reader powered by a 12 V leisure battery. The PIT system was tuned and tested daily, with longitudinal detection distances ranging from 80 – 150 mm.

Barrier passage trials were conducted no sooner than 24 hours after the final personality assays. Individual crayfish were held in a separate 20 litre tank for a period of 0.5 – 1 hour prior to the barrier passage trials, and gradually acclimated to the flume water temperature (mean±SD = 22.2±1.38 °C). Crayfish were placed in a porous container at the downstream end of the flume for an additional 30 minutes to acclimatise to flow conditions. Following the acclimatisation period, crayfish were released at the downstream end of the experimental area (Fig. 6.2a). Trials were terminated once the crayfish had passed upstream beyond the weir crest or after one hour if they failed to do so.

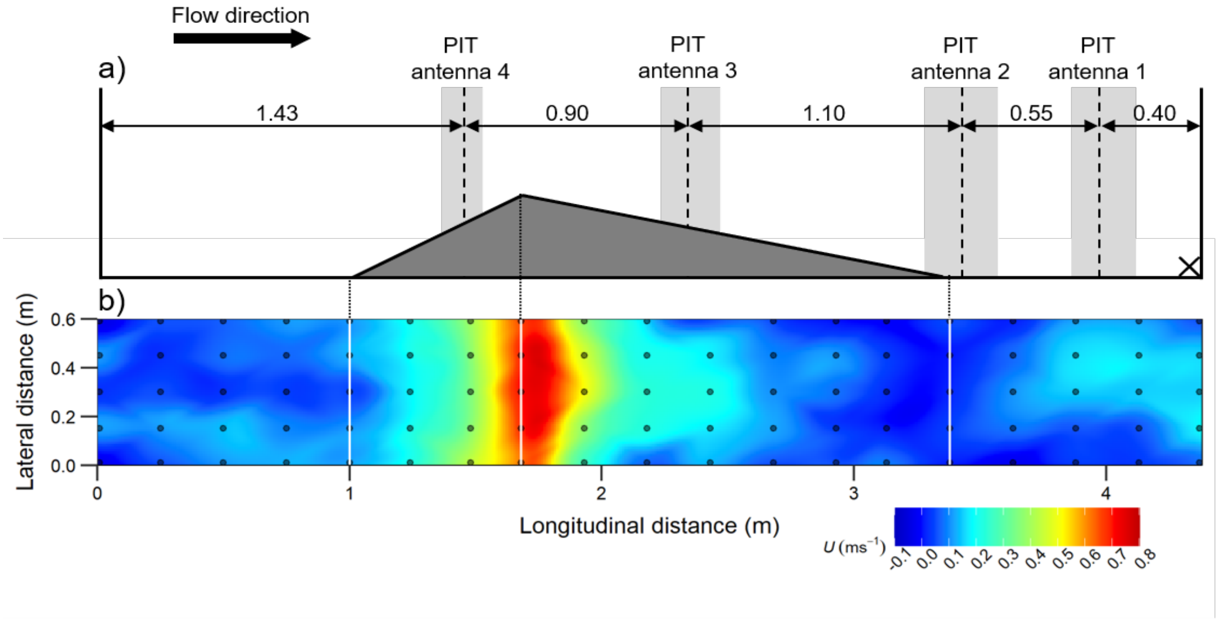

Figure 6.2 – (a) Side view of the experimental area used to assess the behaviour of American signal crayfish at an artificial barrier, showing the model Crump weir (dark grey), PIT antennas (dashed lines), PIT antennas detection distances (light grey shaded area), and release location of the crayfish (cross). (b) Plan view flow velocity map of the experimental area (grey circles represent locations of flow velocity measurements).

6.2.3.2 Assessment of crayfish passage behaviour

Six metrics of crayfish passage behaviour were recorded: 1) number of weir entries, 2) probability of attempt, 3) number of attempts, 4) time to first attempt, 5) maximum distance of ascent, and 6) passage success (Table 6.1). Metrics 1 and 5 were derived from direct observations of the crayfish during the trial under dim red light, with all other metrics calculated from PIT telemetry data. Although observations of barrier passage success were not blinded for personality, each metric was defined objectively prior to the commencement of the trials (Table 6.1).

Table 6.1 – Metrics used to assess the behaviour of American signal crayfish at a model Crump weir installed in a recirculatory flume at the International Centre for Ecohydraulics Research Facility, University of Southampton Boldrewood Campus.

No.	Metric	Definition	Objective	GLM error structure
1	Number of weir entries	The number of times the crayfish progressed onto the weir face.	Motivation	Poisson
2	Probability of attempt	Binary measure of whether the crayfish attempted to pass the weir. An attempt was defined as a detection at PIT antenna 3, as this antenna was positioned at the downstream extent of the high velocity region created by the weir crest.	Motivation	Binomial
3	Number of attempts	The number of times the crayfish attempted to pass the weir.	Motivation	Quasipoisson
4	Time to first attempt	The time interval between the start of the trial and the first attempt to pass the weir (s).	Motivation	Quasipoisson
5	Maximum distance of ascent	The maximum distance moved upstream on the weir face (m).	Motivation	Gaussian
6	Passage success	Binary measure of whether the crayfish successfully passed the weir. Successful passage was defined as a detection at PIT antenna 4, as this antenna was located upstream of the weir crest.	Passage success	Binomial

6.2.4 Ethical note

This study was sanctioned by the University of Southampton Animal Welfare and Ethical Review Board (submission ID: 57510), and all capture/ transport of crayfish was undertaken under licence from the Environment Agency (EP/EW098-H-261/15538/01) and Natural England (IAS permit number 39). To reduce the number of crayfish used in this study, the total to be collected was determined using a power analysis based on a previous study of crayfish passage (Chapter 5), while also accounting for expected high levels of moulting (based on the work of (Taylor, 2016) and previous experience of crayfish husbandry), and uncertainty in the original dataset. Given their invasive status in England, returning signal crayfish to the wild is prohibited by law (The Invasive Alien Species (Enforcement and Permitting) Order 2019), and crayfish were dispatched humanely at the end of the study by freezing at -14°C.

6.2.5 Data analysis

As mass, carapace and chela length were closely correlated, principal components analysis was used to condense these to a single variable. The first principal component (size PC1) explained 86.5% of the variance in these size variables. As this was the only principal component with an eigenvalue greater than 1 it was selected to represent size in further analysis.To assess the repeatability of the behaviours, adjusted repeatability values (R_A) were calculated using the rptR package in R, which estimates R_A based on variance values extracted from mixed-effects models (Stoffel *et al.*, 2017). Poisson error distributions were used in the mixed effects models for boldness and activity, and a gaussian error distribution was used for sociability. Ninety-five percent confidence intervals were determined through parametric bootstrapping (n = 1000) and *P* values were calculated through likelihood ratio tests. To identify confounding variables to be accounted for in repeatability analysis, Generalised Linear Mixed Models (GLMMs) incorporating size PC1, sex, and water temperature as fixed effects, alongside the individual crayfish as a random effect, were constructed for each of the personality traits. Only one relationship between these factors and a personality trait was observed (water temperature and boldness; coefficient = -0.151, SE = 0.055, $p = 0.006$), and therefore temperature was added as a fixed effect to the mixed model used to calculate the repeatability of boldness. For behaviours that were found to be repeatable, the average value for the personality trait across the two trials was used for further analysis. Conversely, behaviours that were not repeatable were not classified as personality traits, and were therefore excluded from further analysis.

To identify the presence of behavioural syndromes, pairwise Kendall's correlations were conducted for each combination of personality traits. Given the non-normal distributions of the personality data, Kendall's correlations were an appropriate method of identifying relationships between personality traits. To account for multiple testing, a Bonferroni correction was applied to the critical *P* value.

To determine how personality traits influenced behaviour at an artificial barrier, generalised linear models (GLMs) were created for each of the key metrics. Initial GLMs contained the three personality traits, size PC1, sex and flume temperature as predictor variables, and the error structure was varied according to the structure of the response variable (Table 6.1). Variance Inflation Factors (VIFs) were calculated for each model to assess multicollinearity between predictor variables, with values > 5 indicating problematic amounts of collinearity (James *et al.*, 2013). All VIF scores were less than 2.52, suggesting the GLMs were unlikely to be affected by multicollinearity. Manual backwards selection of the initial GLMs was conducted by removing variables in descending order of significance until only significant variables remained, or Akaike's Information Criterion was minimised (i.e., the minimum adequate model [MAM] was identified). For all models, the assumptions of normality of residuals and homoscedasticity were assessed through visual inspection of diagnostic plots (Normal Q-Q and Residuals vs Fitted respectively), and no violations were found. A single outlier was removed from the activity variable (number of lines crossed = 351, z score = 4.04), but the remaining data for this individual was retained.

Untransformed latencies were used to represent boldness in each of the GLMs. As a result, negative relationships between the latency to emerge and the metric of interest actually represent a positive relationship with boldness. For example, a negative relationship between latency and the probability of attempt would denote that individuals which take a long time to emerge from the shelter are less likely to attempt passage. Given that longer latencies are associated with shier individuals, this would indicate that bolder individuals are more likely to attempt to pass the barrier. For clarity, statistical results and figures refer to latency to emerge rather than boldness.

6.3 Results

6.3.1 Personality characterisation

6.3.1.1 Repeatability of behaviours

Individuals exhibited repeatable boldness (i.e., latency to emerge from shelter) (n = 56, R_A = 0.286, 95% CI = [0.071, 0.476], p = 0.002, Appendix C Fig. C1.1a) and activity (n = 56, R_A = 0.701, $P < 0.001$, 95% CI = [0.546, 0.806], Appendix C Fig. C1.1b), indicating that these behaviours were personality traits. Conversely, sociability was not repeatable over time (n = 56, R_A = 0.133, 95% CI = [0, 0.367], P =0.176, Appendix C Fig. C1.1c), and was therefore not considered a personality trait in this case.

6.3.1.2 Behavioural syndromes

Higher boldness (shorter emergence latency) was associated with greater activity (τ = -0.281, p = 0.002, Appendix C Fig. C2.1), demonstrating the presence of a boldness-activity syndrome.

6.3.2 Passage behaviour

6.3.2.1 Motivation

Aspects of crayfish motivation were associated with boldness, but not activity (Table 6.2). Bolder individuals were more likely to attempt to pass the weir (Fig. 6.3a), made a greater number of attempts (Fig. 6.3b), attempted more quickly (Fig. 6.3c), and progressed further up the weir (Fig. 6.3d). Activity was included in the MAM as a predictor of time to first attempt (Fig. 6.4) but no association was observed.

For the time to first passage metric, individuals that did not attempt within the trial period were assigned a time to attempt equal to the length of the trial (3600 s). Although common in studies of animal personality, this approach is less commonly applied to fish passage metrics. Therefore, this metric was reanalysed with all individuals that did not attempt removed. In this scenario, no relationship was observed between personality and the time to first attempt (see Appendix C Fig. C3.1).

6.3.2.2 Passage success

Only 3 crayfish (5.4%) successfully passed the barrier in the study, meaning no relationship between personality and passage success was observed under the experimental conditions described (i.e., no variables retained in MAM).

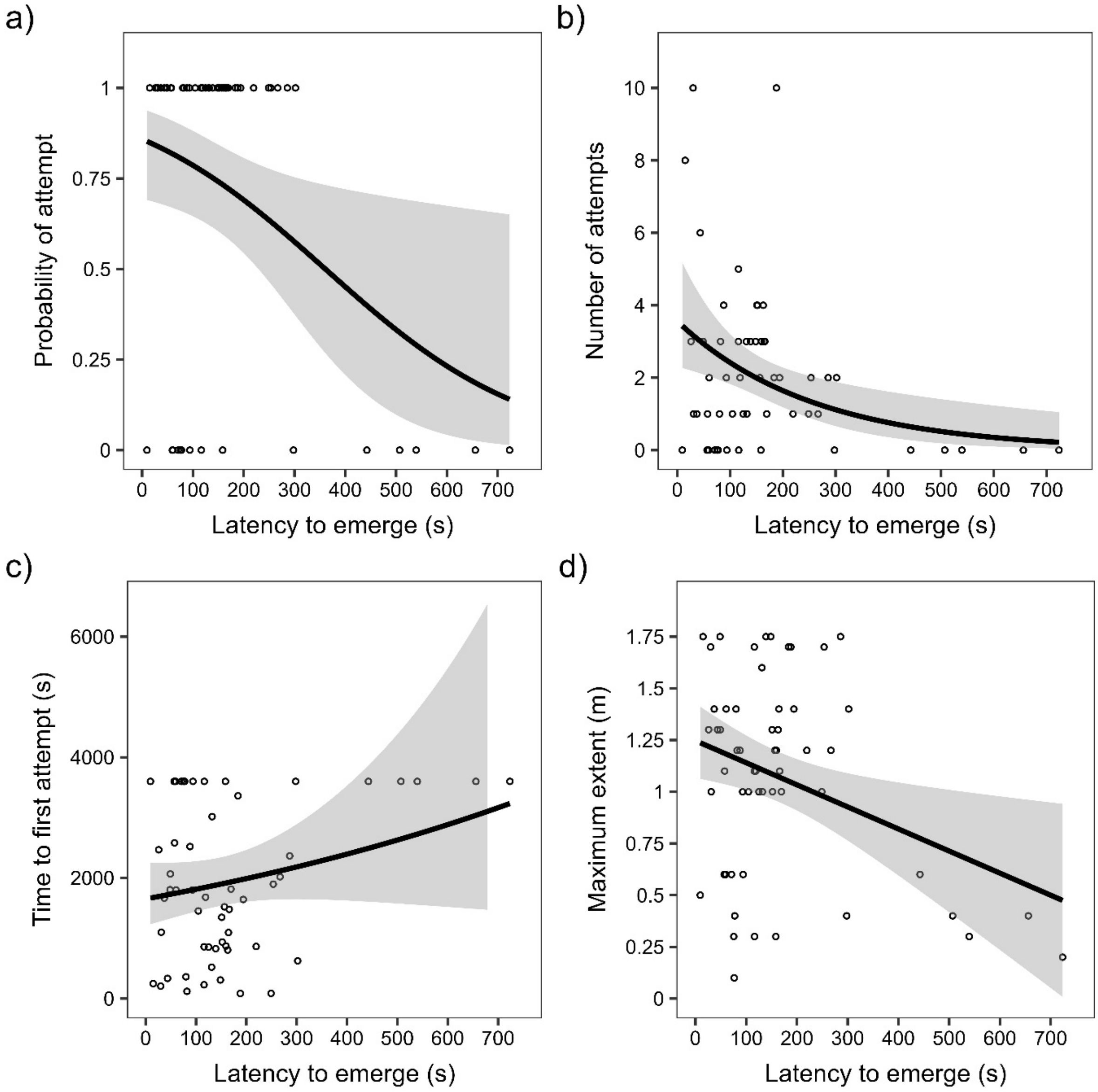

Figure 6.3 - Relationships between the boldness of American signal crayfish and (a) probability of attempting to pass an experimental Crump weir, (b) the number of attempts, (c) the time to first attempt and (d) the maximum distance of ascent. Black lines show GLM predictions and grey shading denotes 95% confidence intervals.

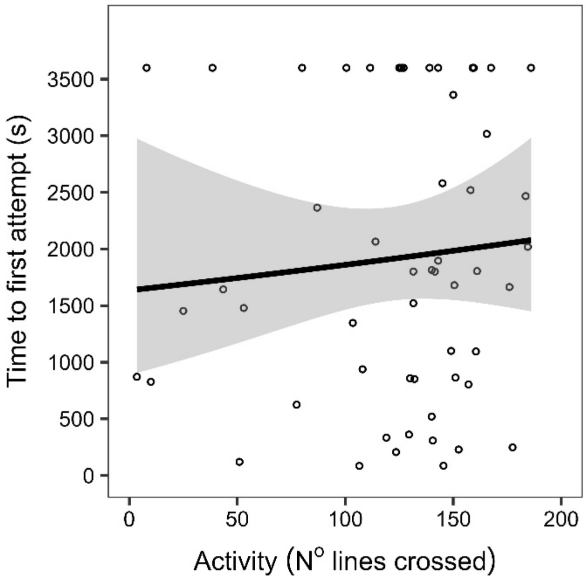

Figure 6.4 – Relationship between the activity of American signal crayfish and the time to the first attempt. Black lines show GLM predictions and grey shading denotes 95% confidence intervals.

Table 6.2 – Variables associated with the motivation of signal crayfish (n = 56) to pass an experimental weir.

Metric	Predictor Variable	Coefficient	SE	*P*
Number of weir entries	-	-	-	-
Probability of attempt	Latency to emerge	-0.007	0.003	**0.014**
	Size PC1	-0.664	0.283	**0.019**
	Sex (male)	-1.971	0.801	**0.014**
Number of attempts	Latency to emerge	-0.004	0.001	**0.004**
Time to first attempt	Latency to emerge	0.002	0.001	**0.031**
	Activity	0.005	0.002	0.069
Maximum distance of ascent	Latency to emerge	-0.001	0.000	**0.012**

Variables present in the table are those retained in minimum adequate models (MAMs) derived from full GLMs. Dashes indicate that none of the predictor variables were retained in the MAM, and bold represents significant associations.

6.4 Discussion

Although personality is known to influence the secondary spread of invasive species, its effects on dispersal in fragmented habitats remain poorly understood. This study quantified personality traits exhibited by American signal crayfish, an important aquatic invasive species in the UK (Holdich *et al.*, 2014) and Europe (Vaeßen & Hollert, 2015), and investigated the influence of personality on passage behaviour at a low-head weir under experimental conditions. Measures of boldness and activity were repeatable over time and positively correlated, indicative of a boldness-activity syndrome. Conversely, sociability was not repeatable and was therefore not classified as a personality trait, potentially as a result of the formation of social hierarchies in the holding tanks. Bolder individuals were more motivated to pass the experimental weir, as indicated by positive relationships between boldness and the probability of attempting to pass the weir, the number of attempts, the distance progressed up the weir face, and the time to first attempt (although this relationship did not hold when individuals that did not attempt were removed). However, this did not result in higher passage success. Activity was not associated with either motivation or passage success. This study provides empirical evidence that personality influences the motivation of an invasive species to pass an anthropogenic dispersal barrier, but further work is recommended to determine how this may affect passage success in natural conditions.

The initial phase of this study quantified aspects of personality in American signal crayfish, and identified the presence of behavioural syndromes in which traits are correlated. Measures of both boldness and activity were repeatable over time, indicating personality traits, while sociability was not. Although the estimate of repeatability (R) for boldness of 0.286 is within the range of that published for other crayfish species [R = 0.16 to 0.49; noble crayfish, *Astacus astacus* (Vainikka *et al.*, 2011); yabby, *Cherax destructor* (Biro *et al.*, 2014); red swamp crayfish, *Procambarus clarkii* (Raffard *et al.*, 2017)], it was much lower than that for activity (R = 0.701). Variation in repeatability between traits is common, and likely driven by differences in the extent to which the trait is influenced by other intrinsic and extrinsic factors (e.g., sex, age, and experimental conditions; Bell *et al.*, 2009). Indeed, Taylor (2016) found that the repeatability of activity and boldness in signal crayfish varies between populations, experimental protocol, and position along the invasion gradient. Furthermore, in this study relatively low variation in water temperature (between 14.5 and 18.6°C) influenced boldness, but not activity.

This study found no evidence for repeatability of sociability in signal crayfish. This finding is in line with Taylor (2016), but it is important to note that crayfish were kept in communal tanks prior to sociability testing in both studies. Signal crayfish are known to form social dominance hierarchies (Ahvenharju & Ruohonen, 2006, 2007), and their establishment in the holding tanks may have confounded the results of the sociability tests, with less dominant individuals avoiding potentially agonistic interactions and therefore being classified as asocial. Future research is recommended to determine the influence of social hierarchy on estimates of sociability.

The observation of a boldness-activity behavioural syndrome in signal crayfish, as indicated by a positive correlation between the two personality traits, has not been widely documented in signal crayfish. Galib *et al.* (2022) found that activity (measured as time in motion) and the distance moved during the trial were not associated with boldness, although this may be explained by the fact that personality assays were conducted during the day in field conditions. Additionally, boldness was assessed using a direct stimulus (pressure applied to the tail), and was calculated differently for individuals classified as 'bold' or 'shy'. Identification of behavioural syndromes may help predict the invasiveness of a non-native species, particularly the success of dispersal (Cote *et al.*, 2010a) and range expansion. For example, the co-occurrence of high boldness and activity in a behavioural syndrome may increase the likelihood of encountering anthropogenic transport vectors, and subsequently enhance the probability of locating and exploiting novel resources and mates within the non-native range (Chapple *et al.*, 2012). Furthermore, boldness and activity are associated with increased aggression and foraging voracity in signal crayfish (Pintor *et al.*, 2008; Pintor *et al.*, 2009), increasing the potential to outcompete and prey on native species within the recipient ecosystems. It is important to note that although similar designs have been used in multiple studies (e.g., Cote *et al.*, 2010b; Lothian & Lucas, 2021), boldness and activity assays conducted consecutively may not be truly independent. This may increase the likelihood of observing boldness-activity syndromes, and future research is encouraged to separate these assays fully.

As predicted, bolder individuals were more likely to attempt to pass, attempted to pass more frequently, and progressed further up the weir face. There is also some evidence to suggest that bolder individuals attempted to pass more quickly, although this relationship did not hold when individuals that did not attempt to pass the barrier were removed from statistical analysis. The practice of assigning the maximum time to individuals which are not observed undertaking an action within the trial period is common in studies of animal personality (e.g., Taylor, 2016; Lothian & Lucas, 2021), as removal of these individuals is likely to be non-random (i.e., less bold individuals are more likely to take longer to complete the action in question, and their removal from the analysis is likely to skew the overall boldness of the population retained in the analysis). However, this practice is less common in the fish passage literature, where it is generally contested that it is not possible to infer times to first attempt or first passage where these events do not occur. As such, the relationship between personality and time to first attempt in this study remains unclear. However, this has little influence on the overall conclusions of this study, as several other metrics (*probability of attempt*, *number of attempts*, and *maximum distance of ascent*) demonstrated that bolder individuals were more motivated to pass the in-stream barrier.

Given the observed relationship with motivation, it is intuitive to predict that bolder individuals are more likely to negotiate barriers in the wild. Indeed, recent studies have demonstrated that higher levels of boldness and exploratory behaviour are associated with increased passage success in brown trout (*Salmo trutta*) and American eels (*Anguilla rostrata*), respectively (Lothian & Lucas, 2021; Mensinger *et al.*, 2021). Similar relationships have been considered for invasive fish, but only in speculative terms, with a positive relationship being predicted (e.g., Cote *et al.* (2010b) for mosquitofish; Hirsch *et al.* (2017) for round gobies). Although not observed directly in this study, the relationship between personality and motivation suggests that personality may influence passage success in crayfish as well as teleosts, although further work is needed to confirm this relationship.

The lack of relationship between personality and passage success in this study may result from the very low number of crayfish that passed the experimental weir (5.4% of those tested). Passage in this study was substantially lower than observed in previous experiments conducted at the same laboratory with comparable weir designs and set-ups (e.g., 14% in Kerr *et al.* (2021) and 38.1% in Chapter 5). The source population for this study has been subjected to a consistent trapping regime since 2015 and, although the ARTs used are known to be less sex- and size-specific than conventional baited traps, this may have led to selective removal of bolder individuals, and subsequently an underrepresentation of these individuals in this experiment. Given that bolder individuals were more motivated to pass the barrier, this potential underrepresentation may have driven the low rates of passage success. Additionally, numerous factors including interpopulation differences, environmental factors (e.g., water temperature) and variation in study design (e.g., water temperature) may drive variation in crayfish passage success (Frings *et al.*, 2013; Rosewarne *et al.*, 2013). Not only should intraspecific variation in behaviour, such as that associated with personality, be considered in invasive species management, but so should the range of intrinsic, extrinsic, and spatio-temporal factors, such as stage of development or range expansion, population, habitat and season.

From the perspective of invasive species management, there are several important implications of this study. Mitigating the negative impacts of anthropogenic barriers to the movement of aquatic organisms represent a substantial conservation challenge, but also provide a means to limit the spread of aquatic invasive species (Jones *et al.*, 2021b). In cases where river infrastructure present partial barriers, they may act as ecological filters that segregate populations based on physiological (e.g., locomotory performance) and behavioural (e.g., personality) characteristics (Jones *et al.*, 2021a). Evidence from this experimental study illustrates how elevated motivation in bolder individuals may enhance the probability of negotiating low-head barriers in fragmented river systems, potentially leading to more bold individuals at the expanding edge of an invasion front compared to the invasion core. This spatial sorting of personality traits has been observed in numerous species, including round gobies (Myles-Gonzalez *et al.*, 2015), cane toads (*Rhinella marina*;

Gruber *et al.*, 2017), common mynas (*Acridotheres tristis*; Burstal *et al.*, 2020; Magory Cohen *et al.*, 2020), and orb-weaving spiders *(Cyrtophora citricola*; Chuang & Riechert, 2022), although evidence for this phenomenon in signal crayfish is mixed (Pintor *et al.*, 2008; Taylor, 2016). Should barrier passage contribute to spatial sorting of personality traits in signal crayfish, this may provide opportunities for the selective removal of bolder individuals (e.g., by trapping), effectively creating an evolutionary trap for individuals at the invasion front (Hale *et al.*, 2016). This could apply a strong selective pressure against boldness, potentially reducing associated impacts (e.g., predation and competition) and rates of range expansion. Avenues of future invasive species research include further consideration of the impacts of personality-biased barrier passage at larger spatio-temporal scales, and the inclusion of personality in dispersal models (Hirsch *et al.*, 2017).

Chapter 7: National-scale drivers of dispersal in a freshwater invasive species.

Abstract:

Invasive species are a major cause of biodiversity loss in freshwater ecosystems, yet their eradication often remains challenging once established. Where eradication is unfeasible, containment is necessary to prevent secondary range expansion and minimise the impact on native communities. Typically, containment approaches focus on preventing long-distance dispersal into new habitats, while local dispersal often goes unmanaged despite being a critical component of secondary range expansion. The drivers of local dispersal remain unclear, preventing the development of effective management techniques. This study investigated the factors driving the local dispersal of a freshwater invasive species using the American signal crayfish (*Pacifastacus leniusculus*) invasion in England as the model system. Records of signal crayfish were collated and a novel hierarchical clustering approach used to identify areas in which local dispersal was occurring (i.e., distinct local invasions). Upstream and downstream invasion rates were calculated for each distinct local invasion, and their relationship with several key predictors (density of river infrastructure, recreational use, anthropogenic pressure, physico-chemical and ecological characteristics of the waterbody) quantified. This approach identified 214 distinct local invasions, and suggested that over 4700 km of river in England are currently occupied by signal crayfish. Faster upstream invasion rates were associated with increased boating pressure, suggesting that anthropogenic vectors exert a strong influence over local dispersal, as well as long-distance movements. Increased downstream invasion rates were associated with higher water temperatures, suggesting that climate change may facilitate faster range expansion in the future. Signal crayfish continue to spread rapidly throughout Europe, North America, and Asia, and these results will facilitate the development of containment techniques that can effectively manage both long-distance and local dispersal.

7.1 Introduction

Biological invasions are a major driver of global environmental change (Pyšek *et al.*, 2020) and can have substantial negative impacts on native biodiversity (Mollot *et al.*, 2017; Blackburn *et al.*, 2019), ecosystem services (Pejchar & Mooney, 2009; Walsh *et al.*, 2016) and the economy (Cuthbert *et al.*, 2021a; Haubrock *et al.*, 2021). Fresh waters, already considered the most degraded of all global ecosystems (Dudgeon *et al.*, 2006), are particularly vulnerable to invasions due to the high density of transport vectors (including recreational angling, e.g., Weir *et al.*, 2022) and interconnectedness of waterways (Moorhouse & MacDonald, 2015), including the connection of previously isolated catchments through extensive networks of engineered canals (Zhan *et al.*, 2015). Invasions of freshwater systems can have severe consequences for native biotic communities, commonly leading to reductions in abundance and diversity (Ricciardi & Macisaac, 2010; Gallardo *et al.*, 2016). In some cases, invasive species are associated with extinction and extirpation of native species (e.g., Witte *et al.*, 1992; Liu *et al.*, 2017), driving an overall trend towards biotic homogenisation in freshwater systems (Villéger *et al.*, 2011). Freshwater invasions also have substantial economic impacts, with recent estimates suggesting that the global costs of aquatic invasive species reached at least $23 billion in 2020 (Cuthbert *et al.*, 2021b). Globally, rates of invasion show no sign of saturation (Seebens *et al.*, 2017; Seebens *et al.*, 2018), meaning the identification and enaction of appropriate management techniques is vital for conservation of freshwater ecosystems (Dudgeon *et al.*, 2006; Reid *et al.*, 2019).

Once aquatic invasive species become established, range expansion can occur through long-distance (i.e., establishment of new populations far from the invasion core) and local dispersal (i.e., expansion into adjacent habitats as a result of population growth and local diffusion) (Shigesada *et al.*, 1995). These processes commonly co-occur (i.e., stratified dispersal; Shigesada *et al.*, 1995), with long-distance movements forming ‘invasion hubs’ (Muirhead & Macisaac, 2005), from which invasive species disperse through the new region (e.g., Bronnenhuber *et al.*, 2011; Mallez & McCartney, 2018; Morissette *et al.*, 2021). Typically, long distance dispersal events are driven by anthropogenic activities such as angling (Anderson *et al.*, 2014), boating (Johnson *et al.*, 2001; Kelly *et al.*, 2013), and long-distance water transfers (Gallardo & Aldridge, 2018), although biological vectors such as birds (Reynolds *et al.*, 2015) and fish (Ricciardi & Hill, 2023) may also play an important role. In contrast, the drivers of diffusive local dispersal remain unclear, with some suggesting that factors such as physico-chemical characteristics of the water body (e.g., Sepulveda & Marczak, 2012; Haubrock *et al.*, 2022), inherent biological traits (e.g., Galib *et al.*, 2022), recreational activities (e.g., Weir *et al.*, 2022), and anthropogenic infrastructure such as dams, weirs, and culverts (e.g., Jones *et al.*, 2021b) may all be influential. However, explicit tests of the effects of these factors on the rate of local dispersal are rare, particularly over large spatiotemporal scales.

Containment (i.e., preventing secondary range expansion) is essential in limiting additional impacts on recipient ecosystems (Britton *et al.*, 2011), particularly in situations where eradication is not feasible for ecological, technological or financial reasons (Simberloff, 2014; Havel *et al.*, 2015; Simberloff, 2021). Currently, containment strategies focus on preventing long-distance movement, utilising approaches such as biosecurity campaigns (e.g., ‘*Check Clean Dry*’ in the UK; Great Britain Non-Native Species Secretariat, 2010), and targeted management of satellite populations with high dispersal potential (e.g., Gozlan *et al.*, 2010). However, there is growing recognition that prevention of local dispersal is also vital to limit range expansion, with techniques such as exclusion barriers (i.e., river infrastructure that inhibits the migration of invasive species) increasingly being employed to this effect (Jones *et al.*, 2021b). Further development of these techniques relies on a strong understanding of the factors driving local dispersal, particularly over large spatiotemporal scales.

Using the invasion of American signal crayfish (*Pacifastacus leniusculus*) in England as a model system, this study investigated the factors associated with the local dispersal of freshwater invasive species. To achieve this, all observations of signal crayfish in England were collated and used to: 1) identify distinct local invasions (i.e., areas in which local dispersal occurred, rather than long distance movement), 2) calculate invasion rates for each local invasion, and 3) identify the factors associated with differences in invasion rate.

7.2 Methodology

7.2.1 Model system

As discussed in detail in Chapter 4, signal crayfish were deemed to be an appropriate model species for this study. Signal crayfish were introduced to England in the 1970s for aquaculture (Richards, 1983), and their range expansion has been extensively documented (Goddard & Hogger, 1986; Holdich & Reeve, 1991; Rogers & Watson, 2011; Holdich et al., 2014). The ecological impacts of repeated introductions have been overwhelmingly negative (Holdich et al., 2014), including widespread extirpations of native white-clawed crayfish (*Austropotamobius pallipes*; Füreder et al., 2010) populations and reduced abundance and richness of fish and macroinvertebrate communities (Galib et al., 2021). Signal crayfish are estimated to cause economic losses of up to £13.9 million per year in the UK through damage to important resources (e.g., fisheries) and the associated management (Kouba et al., 2022). Although some localised eradications have been achieved using biocides (Ballantyne et al., 2019; Peay et al., 2019), widespread application of this approach remains unlikely in the UK due to the risk of non-target effects and high costs (Stebbing et al., 2014; Peay et al., 2019). Instead, it is likely that future management and control will depend to some extent on containment (Krieg & Zenker, 2020), making signal crayfish a useful model species for this study.

7.2.2 Identifying distinct local invasions

7.2.2.1 Crayfish data collection and mapping

Records of the spatial distribution of signal crayfish in Great Britain (n = 9299) were obtained from the National Biodiversity Network (NBN) Atlas (https://nbn.org.uk/), which collates and hosts biodiversity information from a variety of expert organisations (e.g., government agencies, conservation groups, and local ecological records centres) and citizen science projects. Focusing only on data relating to England, all duplicate (e.g., those collected from the same location on the same date), and incomplete records were removed. Observations that dated to earlier than 1975, the official date of first crayfish invasion reported by the Great Britain Non-Native Species Secretariat, were also removed, resulting in a final dataset containing 7127 records.

To ensure that subsequent spatial calculations could be constrained to movements through rivers, a map of the English river network was obtained using Ordnance Survey (OS) open rivers data. Connectivity was assessed manually using the Trace Network function in ArcGIS Pro (Version 2.7.1; Esri Inc.), with any disconnected river segments being checked using Google Earth satellite imagery and reconnected manually if appropriate.

7.2.2.2 Hierarchical clustering

As this study focused on local dispersal, it was important to differentiate these from long-distance movements. For each catchment in England (catchment maps obtained from the Environment Agency with the downstream extent of the river defined as the normal tidal limit), distinct invasions were identified using a hierarchical clustering approach (using the *hclust* function in R, (Müllner, 2013)). First, a matrix containing the distances (calculated along the river network) between every possible pair of observations of signal crayfish in the catchment was generated using the *riverdist* package in R (Tyers, 2020). A similar matrix was created to give the difference in time between each possible pair of observations. These matrices were then combined (distance matrix / time matrix) to calculate a theoretical invasion rate (i.e., the speed at which the invasion front would have needed to advance if the records were part of the same introduction event) for every pair of observations within the catchment. Agglomerative clustering with single linkage (Murtagh & Contreras, 2012) was applied to these data to generate a hierarchical tree showing spatiotemporal relationships between individual records (Fig. 7.1a). To identify individual clusters (i.e., distinct local invasions), hierarchical trees were divided into separate groups (Fig. 7.1b) using a pre-defined threshold based on available literature that reported the total linear

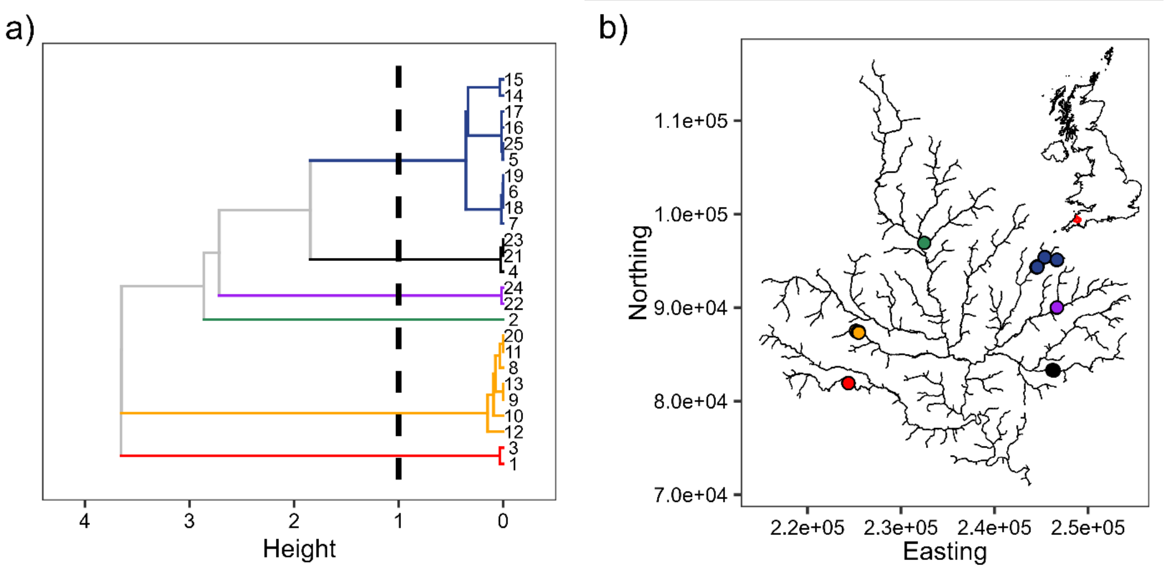

Figure 7.1 – The hierarchical clustering approach used to identify distinct local invasions of American signal crayfish (*Pacifastacus leniusculus*) in England, exemplified using the River Tamar Catchment. a) Dendrogram showing the relationships between individual records. Numbers at each branch terminal represent a single record. b) Records of signal crayfish overlayed on a map of the river network in the catchment. Different colours represent separate clusters.

expansion rate (TLER) of signal crayfish in the wild in the UK (Bubb *et al.*, 2005; Peay *et al.*, 2009a; Imhoff *et al.*, 2011). The maximum TLER (2.20 km year^{-1}) did not effectively delineate local invasions while the minimum TLER (0.24 km year^{-1}) proved over-conservative. Therefore, the average TLER of signal crayfish (1.00 km year^{-1}) was used to define the threshold for clustering.

7.2.3 Calculating invasion rate

To calculate the invasion rate for each cluster, the earliest record was identified and considered the initial introduction event (henceforth 'first record'). The furthest upstream and downstream records (i.e., the invasion fronts) within the cluster were identified, and their distance from the first record calculated (henceforth 'invasion distance'). Additionally, the total duration of the upstream and downstream invasion (henceforth 'invasion duration') was calculated by determining the time difference between the first record and the most recent record in each direction. Upstream and downstream invasion rates were calculated as the quotient of the invasion distance and the invasion duration.

7.2.4 Factors associated with invasion rate

7.2.4.1. Data collection

To identify factors potentially associated with secondary spread, eight predictor variables were quantified within a 300 m buffer zone (Fig. 7.2) around each cluster: 1) barrier density, 2) boating pressure, 3) angling pressure, 4) human influence, 5) human population density, 6) water temperature, 7) pH, and 8) river flow (Table 7.1). This distance of the buffer zone was chosen because the landscape characteristics within 300 m of the river are known to strongly influence water quality (Li *et al.*, 2018). For predictors that reflected mean measurements within the buffer zone (population density, human influence, water temperature, pH and river flow) the temporal extent of the predictor variables was matched to that of the cluster wherever possible (i.e., data points were only retained if they were taken between the dates of the earliest and most recent records in the cluster; Table 7.1). However, predictors that relied on count data (barrier density, boating pressure, angling pressure) were likely to be influenced by the temporal scale of the cluster (i.e., clusters covering longer periods of time would inevitably include a greater number of points). Therefore, no spatial matching was implemented for these predictors, ensuring that the final values were comparable across clusters with different temporal scales.

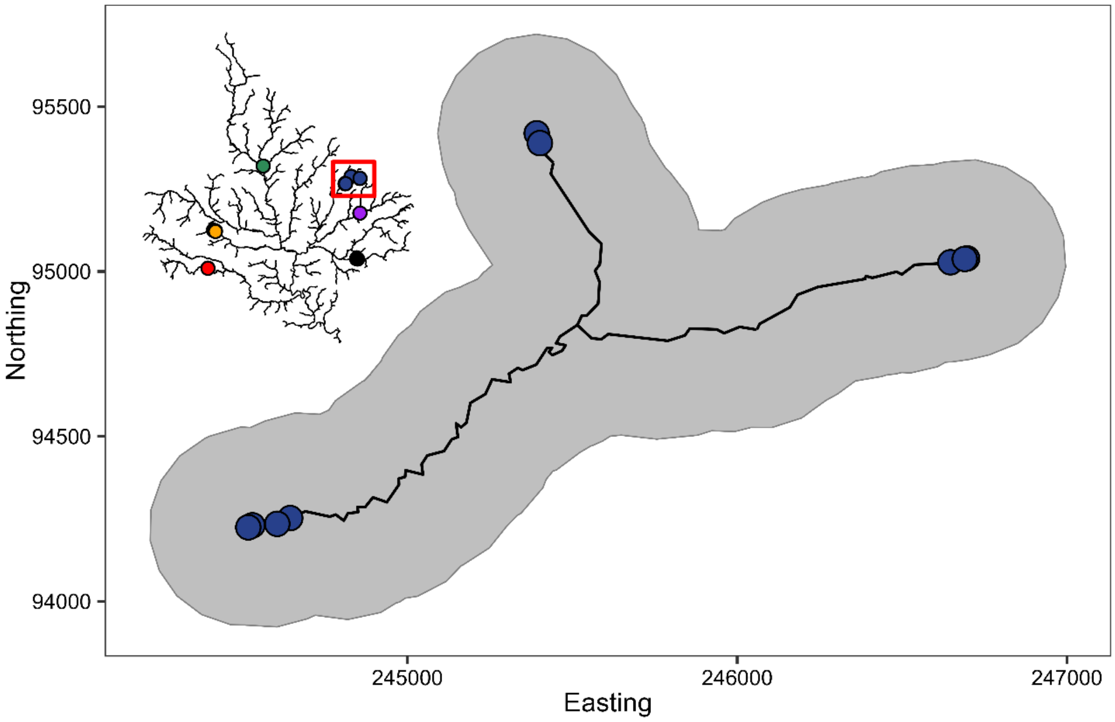

Figure 7.2 – An example of a distinct introduction of American signal crayfish (*Pacifastacus leniusculus*) in the River Tamar catchment (inset), identified using a hierarchical clustering approach. The grey shaded area denotes the 300 m buffer zone in which predictors of secondary spread were calculated. Blue points show records of signal crayfish, and the black line represents the river network.

Table 7.1 – Summary of metrics used to assess factors associated with local dispersal in American signal crayfish (*Pacifastacus leniusculus*) in England.

Anthropogenic Driver	**Metric**	**Data Source**
Anthropogenic barrier density	Number of anthropogenic dispersal barriers per river km.	AMBER Consortium (2020)
Boating pressure	Total number of verified photographs.	Flickr. Images accessed through *photosearcher* (Fox *et al.*, 2020) and verified using *googleCloudVisionR* (Pal *et al.*, 2020).
Angling pressure	Total number of verified photographs.	Flickr. Images accessed through *photosearcher* (Fox *et al.*, 2020) and verified using *googleCloudVisionR* (Pal *et al.*, 2020).
Human influence	Average human footprint (normalised scale from 0 -100).	Wildlife Conservation Society (WCS) & Center for International Earth Science Information Network (CIESIN) Columbia University (2005)
Population density	Average population density (1000 people km^{-2}).	Rose *et al.* (2020)
Water temperature	Mean water temperature (°C).	Environment Agency (2022b)
pH	Mean pH value.	Environment Agency (2022b)
River flow	Mean river flow rate (m^3 s^{-1}).	The National River Flow Archive, accessed through *rnrfa* (Vitolo *et al.*, 2016)

Data on anthropogenic river infrastructure in the UK, including dams, weirs, culverts, fords, sluices, and ramps, were obtained from the EU AMBER Atlas (AMBER Consortium, 2020). The Atlas provides the most comprehensive information available on instream barriers to the movement of aquatic species in Europe with over 1.2 million records (Belletti *et al.*, 2020).

Boating and angling pressure were quantified through a ‘passive citizen science’ approach using the photo sharing site Flickr. The *photosearcher* package in R (Fox *et al.*, 2020) was used to access the Flickr database and download metadata for all geotagged photographs taken in the UK with tags relevant to the activity of interest. For boating pressure, relevant tags were "boat", "barge", "paddleboard", "kayak", "canoe", "riverboat", "canal boat", "rowing boat", “sail”, “sailing” and "dinghy". For angling pressure relevant tags were “fishing”, “angling”, “fishing rod”, “fly fishing”, “coarse fishing”, “fisherman”. Given the potential inaccuracies of user-defined tags, automated image verification was implemented using the Google Cloud Vision (GCV) application programming interface (API) (Edwards *et al.*, 2021). The URL of each relevant image was passed to the GCV API using the R package *googleCloudVisionR* (Pal *et al.*, 2020), and a list of annotations returned. Images were discarded if the annotations did not contain at least one relevant keyword (see Appendix D.1 for full list of keywords), resulting in a final set of verified images. Boating and angling pressure were both calculated as the total number of verified photographs contained within the buffer zone surrounding each cluster.

Human influence was quantified using the Global Human Influence Index (Wildlife Conservation Society (WCS) & Center for International Earth Science Information Network (CIESIN) Columbia University, 2005). This dataset assigns an overall human influence score to 1 km grid cells (ranging from 0 in areas of no human influence to 64 in maximally influenced areas) based on a weighted composite of eight variables (population density, night lights, land cover, urban extent, and proximity to roads, railroads, navigable rivers and coastlines). For the purposes of this study, human influence was quantified as the average score within the buffer zone of each cluster. Although partially accounted for in the measure of human influence, population density was also included due to its strong potential impacts on the spread of invasive species (Chytrý *et al.*, 2009; Pyšek *et al.*, 2010; Lee *et al.*, 2017). Population density was obtained from the Oak Ridge National Laboratory (Rose *et al.*, 2020) at a 1 km resolution, and the average density in the buffer zone used as the final metric. To ensure that the inclusion of population density did not lead to undue collinearity in the final models, variance inflation factors (VIFs) were calculated. VIFs indicated minimal collinearity, meaning the addition of population density was appropriate (see Section 7.2.4.2). Each of these datasets was supplied as a single raster layer, meaning it was not possible to match the temporal extent of the data with that of the cluster.

Water temperature, pH (Water Quality Data Archive; Environment Agency, 2022b) and river flow (National River Flow Archive; Vitolo *et al.*, 2016) were chosen to represent the physicochemical characteristics of the river, as each is known to influence signal crayfish abundance and/or distribution (Bubb *et al.*, 2004; Usio *et al.*, 2006; Vedia *et al.*, 2017). Due to limitations of the water quality data, it was not possible to fully match the temporal extent for clusters with a start date prior to 2000. In cases where the cluster ended after 2000, partial temporal matching was implemented by only including data points taken between 1 January 2000 and the end date of the cluster. In cases where the cluster started and ended before 2000, or where no data points were contained within the buffer zone, water quality data was regarded as missing (n = 28). Flow data consists of quality controlled daily flow measurements taken at gauging stations across the UK and was calculated as the average daily flow for points contained within the buffer zone. However, there were numerous cases (n = 82) where no flow data was available within the buffer zone as a result of the low spatial resolution of this database (n = 1600 gauging stations). Under these scenarios, the average daily flow for points contained within the rest of the catchment was used to derive a measure of river flow. In cases where no gauging stations were present in the catchment (n = 7), flow data was recorded as missing. For each variable, the average of the temporally matched data points contained within the buffer zone was used as the final metric for the cluster.

7.2.4.2 Statistical Analysis

Initial data screening indicated a single outlier in upstream invasion rate (invasion rate = 124 km year^{-1}, z score = 10.33), which was subsequently removed from further analysis. Similarly, pilot analyses showed two outliers in barrier density (barrier density = 34.9 barriers km^{-1} & 7.5 barriers km^{-1}, z scores = 9.17 & 7.49 respectively) exerted strong influence over all models, and these points were also removed.

Due to potential non-independence of clusters from within the same river catchment, generalised linear mixed models (GLMMs) with a Gamma error structure and log link function were constructed separately for the upstream and downstream invasion rates. GLMMs contained catchment as a random effect and each of the eight predictor variables as fixed effects. To determine the importance of including catchment as a random effect, GLMMs were compared to equivalent generalised linear models (GLMs) that excluded the random effect of catchment. Comparisons were conducted using an F test and indicated that the inclusion of catchment did not affect the model (upstream models: Δlog-likelihood = 1.00, p = 1.00, downstream: Δlog-likelihood = 0.88, p = 1.00), meaning mixed effects models were not required.

Assessment of diagnostic plots for the initial GLMs (residuals vs fitted, QQ plots, residuals vs leverage) revealed several observations with particularly strong influence over model fit, and therefore a robust GLM approach was implemented using the *robustbase* package in R (Maechler *et al.*, 2023). In this approach, points are weighted based on leverage using the methods described by Cantoni and Ronchetti (2001) and Cantoni and Ronchetti (2006), reducing the influence of those with particularly high-leverage. Full models containing all eight predictor variables were constructed and variable inflation factors (VIFs) indicated no collinearity between the predictors (upstream maximum VIF = 2.29, downstream = 2.25). Model simplification was then conducted by removing variables in order of significance, with the minimum adequate model deemed to be reached when removal of further variables caused a significant decrease in model fit (assessed using a Wald test) or only significant predictors remained.

7.3 Results

7.3.1 Identifying distinct local invasions

Overall, 214 clusters were identified, with 21 composed of single observations and 193 consisting of multiple records (mean ± SE: 31.45 ± 6.48). For the clusters with multiple records, the mean length was 24.09 km (SE = 4.98), and the mean duration was 11.77 years (SE = 0.83). In total, 4716 km of river in England were found to be currently occupied by American signal crayfish (Fig. 7.3).

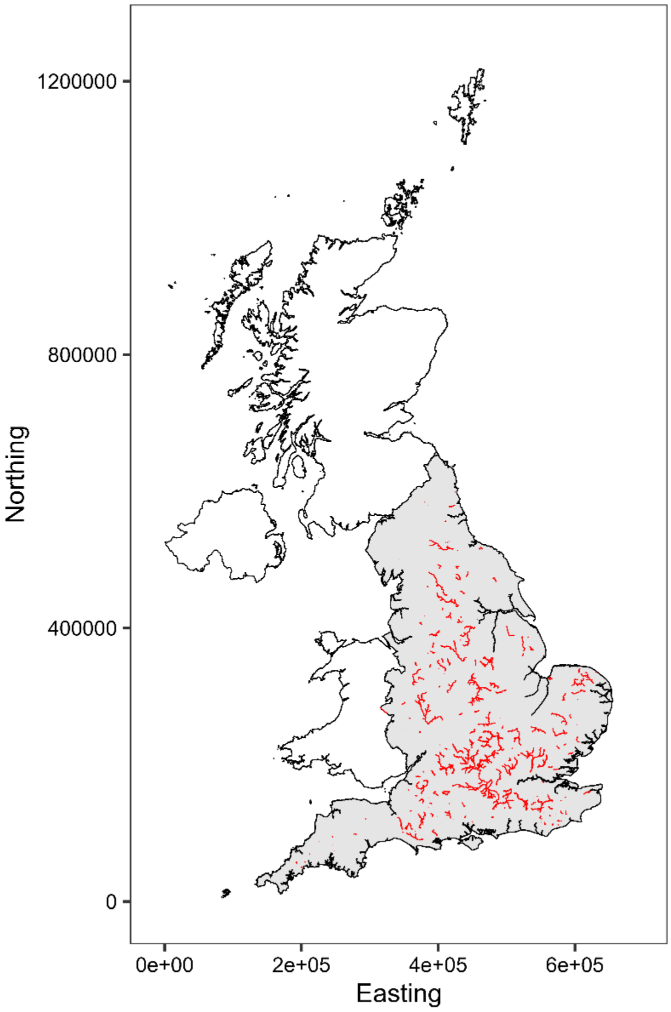

Figure 7.3 – Sections of river in England (grey shaded area) which are currently occupied by American signal crayfish *(Pacifastacus leniusculus*; red lines), identified using a hierarchical clustering analysis of all publicly-available records.

7.3.2 Calculating invasion rates

Of the clusters identified, 154 contained more than one record, allowing for the calculation of an invasion rate (upstream: n = 106, downstream: n = 108). Across these clusters, the average upstream and downstream invasion rates were 0.675 km year^{-1} (SE = 0.064) and 0.708 km year^{-1} (SE = 0.050), respectively (Fig. 7.4).

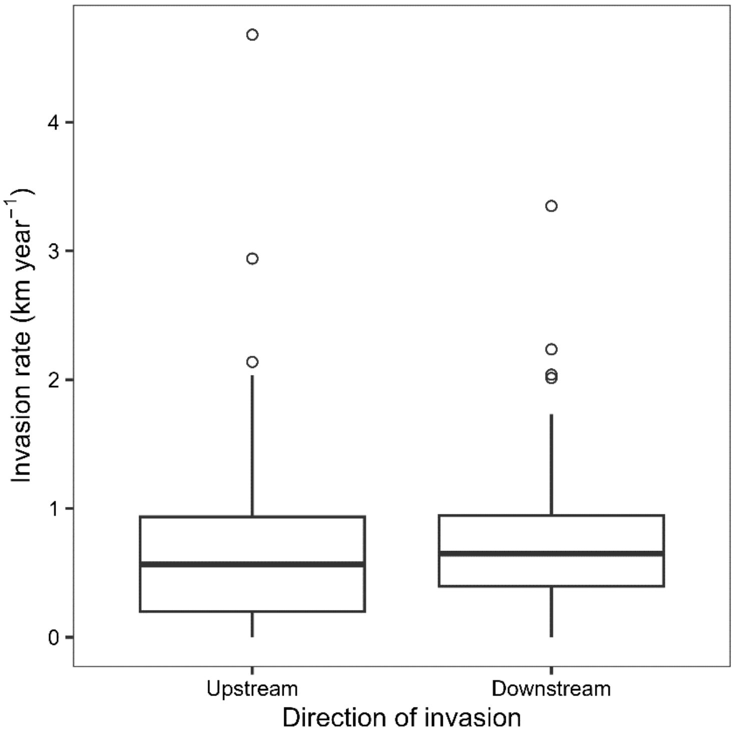

Figure 7.4 – Distribution of upstream and downstream invasion rates of American signal crayfish (*Pacifastacus leniusculus*) in English rivers.

7.3.3 Factors associated with invasion rate

All predictor variables could be quantified for a relatively high proportion of clusters (upstream: n = 84, downstream: n = 89). For upstream invasion rates, a greater boating density was associated with faster range expansion (estimate = 0.527, SE = 0.214, p = 0.014; Fig. 7.5a), but no additional variables were retained in the MAM. Similarly, only water temperature was retained in the MAM for downstream invasion rates, with higher temperatures associated with faster expansion (estimate = 0.165, SE = 0.065, p = 0.011; Fig. 7.5b).

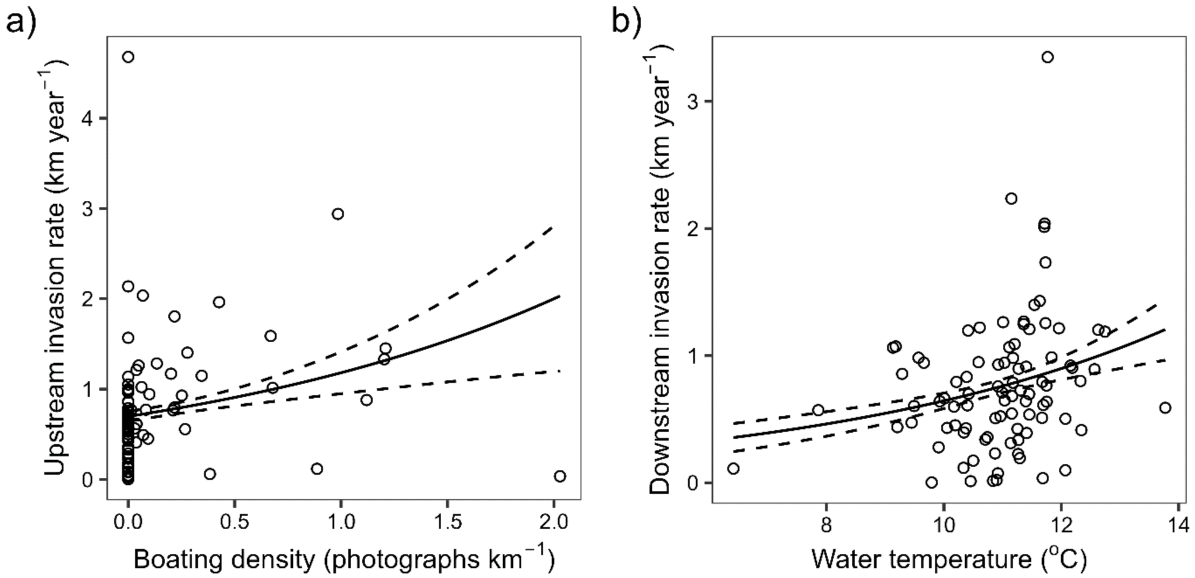

Figure 7.5 – Factors associated with the secondary spread of American signal crayfish (*Pacifastacus leniusculus*) in England, showing the relationships between a) boating density and upstream invasion rate, and b) water temperature and downstream invasion rate. Points denote distinct invasion events identified using a hierarchical clustering analysis of available records, solid lines show predictions obtained from a robust GLM, and dashed lines show the standard errors of the predictions.

7.4 Discussion

Understanding the factors associated with secondary range expansion is vital to effectively contain freshwater invasive species and minimise their impact on native biodiversity. Currently, the drivers of long-distance dispersal are well recognised and numerous methods have been developed to limit these movements. However, the factors associated with local dispersal remain poorly understood, preventing the enaction of effective management techniques. This study utilised multiple national-scale datasets and a novel hierarchical clustering approach to identify the factors associated with the secondary spread of American signal crayfish in England. Faster upstream invasions corresponded with intense boating pressure, whereas increased downstream invasion rates were related to higher water temperatures. These results demonstrate the importance of anthropogenic activities as vectors for local dispersal, as well as long-distance movements, highlighting the need for effective legislation and biosecurity campaigns. Additionally, the identification of temperature-dependent dispersal as a driver of secondary range expansion suggests that signal crayfish spread may accelerate due to climate change, emphasising the need for rapid development of effective containment strategies. Further field studies and modelling with a greater temporal resolution are recommended to provide additional insight into the drivers of local dispersal.

7.4.1 Identifying distinct local invasions

Overall, this study identified 214 distinct local invasions, suggesting that long-distance movements or new introductions have occurred frequently in England. Coupled with the clear evidence of ongoing local dispersal, this study suggests that signal crayfish follow a stratified dispersal pattern (Shigesada *et al.*, 1995). This combination of short- and long-distance dispersal can substantially increase the rate of secondary expansion (Shigesada *et al.*, 1995), potentially explaining the rapid spread of signal crayfish across Europe (Kouba *et al.*, 2014). Given the overwhelmingly negative ecological (Galib *et al.*, 2021) and socioeconomic (Kouba *et al.*, 2022) impacts of signal crayfish, as well as the current lack of effective eradication techniques (Manfrin *et al.*, 2019), preventing the further spread of signal crayfish over both short and long distances is essential. Management of local dispersal may be achieved through the construction of 'exclusion barriers', which can either be purpose-built downstream of areas with high conservation interest, or retrofitted to existing barriers (Krieg *et al.*, 2021). Some suggest that exclusion barriers are the most effective method for containing signal crayfish (Krieg & Zenker, 2020), although their efficacy against downstream dispersal is low and tests of their long-term effectiveness remain rare (Chapter 5). Prevention of long-distance dispersal is typically attempted through the introduction of targeted legislation (e.g., European Union [EU] Regulation 1143/2014 (EU, 2014), Convention on Biological Diversity (Secretariat of the Convention on Biological Diversity, 2010)) and generic biosecurity campaigns (e.g., 'Check Clean Dry'; Great Britain Non-Native Species Secretariat, 2010). There is evidence to suggest that simple biosecurity measures such as immersion in hot water may be sufficient to prevent the spread of signal crayfish during recreation (Anderson *et al.*, 2015), but there are numerous barriers to widespread public uptake (Sutcliffe *et al.*, 2018). The ongoing spread of signal crayfish throughout Europe suggests that current containment techniques are insufficient, and rapid further development is needed to prevent additional impacts on native ecosystems.

Although the clusters identified in this study are treated as separate introductions, it is possible that their designation could be influenced by incomplete data in main river channels. Indeed, current crayfish survey techniques are generally limited by water depth and flow rates (Pritchard *et al.*, 2021), meaning effective sampling is more challenging in deep, fast-flowing waters. As a result, it is possible that some clusters may be connected by unsampled populations in the main channel, and are therefore incorrectly identified as distinct invasions. Modern techniques such as eDNA sampling may provide a more comprehensive assessment of crayfish presence in larger rivers (Robinson *et al.*, 2019), and the availability of this data would help to inform future work aiming to quantify large-scale dispersal.

7.4.2 Calculating invasion rates

The average invasion rates calculated in this study (upstream: 0.675 km year^{-1}; downstream: 0.708 km year^{-1}) are within the range of those reported in field studies (upstream: 0.06 – 2.68 km year-1: downstream 0.18 – 3.63 km year-1; Sibley, 2000; Bubb *et al.*, 2005; Peay *et al.*, 2009a; Bernardo *et al.*, 2011; Hudina *et al.*, 2013; Hudina *et al.*, 2017). However, it is likely that the invasion rates reported in this study underestimate the true invasion rates as they rely on presence-only data and sporadic sampling, rather than the more rigorous presence-absence data and systematic surveying used in field studies. Additionally, long-term field studies with greater temporal resolution can generate more detailed insights into invasion dynamics, including the identification of lag phases (Bubb *et al.*, 2005) and more accurate quantification of size and sex structures (Hudina *et al.*, 2017). Similar insight can be achieved through the use of spatially-explicit modelling techniques (e.g., individual-based modelling; Chapter 5). Fieldwork and modelling studies are recommended as a focus for future research, as the greater temporal resolution may provide additional insights into the drivers of local dispersal.

7.4.3 Drivers of invasion rate

Interestingly, increased boating pressure was associated with faster upstream invasions. Typically, anthropogenic vectors such as boating are associated with long-distance dispersal within (e.g., Kelly *et al.*, 2013) or between catchments (e.g., Johnson *et al.*, 2001; Smith *et al.*, 2020). This is particularly true for juvenile signal crayfish, whose high desiccation tolerance and small size means they can survive long-distance movements when undetected on recreational equipment (Holdich *et al.*, 2014; Anderson *et al.*, 2015). However, the results of this study suggest that recreational activities can also affect local dispersal. This supports a recent study of angling activity in the contiguous United States, which demonstrated that short-distance movements by anglers created ‘invasion superhighways’ that can substantially increase invasion rates (Weir *et al.*, 2022). Indeed, recreational boaters typically make repeated visits to areas which are close to their homes (Hunt *et al.*, 2019), and may be less likely to thoroughly clean equipment during such visits, increasing the risk of local spread. The ability of anthropogenic vectors to drive both long-distance and local dispersal of invasive species highlights the need for effective biosecurity measures (Barker, 2021). These techniques have proved successful for a variety of freshwater invasive species (e.g., Shannon *et al.*, 2018; Bradbeer *et al.*, 2020; Coughlan *et al.*, 2020), but there is a strong need to develop further measures for a wider range of species and to increase public awareness of the need for biosecurity (Sutcliffe *et al.*, 2018; Smith *et al.*, 2020).

Higher water temperature was associated with greater downstream invasion rates, supporting previous field studies that have suggested signal crayfish movements are strongly temperature dependent (Bubb *et al.*, 2004). Water temperature is known to exert a strong influence over crayfish physiology (Ruokonen & Karjalainen, 2022), behaviour (Johnson *et al.*, 2014), and population dynamics (Bohman *et al.*, 2016), meaning the observed relationship with downstream dispersal is somewhat unsurprising. However, the lack of relationship between water temperature and upstream dispersal is unexpected, particularly given the strong influence of temperature on upstream dispersal rate observed by Bubb *et al.* (2004). Further work to elucidate the relationship between water temperature and upstream dispersal rates is recommended, particularly due to the continuing increases in water temperature as a result of climate change (Paul *et al.*, 2019). Climate change is already predicted to increase the overall habitat available for signal crayfish (Zhang *et al.*, 2020) and facilitate greater feeding performance in recipient regions (Rodríguez Valido *et al.*, 2021), meaning greater dispersal rates could have higher impacts than previously anticipated.

Additional physico-chemical factors tested in this study (flow and pH) showed no association with invasion rate. Given that signal crayfish exhibit strong positive rheotaxis in both laboratory (Kerr *et al.*, 2021; Chapter 5) and field (Chucholl *et al.*, 2022) conditions, and that pH is known to be a strong predictor of habitat suitability (Usio *et al.*, 2006), this result appears unexpected. However, this may be a result of the way in which the variables were calculated. River systems exhibit substantial seasonal fluctuations in flow and pH (Neal *et al.*, 2002; Huang *et al.*, 2009), and averaging the variables over the total time of the cluster fails to capture this temporal variation. Future work with a greater temporal resolution may be able to detect a relationship between these variables and invasion rate, although this was not possible within the limitations of this study.

The density of anthropogenic movement barriers did not affect the secondary spread of signal crayfish, contrary to the predictions of several key reviews (e.g., Rahel, 2013; Krieg & Zenker, 2020). This may be a result of the high dispersal capability of signal crayfish. Indeed, crayfish are known to disperse overland (Thomas *et al.*, 2019b) and may utilise algal build-ups (Frings *et al.*, 2013) and flood events (Kerr *et al.*, 2021) to pass barriers. These results demonstrate that it is not possible to rely on existing infrastructure to limit the secondary spread of signal crayfish, and suggest that barriers are unlikely to be an effective containment technique unless constructed and maintained specifically for this purpose (Jones *et al.*, 2021b). Indeed, purpose-built barriers incorporating features such as smooth surfaces, overhanging lips, and wing walls have been successfully used to prevent upstream invasion by signal crayfish (Krieg *et al.*, 2021) and red swamp crayfish (*Procambarus clarkii*; Dana *et al.*, 2011). Despite their inability to limit the spread of signal crayfish, existing barriers may still be effective against freshwater invasive species with lower dispersal abilities. For example, a network of over 1000 barriers, of which only 77 have been purpose-built, is vital for preventing the spread of invasive sea lamprey (*Petromyzon marinus*) in the Great Lakes (Zielinski *et al.*, 2019). Further work is needed to determine the ability of existing barriers to contain a wider variety of freshwater invasive species, and consideration of invasive species is vital when removing infrastructure as part of river restoration projects (Tullos *et al.*, 2016).

Unexpectedly, neither of the variables chosen to represent anthropogenic pressure (population density and human influence) were related to the rate of secondary spread.

Urban areas with high population density (i.e., towns and cities) act as a nexus for the flow of people and trade, meaning they are particularly susceptible to the introduction of invasive species (Francis & Chadwick, 2015). These areas therefore act as a source of invasive species, and can disseminate them into the surrounding landscape (Francis *et al.*, 2019) However, the processes by which invasive species typically move into urban environments (e.g., recreation, aquarium release, shipping) often represent long-distance dispersal rather than diffusive local processes, which may explain why population density and human influence were not associated with invasion rate in this study.

7.4.4 Conclusion

Preventing the secondary range expansion of invasive species is vital to minimise their impact on native communities, but this can only be achieved by understanding and appropriately managing the potential drivers. This study used national-scale datasets to quantify the factors affecting the rate of local dispersal, showing that secondary range is associated with both anthropogenic vectors (i.e., boating) and natural processes (i.e., temperature dependent dispersal). The ongoing spread of signal crayfish suggests that current containment techniques are insufficient, and rapid further development is needed to prevent accelerated range expansion due to climate change. In particular, wider uptake of biosecurity measures is needed to prevent both long-distance and local dispersal via recreational activities. Fieldwork and modelling studies with greater temporal resolution will provide further information about the drivers of local dispersal, and this recommended as a focus for future research.

Chapter 8: Optimising the installation of invasive species exclusion barriers under multiple conservation objectives

Abstract: In freshwaters, containment of impactful invasive species is increasingly achieved through construction, modification or maintenance of river infrastructure (i.e., exclusion barriers), yet these structures can also inhibit the migration of native fishes. Understanding of these trade-offs over large spatio-temporal scales is limited due to a focus on quantifying passability of individual structures, meaning the role of exclusion barriers in catchment-scale management remains unclear. This study combined an individual-based model (IBM) with multi-criteria decision analysis (MCDA) to quantify the trade-offs between invasive species containment, native fish migration, and cost at a catchment scale, using the American signal crayfish (*Pacifastacus leniusculus*) invasion in the river Glaven catchment (Norfolk, UK) as a model system. The IBM accurately reproduced the historical invasion in the Glaven, and was used to predict the effects of 104 potential combinations of barrier modifications on signal crayfish spread over a 15-year period. Accessibility-weighted habitat availability (AWHA) for three native fishes (European eel [*Anguilla anguilla*], brown trout [*Salmo trutta*], and brook lamprey [*Lampetra planeri*]) was assessed for each combination, and costs were derived from previous studies. MCDA was used to quantify the overall performance of each combination by integrating quantitative assessments with value-based information regarding their relative importance. Barrier modification limited signal crayfish spread within the catchment, but modifications were costly and negatively impacted AWHA for two native fishes (European eel and brown trout). The MCDA identified an optimal solution involving modification to a single large barrier, although rankings were sensitive to uncertainty in IBM predictions, differences in the length of time over which the prediction occurred, and variation in weights. These results demonstrate that exclusion barriers are a useful tool for catchment-scale invasive species management, but highlight the importance of explicitly considering the trade-offs with other conservation objectives.

8.1 Introduction

Invasive species have overwhelmingly negative ecological (Gallardo *et al.*, 2016) and economic (Cuthbert *et al.*, 2021b) impacts in freshwater ecosystems, yet eradication of established populations remains challenging due to a variety of ecological, financial, or technological limitations (Simberloff, 2021). In cases where eradication is not feasible, limiting secondary range expansion (i.e., containment) is essential to minimise the impacts on native ecosystems (Britton *et al.*, 2023). In freshwaters, this can be achieved by the construction or maintenance of river infrastructure which can impede the movement of invasive species (i.e., exclusion barriers; Jones *et al.*, 2021b). Indeed, exclusion barriers form an integral part of integrated pest management (IPM) approaches for a number of high-impact freshwater invasive species, including sea lamprey (*Petromyzon marinus*; Zielinski *et al.*, 2019), common carp *(Cyprinus carpio*; Stuart & Conallin, 2018), American signal crayfish (*Pacifastacus leniusculus*; Krieg *et al.*, 2021), and numerous salmonids (e.g., Fausch *et al.*, 2009; Franklin *et al.*, 2018). However, modern rivers are already heavily fragmented by river infrastructure (Belletti *et al.*, 2020), and these structures are known to degrade freshwater ecosystems by disrupting natural flow (Gierszewski *et al.*, 2020) and sediment (Kondolf *et al.*, 2014) regimes, altering physico-chemical conditions (Winton *et al.*, 2019), and acting as barriers to the movement of fish and other species (Brooks *et al.*, 2018; Jones *et al.*, 2020; Jones *et al.*, 2021a). As a result, there has been a global drive towards infrastructure removal, with over 3800 dams removed since 1953 (Ding *et al.*, 2019b). This tension between the need to limit the spread of invasive species while simultaneously improving connectivity for native species (i.e., the "connectivity conundrum"; Zielinski *et al.*, 2020) represents a significant concern for conservation managers (Tullos *et al.*, 2016), yet few studies have attempted to quantify this trade-off at the broad spatial scales over which biological invasions and freshwater fish migrations occur (Cooper *et al.*, 2021).

Trade-offs between opposing management goals are common in conservation, meaning numerous techniques have been developed to facilitate defendable, informed, and transparent decision-making (Hemming *et al.*, 2022). In particular, multi-criteria decision analysis (MCDA) provides a formalised framework to explore trade-offs between disparate objectives, and has been widely used to support effective decision-making in conservation (Cegan *et al.*, 2017; Kurth *et al.*, 2017). This approach involves assessing various management alternatives against a set of pre-defined criteria to determine their overall performance, and provides an effective method of integrating objective information derived from surveys and modelling with value-based information obtained from stakeholders (Adem Esmail & Geneletti, 2018). Indeed, MCDA has previously been used to identify barrier removals which can maximise habitat connectivity for native fishes, while minimising potentially negative outcomes (e.g., changes in water quality, socio-economic losses, spread of invasive species; Zheng *et al.*, 2009; Terêncio *et al.*, 2021) However, this approach relies on landscape-scale assessments regarding the performance of each alternative, which are typically unavailable for the construction of exclusion barriers (Jones *et al.*, 2021b).

Individual-based models (IBMs) provide a powerful tool for assessing the impacts of invasive species management techniques over large spatio-temporal scales (Thompson *et al.*, 2021). Complex interdependent factors such as growth, reproduction, movement, and mortality are incorporated at the individual level, allowing for emergent population-level effects such as secondary range expansion to be studied (DeAngelis and Grimm 2014). Indeed, IBMs have been used to assess the effectiveness of a variety of management techniques for freshwater invasive species, including electrofishing and exclusion barriers for eastern brook trout (*Salvelinus fontinalis*; Day *et al.*, 2018), culling for bitterling (*Rhodeus sericeus*; Dominguez Almela *et al.*, 2021) and trapping for rusty crayfish (*Faxonius rusticus*; Messager & Olden, 2018). Each of these studies demonstrated that management techniques were most effective when applied early in the invasion, and showed the utility of IBMs as a tool for informing decision-making. However, these studies did not directly consider the economic costs (but see Messager & Olden, 2018) or potential non-target effects of the management strategies in question, meaning trade-offs between other conservation goals were not explicitly considered.

This study aimed to identify a cost-effective combination of exclusion barriers that could limit the spread on an aquatic invasive species while minimising the associated impact on native fishes by integrating individual-based modelling with MCDA. To achieve this, the American signal crayfish was used as a model species due to its widespread invasive range (Kouba *et al.*, 2014; Usio *et al.*, 2016), and overwhelmingly negative ecological (Vaeßen & Hollert, 2015) and economic (Kouba *et al.*, 2022) impacts. In-stream infrastructure can reduce upstream movement of signal crayfish under laboratory (Frings *et al.*, 2013; Kerr *et al.*, 2021; Chapter 5) and field (Rosewarne *et al.*, 2013) conditions, and recent evidence suggests that the installation of low-cost barrier modifications (e.g., installation of stainless steel plates, construction of overhanging lips) may completely prevent upstream movements over short timescales (Krieg *et al.*, 2021; Chucholl *et al.*, 2022). Additionally, an IBM operating on a 70 km virtual single-channel river predicted that a single partial barrier (blocking 78% of males and 88% of females) could delay upstream invasion by 1.73 years (Chapter 5). This IBM can accurately replicate the spatio-temporal dynamics of signal crayfish invasions (Chapter 5), meaning its integration with MCDA can provide vital information for managers of invaded catchments. In this study, two key objectives were addressed: 1) update and develop the IBM in Chapter 5 to function on a real river network (river Glaven, Norfolk, UK) with multiple barriers, and 2) identify the optimal configuration of barrier modifications within a river catchment to limit the spread of signal crayfish, while operating within budgetary constraints and maximising the habitat available for native fish species.

8.2 Methodology

8.2.1 IBM development

8.2.1.1 Study system

The river Glaven is a small (length = 17 km, catchment area = 115 km^2), lowland (<50 metres above sea level) river in North Norfolk, UK (Fig. 8.1). The Glaven is classified as a partial chalk stream due to the chalk-dominated geology in the middle and lower reaches (Pawley, 2008) and, given the global scarcity and poor condition of these habitats (85% of the world's chalk streams are located in England, and only 15% are in good ecological condition (Environment Agency, 2022a)), is an area of high conservation importance. The catchment supports populations of several species listed in Annex II of European Habitats Directive (92/43/EEC of 21 May 1992), including European eel (*Anguilla anguilla*), brook lamprey (*Lampetra planeri*) and white-clawed crayfish (*Austropotamobius pallipes*). However, populations of these species are currently threatened by an ongoing invasion of American signal crayfish. Signal crayfish were first detected in the river channel in 2009 (Fig. 8.1) after escape from a local aquaculture pond, and have since spread both up- and downstream. Active management is ongoing in the catchment, and there is strong local interest in leveraging existing barriers to slow the invasion (U. Juta *pers. comm.*). Indeed, stainless steel lips were installed at two weirs in the town of Letheringsett (52.906904°N, 1.063839°E) in 2016 in an attempt to limit the upstream spread (U. Juta *pers. comm.*).

The River Glaven has been extensively modified through various anthropogenic activities, including construction of mills and weirs, straightening and relocation of the channel, removal of woody debris and in-stream vegetation, and the erection of embankments for flood defence (Clilverd *et al.*, 2013). Angling is known to occur within the catchment, but boating activity is limited due to the relatively narrow width and frequent impoundments.

The structures present in the River Glaven catchment (n = 36; 2 additional structures not assessed due to lack of landowner permission) were formally assessed using the SNIFFER protocol (SNIFFER, 2010a) during January 2023. The SNIFFER protocol is a coarse-resolution rapid assessment methodology for assessing the passability of in-stream barriers to nine species/life stages of fish. Ten factors are recorded at each structure (drop height, slope, water depth through the structure, plunge pool depth, water velocity, and turbulence, as well as the presence/absence of standing waves, debris, fish passes, and any factors that may block downstream migration), alongside numerous structure- and species-specific metrics (e.g., the total length of culverts, overhanging lips at culverts/weirs, the presence of climbing substrate for eels). The passability of a barrier for a given species is calculated using a set of criteria derived from published literature describing the swimming, leaping, and climbing ability. Based on these criteria, the barrier is assigned as 0 (impassable), 0.3 (partial barrier with high impact), 0.6 (partial barrier with low impact), or 1 (no barrier) for the species in question. In this study, passability scores were calculated for three species (European eel, brook lamprey, and brown trout [*Salmo trutta*]) chosen for their presence in the catchment, high socio-economic and conservation interest, and high probability of being affected by barrier modification (see section 8.2.2.1).Although the SNIFFER protocol does not provide an estimate of barrier passability for signal crayfish, the comprehensive measurements collected during the assessment could be used to predict crayfish passage success in the IBM (see section 8.2.1.5).

8.2.1.2 IBM development

The IBM used in this study builds on the work described in Chapter 5, and provides a framework within which individual crayfish can move, grow, and interact. The underlying population and movement dynamics (density- and temperature-dependence, movement distances, reproductive rates, mortality, etc.) are described fully using the Overview, Design concepts and Details (ODD) protocol (Grimm *et al.*, 2020) in Chapter 5, and remained unchanged for the purposes of this study.

A map of the river Glaven catchment was obtained from the Ordnance Survey (OS) MasterMap Water Network (Ordnance Survey, 2022). Initial processing was conducted in ArcGIS Pro 2.7.1; side channels less than 100 m in length were removed and any braided sections (other than those which bypassed an existing barrier) were reduced to a single line representing the main river channel. Any sections that were disconnected from each other were assessed using google maps imagery and reconnected if appropriate. This dataset was then imported to R v4.1.1 and spatially dissolved using the package *riverdist* (Tyers, 2020). The final river network consisted of 92 segments, each of which represented a single-channel, unbranching river section of constant width, bounded by either a confluence or the end of the river network (Appendix E Fig. E1.1). The length of each segment was calculated internally by *riverdist* and then rounded to the nearest 100 m for the purpose of breeding calculations, whereas widths were derived manually from the original data. As the spatial dissolve combined several shorter sections of river, the width of the final segment was calculated as the average width of the combined sections, weighted by their relative lengths according to the formula $W_{SEG} = \Sigma((W_{SEC} \times L_{SEC}) / L_{SEG})$, where W_{SEG} = the width of the final river segment, W_{SEC} = the width of the section to be combined, L_{SEC} = the length of the section to be combined, and L_{SEG} = the total length of the final river segment. Additionally, the connections between the segments were identified using *riverdist*, which provides a matrix showing which segments are connected and whether they are connected at the upstream or downstream confluence.

To implement the IBM on the river Glaven catchment, each river segment was treated as a separate sub-model for the purpose of biomass and breeding calculations, but crayfish were able to move freely between segments. For efficient computation, abundance measurements (density [number of individuals m^{-2}] and biomass [g m^{-2}]) were calculated within 10 m sections of river, and breeding calculations were conducted in 100 m sections. At confluences, crayfish had an equal probability of entering each channel. This was implemented by assigning each crayfish a random number between 0 and 1, and determining which segment to move to by evaluating whether this value was below or above 0.5 (value reset after each movement between segments to ensure the direction was randomly selected each time). The location within the new segments was calculated using the distance by which the movement exceeded the length of the previous segment. In cases where there were no connected segments (i.e., downstream of the river mouth or upstream of the tributary source), crayfish that exceeded the extent of the segment were removed from the model. Although boating activity is known to drive both short- and long-distance dispersal by signal crayfish (see Chapter 6), this was not implemented in the IBM due to its low frequency within the catchment.

To enhance computational efficiency, individual juvenile crayfish (carapace length [CL] < 39 mm) were aggregated into 'super-individuals' (Scheffer *et al.*, 1995). When initially created, each super-individual represented six crayfish (implemented in the model through creation of an additional variable storing the number of crayfish represented by each super-individual) which grew and moved together. Density and biomass calculations were conducted at an individual level (i.e., a super-individual containing six individuals each with a biomass of 7 g would contribute a total of 42 g to the overall calculation). To implement mortality, each individual represented by the super-individual was assigned a random value, and was deemed to have died if this was less than the probability of mortality (calculated as described in Chapter 5). The number of individuals represented was decreased accordingly, and the super-individual was removed from the model if this value fell to 0. Upon reaching maturity, super-individuals were converted to individuals by releasing mature crayfish at the super-individual's current location, with the number released equal to the number of crayfish represented. Sensitivity analysis indicated that this approach was consistent with the original approach (2.40% difference in total invaded area after 20-year simulation; Appendix E Fig. E2.1), but substantially reduced overall computing requirements.

The model was implemented in R v4.1.1 and final model runs were batch processed (1 model run per core) using the University of Southampton's high-performance computing unit (IRIDIS 5). Final runs simulated a release of 200 crayfish at the original introduction location (Fig. 8.1) in April 2009. The model operated in two-day time steps and was used to predict the distribution of crayfish in 2038 (i.e., 15 years from present). At each timestep, seven key processes occurred:

1. **Incrementation of time-dependent factors**. The age of each crayfish was incremented by two days and correlated factors (CL and mass) were recalculated accordingly. Any super-individuals that reached maturity were converted to individuals. The gestation period of gravid crayfish was increased by two days.
2. **Population calculations**. Abundance measurements (density and biomass) were calculated for each 10 m river section.
3. **Movement**. When generated, each crayfish was randomly assigned a predisposition towards upstream or downstream movement (80% of movements in the given direction). At each timestep, crayfish were randomly allocated a movement distance based on daily movement patterns observed by Bubb *et al.* (2004).

Movement distances were then scaled according to seasonal temperature changes (movements greater in warmer summer periods) and local population density (larger movements in high-density areas).

4. **Barrier passage**. If crayfish attempted to pass a barrier (i.e., the movement caused them to move from downstream to upstream of a structure), their physiological ability and motivation to pass the barrier was assessed according to the criteria described in section 8.2.1.3. If crayfish were unable to pass the barrier, they were reflected downstream by a randomly allocated distance of between 0 and 20 m.
5. **Trapping**. If crayfish were present in the same 10 m section of river as a trap, the likelihood of capture was assessed using the criteria described in section 8.2.1.5. Trapped crayfish were removed from the model.
6. **Mortality**. At each timestep the probability of mortality was calculated according to crayfish size (higher probability of mortality for smaller individuals) and local population density (greater probability of mortality in high density areas). Each crayfish was assigned a random value between 0 and 1, and were removed from the model if this value was less than the probability of mortality. Crayfish were also removed from the model if their location exceeded the boundaries of the river, or if they exceeded a maximum predefined age (7 years).
7. **Reproduction**. Females became pregnant if the Julian day was within the breeding season, they were sexually mature (CL > 39 mm), and there was an adult male present in the same 100 m breeding section. Fecundity (i.e., the number of eggs released) was calculated based on CL, with larger females producing a greater number of young.
8. **Population expansion**. To calculate the total length of the river system invaded by signal crayfish in kilometres, the number of occupied 10 m river segments was summed and divided by 100.

8.2.1.3 Implementation of barrier passage

The SNIFFER protocol used to evaluate barrier passability for native fish species does not provide an estimation for signal crayfish, meaning a novel approach for quantifying crayfish passage ability was developed. The approach developed here considers the physiological possibility of passage separately for slope-based (e.g., sloping weirs, culverts) and drop-based (e.g., overshot sluices, stepped structures) barriers, while also explicitly accounting for motivation and the possibility of passage via terrestrial routes (Fig. 8.2).

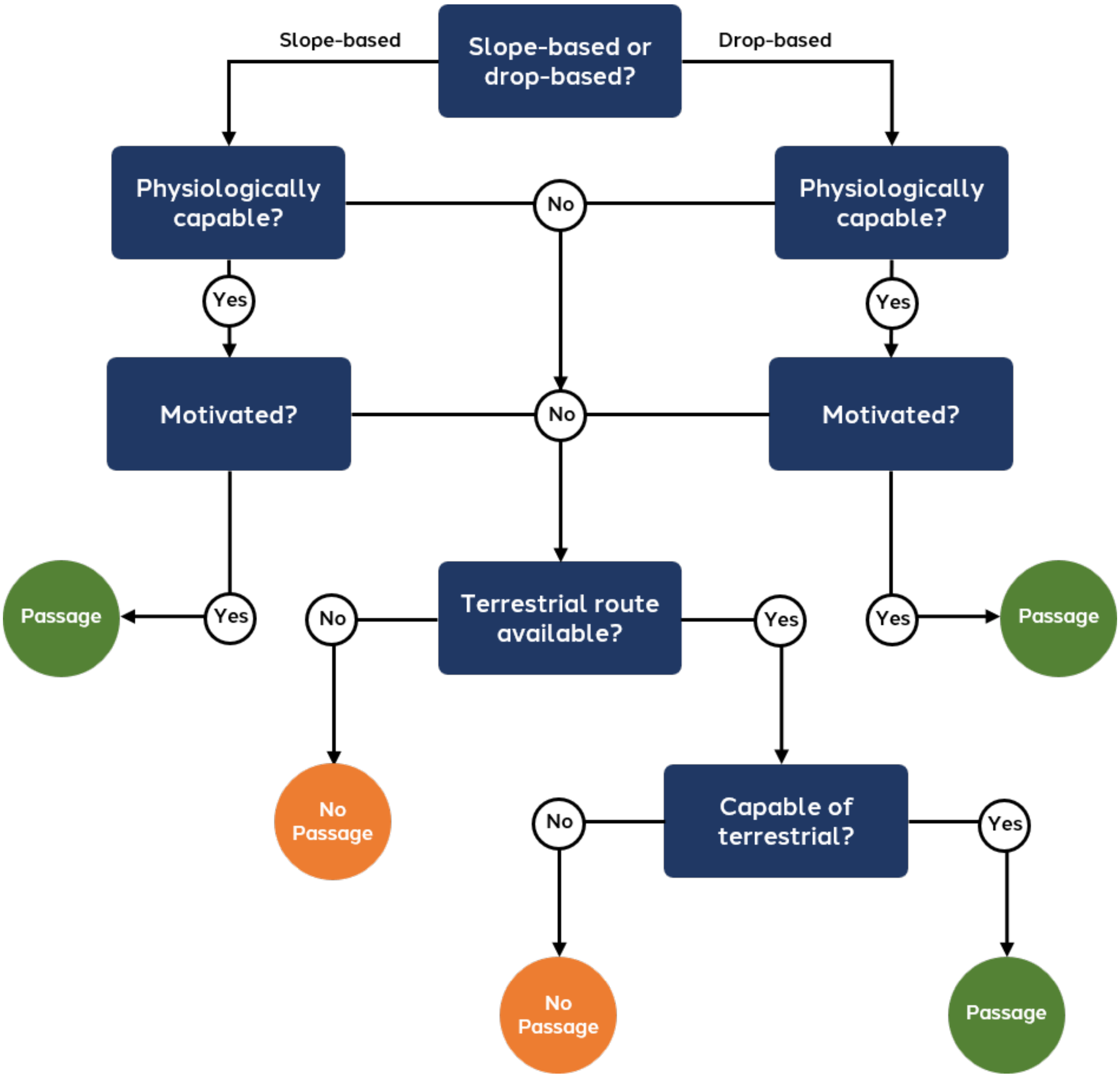

Figure 8.2 – The workflow used to determine whether American signal crayfish (*Pacifastacus leniusculus*) can pass a riverine barrier.

For slope-based barriers, Frings *et al.* (2013) used fundamental principles to predict barrier efficacy for signal crayfish, suggesting that a barrier would be effective against walking crayfish if:

$$\sin(\alpha) - \mu\cos(\alpha) > \frac{F_m - 0.5\rho C_d A u^2}{(\rho_c - \rho)VG} \qquad \text{Equation 8.1}$$

Where α = barrier slope (°), μ = the Coulomb friction factor, F_m = the muscular force of the crayfish (N), ρ = water density (998 kg m^{-3}), C_d = drag coefficient, A = frontal surface area of the crayfish (m^2), u = flow velocity at the barrier crest (m s^{-1}), ρ_c = signal crayfish density (1105 kg m^{-3}, measured in their study), V = crayfish volume (m^3), and G = gravitational acceleration (9.81 m s^{-1}). Of these 10 parameters, three (μ, F_m, and C_d) have not been measured in sufficient detail in the scientific literature. Frings *et al.* (2013) conducted laboratory trials with numerous combinations of barrier slope, flow velocity, and surface roughness, then adjusted these parameters until the predictions of the equation matched the experimental results (final values: μ = 1.3, F_m = 0.01, C_d = 0.2; Fig. 8.3a). However, recent studies (Kerr *et al.*, 2021; Chapters 5 & 6) have observed successful passage under conditions (slope = 11.3°, flow velocity at crest = 0.68 – 0.74 m s^{-1}) which the equation predicts to be impassable, suggesting that the parameters chosen by Frings *et al.* (2013) are too conservative. Therefore, these parameters were iteratively readjusted until the predictions of the equation accurately reflected the initial experimental results of Frings *et al.* (2013), as well as the more recent experimental results of Kerr *et al.* (2021), and those presented in chapters five and six (final values: μ = 1.3, F_m = 0.005, C_d = 0.145; Fig. 8.3b). Frings *et al.* (2013) also noted that crayfish could pass barriers by swimming, and therefore predicted that a barrier would not be effective unless the flow velocity exceeded the maximum velocity against which crayfish could swim during experiments (0.44 m s^{-1}; Fig. 8.3a). However, it was observed in Chapter 5 that crayfish successfully passed a barrier by

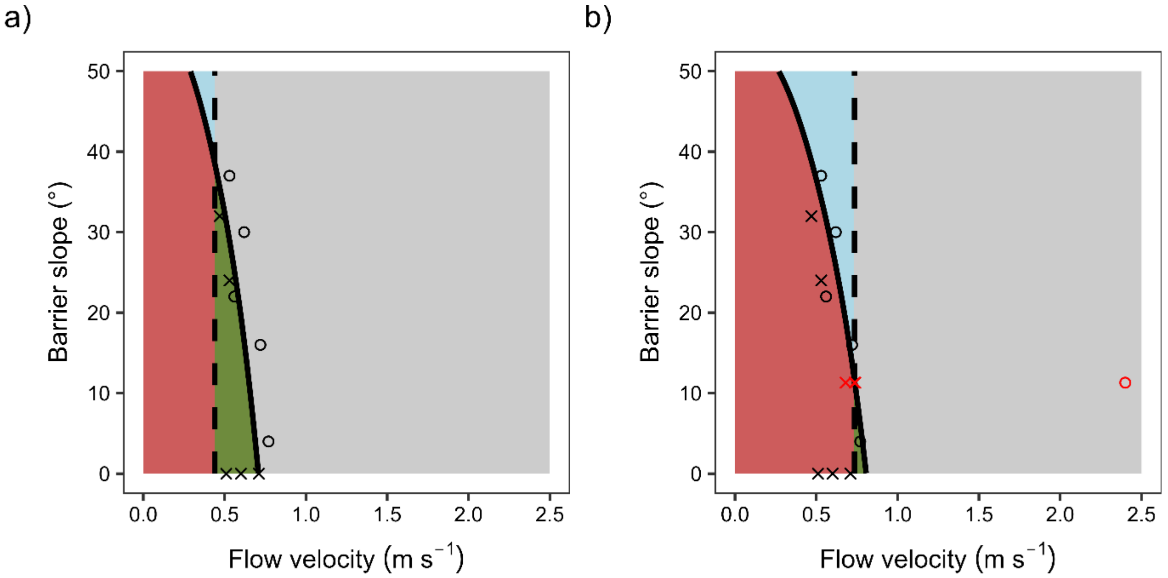

Figure 8.3 – Predictions from first principles as to whether American signal crayfish (*Pacifastacus leniusculus*) can pass a flow-based barrier by walking or swimming (red), walking only (green), swimming only (blue), or are unable to pass (grey), showing a) predictions made using the original parameters proposed by Frings *et al*. (2013), and b) the updated parameters developed in this study. Solid lines show the maximum velocity against which crayfish can walk at different barrier slopes, and dashed lines show the maximum flow velocity which crayfish can swim against. Black circles denote the original trials conducted by Frings *et al*., (2013), with crosses showing successful passages and circles showing trials with no passages. Red points show the results of additional, more recent studies (Kerr *et al*. 2021, Chapters 5 and 6) which were used to adjust the

swimming against a crest velocity of 0.735 m s^{-1}, meaning the maximum swimming speed threshold used by Frings *et al.* (2013) was also adjusted (Fig. 8.3b).

In the IBM, crayfish volume was calculated at each time step based on mass ($V = m / \rho_c$). Volume was subsequently used to calculate frontal area using the formula $A = V / CL$, which assumes the carapace of the crayfish to be cylindrical. If crayfish attempted to pass a barrier in the model, equation 8.1 (incorporating the barrier slope and flow velocity values measured in the field) and the maximum swimming speed threshold were used to determine whether it was physiologically possible for the crayfish to pass the barrier (Fig. 8.3b).

Evidence regarding fine-scale crayfish passage behaviour at vertical barriers is limited, and therefore these structures were conceptualised as a climb, followed by movement against the water flow along a flat surface. The climb was deemed physiologically passable if the maximum step was less than or equal to 0.4 m, as signal crayfish have been observed to climb to this height under laboratory and field conditions (Peay & Dunn, 2014). Subsequently, the possibility of moving against the flow upstream of the drop was quantified using equation 8.1, with barrier slope set to 0°.

For structures that presented sloped and vertical barriers in series (e.g., a culvert with a vertical drop at the downstream opening), crayfish were only deemed to be able to pass if they were physiologically capable of passing both elements. Conversely, if a single structure presented a vertical or sloped barrier in parallel (e.g., a sloping weir with a stepped fish pass alongside), crayfish were able to pass if they were physiologically capable of passing either element.

Given the importance of flow in determining the passability of both slope- and drop-based barriers, the effect of seasonal variation in flow rate was incorporated in the IBM by scaling the values measured in the field according to long-term flow data. No gauging stations with long-term, publicly available data were present within the Glaven catchment, meaning flow data was obtained from the neighbouring river Stiffkey catchment. The river Stiffkey has similar geological and physico-chemical characteristics to the river Glaven (Campos *et al.*, 2018), and was therefore deemed as an appropriate proxy. Daily flow data from 1st April 2009 (i.e., the model start date) to 21st March 2023 were obtained from the National River Flow Archive using the R package *rnrfa* (Vitolo *et al.*, 2016). To calculate the scaling factor, the average daily flow was quantified for each Julian week, and then divided by the flow value corresponding to the week in which field measurements of the barriers were conducted (Julian week 3). The final scaling factor (Appendix E Fig. E3.1) was applied to the flow measurements during barrier passability calculations at each timestep.

The motivation of signal crayfish to pass a barrier varies between individuals, and can be predicted by consistent intraspecific differences in personality traits such as boldness (Chapter 6). To account for this in the IBM, each crayfish was assigned a fixed random value between 0 and 1 reflecting their motivation, and were only able to pass the barrier if this value was less than a predefined threshold of 0.745. This threshold was based on two laboratory studies that used similar barriers and flow regimes and explicitly measured whether crayfish attempted to pass the barrier (Chapters 5 and 6). The raw data from these studies was combined, and the total proportion of crayfish that moved upstream onto the barrier face (i.e., were motivated to pass the barrier) in these two studies (310 of 416 individuals) was calculated. Crayfish were only deemed to be able to pass the barrier if they were both physiologically capable and motivated.

If crayfish were unable to pass using the barrier itself but the banks were deemed to be accessible during the field survey, they were also able to move upstream via terrestrial dispersal. Each crayfish was assigned a random number between 0 and 1 reflecting its ability to disperse terrestrially. Thomas *et al.* (2018) found that CL was positively associated with the number of times juvenile crayfish (CL 8.5 – 26.5 mm) emerged onto land, with crayfish with CL ≤ 13.7 mm never leaving the water. However, this relationship did not generalise to a study with adult crayfish (CL 38.6 - 59.3 mm; Thomas *et al.*, 2019b). Therefore, any crayfish with CL ≤ 13.7 mm were deemed unable to pass the barrier, whereas all other crayfish were able to use terrestrial routes if their randomly assigned terrestrial passability value was less than a predefined threshold (0.133). This threshold was based on the work of Krieg *et al.* (2021), who conducted a field study at a purpose-built waterfall barrier and found that 13.3% of signal crayfish attempted to pass the structure via terrestrial dispersal.

8.2.1.4 Implementation of barrier modifications

Modifications were introduced to the model in August 2023, and varied by barrier type (Fig. 8.4). However, all modifications included the addition of stainless steel plates and an overhanging lip, as well as the elimination of terrestrial passage routes (as described by Krieg *et al.* (2021) and Chucholl *et al.* (2022)). Modified barriers were assessed using the same workflow and calculations as described in section 8.2.1.3, with some parameters changed or added to reflect the modifications. To account for the addition of stainless steel plates, the Coulomb friction factor (μ) in equation 8.1 was changed to 0.4 (i.e., the friction coefficient for stainless steel; Artoos *et al.*, 1994). Similarly, the addition of an overhanging lip was implemented into the assessment of physiological capacity for passage by assigning each individual a random value between 0 and 1, and preventing passage if this value was less than 0.997. This threshold reflects the work of Krieg *et al.* (2021), who found that 1 of 300 tagged crayfish (99.7%) was able to pass an overhanging lip at a modified barrier.

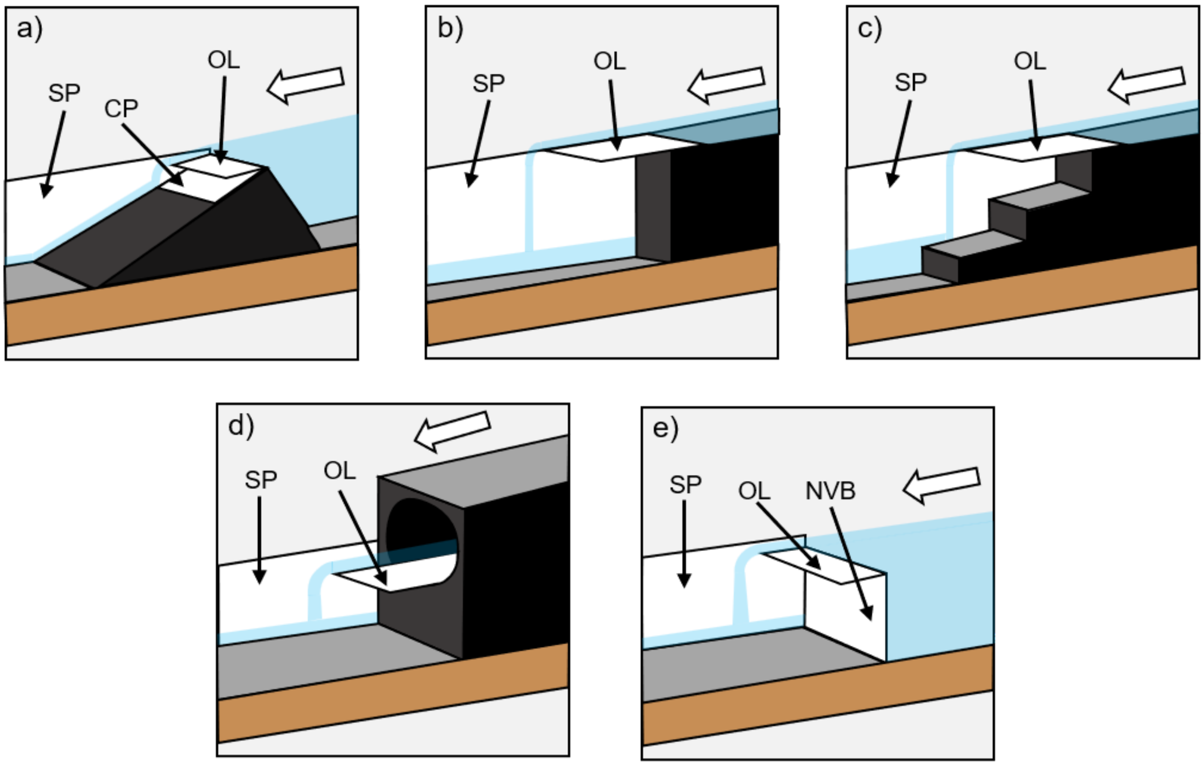

Figure 8.4 – Modifications applied to a) sloped weirs, b) vertical weirs, c) stepped weirs, d) culverts, and e) fords (without vertical drops or steps) to limit the upstream movements of American signal crayfish (*Pacifastacus leniusculus*) in an individual-based model. Diagrams show existing structures (dark grey and black), the direction of water flow (white arrow), side plates extending downstream along the river banks (SP), overhanging lips (OL), plates at the crest of sloping weirs (CP), and new vertical barriers (NVB), with all modifications made of stainless steel. Modifications are based on Krieg *et al.* (2021) and Chucholl *et al.* (2022).

8.2.1.5 Replication of previous management approaches

To ensure the IBM accurately reflected the historical signal crayfish invasion in the river Glaven, previous management approaches were included in the model. Weekly trapping was implemented between 1st May and 1st September for each year between 2011 and 2021. Initially, ten traps were placed every 10 m along a section of river 1.4 km downstream of the initial release point, and the number of traps was reduced by one per year to reflect a reduced intensity of trapping over time. When generated, each crayfish was assigned a random value between 0 and 1 reflecting the likelihood of being trapped. Crayfish were deemed to be trapped if they were within 10 m of a trap, CL exceeded 35 mm (the minimum size that can be caught in conventional traps; Chadwick *et al.* (2021)), and the random value was less than 0.748 (based on the work of Chadwick *et al.* (2021) who showed that traps catch 74.8% of individuals with CL > 35 mm). Trapped crayfish were subsequently removed from the model.

Additionally, stainless steel plates with overhanging lips were added to two barriers (GLA1 and GLA2 in Fig. 8.1) in April 2016. These barriers were implemented in the IBM as described in section 8.2.1.4. However, the stainless steel plates did not extend downstream along the river banks, meaning terrestrial passage routes remained available.

8.2.1.6 Model validation

The underlying movement and population dynamics for a single 75 km virtual river channel were validated in Chapter 5. The accuracy of the modified IBM presented in this study was assessed by determining its ability to replicate the historical signal crayfish invasion in the river Glaven. Regular crayfish surveying is undertaken directly upstream of Letheringsett mill (GLA11 in Fig. 8.1), and American signal crayfish were first observed at this location in 2021 (H. Crawley *pers. comm.*), 12 years after their initial introduction in the catchment. Ten full model runs including only the historic management approaches were conducted to assess IBM performance, and the date at which crayfish first passed this barrier was recorded and compared to the known invasion history.

8.2.2 Multi-criteria decision analysis

8.2.2.1 Problem structuring

The objective of this MCDA (to identify the combination of barrier modifications that represents the optimal trade-off between limiting the spread of signal crayfish and other conservation goals) was developed after consultation between the four experts who co-developed this project (comprising three academics from the University of Southampton and one conservation practitioner from the Norfolk Rivers Trust). Verbal agreement was given by all experts for their views to be incorporated into the study. Three main criteria were formulated to assess the performance of each alternative in achieving this objective: 1) the river length occupied by signal crayfish, 2) the river length available to native fish species, and 3) the total cost of implementing the modifications (Fig. 8.5). The habitat available to native fish was further subdivided to reflect three species of high socio-economic and conservation interest that are likely to be affected by barrier modification (European eel [*Anguilla anguilla*], brook lamprey [*Lampetra planeri*], and brown trout [*Salmo trutta*]).

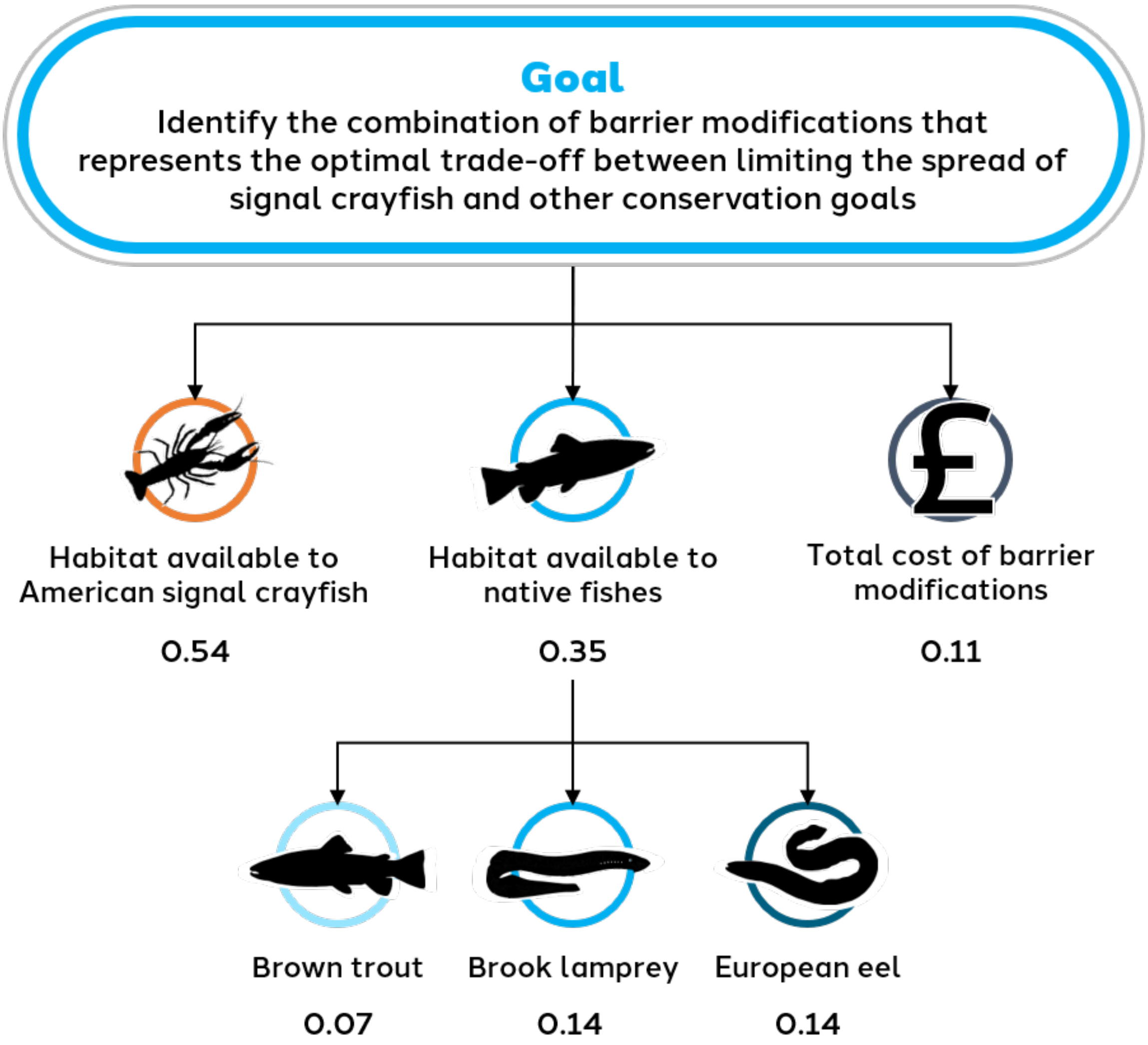

Figure 8.5 – Hierarchical decision tree used to inform a multi-criteria decision analysis aiming to quantify the trade-offs of management techniques used to manage the spread of American signal crayfish (*Pacifastacus leniusculus*). Numbers denote the weights applied to each criteria, as determined by swing weighting.

8.2.2.2 Identification of alternatives

Initially, alternatives defined in this MCDA represented all potential combinations of barrier modifications, ranging from a scenario in which all barriers remained in their current state to one where all structures were modified. To reduce the total number of alternatives, only barriers upstream of the current invasion front (i.e., upstream of barrier GLA11 in Fig. 8.1) were considered potential candidates for modification. Additionally, any barriers that could not be modified due to their ongoing functionality (e.g., working mills, gauging stations) or lack of landowner consent were excluded.

To ensure that management recommendations were feasible, combinations were also filtered by cost. Cost estimates reported by (Krieg *et al.*, 2021) were combined with the previously incurred costs of modifying barriers within the river Glaven catchment (U. Juta *pers. comm.*) to estimate the average cost of modifications per metre of barrier width. Cost estimates per metre were derived separately for barriers that only required basic modification (i.e., sloped weirs, vertical weirs, stepped weirs, culverts; cost = £1668.86 m^{-1})

and those that also required a vertical drop to be manufactured using steel plates (i.e., fords; cost = £1066 m^{-1}). The cost of each alternative was calculated by summing the costs of the barrier modifications it represented, and only combinations with a total cost of less than £10,000 (a typical conservation budget for river management in the area; U. Juta *pers. comm.*) were retained. This process resulted in a total of 104 potential alternatives.

8.2.2.3 Criteria assessment

To assess the ability of each alternative to limit the spread of signal crayfish, 10 replicate IBM runs were conducted for each combination of modifications, and the average river length occupied by signal crayfish at the end of the simulation period calculated. The cost of each alternative was calculated as part of the alternative identification process (see section 8.2.2.2).

To determine the impacts of barriers on native fishes, the accessibility-weighted habitat availability (AWHA) was calculated for each fish species as described by Milt *et al.* (2018). Although it can describe habitat accessibility at a catchment scale, the AWHA metric does not incorporate the suitability of different habitats. Therefore, for the purposes of this study it is assumed that the all river sections in the Glaven catchment contained habitat suitable for the species of interest. This assumption may be oversimplistic, and future field studies are recommended to assess catchment-scale habitat suitability. Similarly, it is assumed that colonisation and population maintenance in the target species is driven by upstream movements of adults to spawning sites. This may also be an oversimplification, particularly for brook lamprey where a large proportion of the movement within the population is driven by downstream dispersal of the larval stages to silty habitats (Kelly & King, 2001; Bracken *et al.*, 2015).

To calculate AWHA, each river segment (as described in section 8.2.1.1) was split at any intersection with a barrier, resulting in a final river map containing 125 river segments bounded by either a confluence or the presence of a structure (Appendix E Fig. E4.1). For each of these segments, the cumulative accessibility was calculated by multiplying the passability values of all downstream barriers (as defined during the SNIFFER assessment described in section 8.2.1.1). To incorporate the impacts of proposed modifications on AWHA, the passability scores derived from SNIFFER were recalculated for each scenario based on the hypothetical modifications described in section 8.2.1.4. Each of the proposed modifications that could affect fish passage (overhanging lips and the removal of climbing substrate) is included as a binary factor (i.e., present or absent) in the SNIFFER criteria, and therefore it was possible to recalculate the passability scores for modified barriers without additional data collection. Although the inclusion of these factors as binary may appear coarse, the SNIFFER protocol provides a more detailed assessment of barrier characteristics than comparable alternatives such as the ICE protocol (Barry *et al.*, 2018). For each scenario, the cumulative accessibility (and subsequently AWHA) were recalculated based on the modified passability scores. In cases where it was possible to bypass barriers (i.e., braided sections of river), it was assumed that fish would use the alternative route and the barrier was therefore not included in AWHA calculations. The cumulative accessibility was then multiplied by the length of the segment to give the AWHA for the segment, and these values were summated across the full river network. To account for potential changes to the passability scores (and subsequently AWHA) as a result of barrier modification, SNIFFER assessments for each barrier were reconducted with consideration of the changes.

8.2.2.4 Weighting

To quantify the relative importance of each criteria, the swing weighing method was used (Von Winterfeldt & Edwards, 1993). This method aims to quantify the relative importance of a criteria 'swinging' from its worst to its best possible value (e.g., a swing from the entire catchment being occupied by signal crayfish to no expansion from the current invasion front; Von Winterfeldt & Edwards, 1993). For each level of the decision tree (Fig. 8.5), each expert ranked the criteria from most to least important. These rankings were then discussed until a consensus was obtained. The most important variable was assigned 100 points, and each author then assigned points to the remaining points based on their relative importance (i.e., a criteria half as important would receive 50 points). As previously, points scores were discussed until a consensus or compromise was achieved for each criterion. To calculate the final weights (*w*, Fig. 8.5), each score was divided by 100, and weights for criteria at lower levels were multiplied by the weight of the parent criteria.

8.2.2.5 Criteria aggregation

The raw data from criteria assessments were standardised using linear value functions (Appendix E Fig. E5.1) based on the swing weighting procedure, such that a value of 0 was equivalent to the previously defined worst possible scenario, and a value of 1 was equivalent to the best scenario. The gradient (*m*) and intercept (*c*) of a line intersecting the graphical coordinates of the best and worst scenarios were calculated, and used to calculate the standardised value v_{std} using the equation: $v_{std} = mv_{raw} + c$, where v_{raw} represents the raw value.

The weighted linear combination (Malczewski, 2000) was used to calculate the final score (*s*) for each alternative (*i*) by combining the criteria (*j*) using the formula:

$$s_i = \sum_{i,j} v_{std,i,j} w_j$$

8.2.2.6 Sensitivity analysis

The influence of uncertainty in IBM predictions on the results of the MCDA was assessed using a one-at-a-time (OAT) approach. For each alternative in turn, the mean length of river occupied by signal crayfish predicted by the IBM was replaced by the upper 95% confidence limit, while the values for all other alternatives were kept the same. Final ranks were recomputed, and the change in rank was calculated for the alternative being tested. This process was subsequently repeated using lower 95% confidence limits.

To assess whether MCDA results were consistent over time, the total habitat occupied by signal crayfish was extracted from the IBM after a 5- and 10-year forecast (equivalent to years 2028 and 2033, respectively). Ranks were recalculated using the 5- and 10-year predictions, and these values were compared to rankings obtained from the full 15-year predictions using a Spearman’s rank test.

To assess the robustness of the final rankings to weight changes, several weighting scenarios were tested using an OAT approach (Table 8.1). First, an equal-weight scenario was tested, then the weight of each criterion in turn was increased to 60% with the remaining weights equally divided between the remaining criteria. The rankings were recomputed for each weighting scenario, and compared to the original ranks using a Spearman’s rank test.

Table 8.1 – Criteria weights used in a sensitivity analysis to assess the robustness of a multi-criteria decision analysis aiming to identify containment solutions for American signal crayfish (*Pacifastacus leniusculus*).

	Weights						
	Original scenario	Equal scenario	Crayfish scenario	Trout scenario	Lamprey scenario	Eel scenario	Cost scenario
Signal crayfish habitat occupied	0.54	0.2	0.6	0.1	0.1	0.1	0.1
Brown trout AWHA	0.07	0.2	0.1	0.6	0.1	0.1	0.1
Brook lamprey AWHA	0.14	0.2	0.1	0.1	0.6	0.1	0.1
European eel AWHA	0.14	0.2	0.1	0.1	0.1	0.6	0.1
Cost	0.11	0.2	0.1	0.1	0.1	0.1	0.6

8.3 Results

8.3.1 IBM development

8.3.1.1 Model validation

At the end of the 29-year model period, crayfish occupied a total of 71.50 km (standard deviation [SD] = 0.38) of river, equivalent to 97.1% of the Glaven catchment (Fig. 8.6a). The speed of range expansion varied across the 29-year model period, remaining below 2.50 km year^{-1} over the first 15 years, before rising rapidly to a peak of 9.03 km year^{-1} after 20 years, and falling to an average of 2.57 km year^{-1} over the final 5 years (values represent 365-day rolling averages; Fig. 8.6b). There was also substantial seasonal variation in the

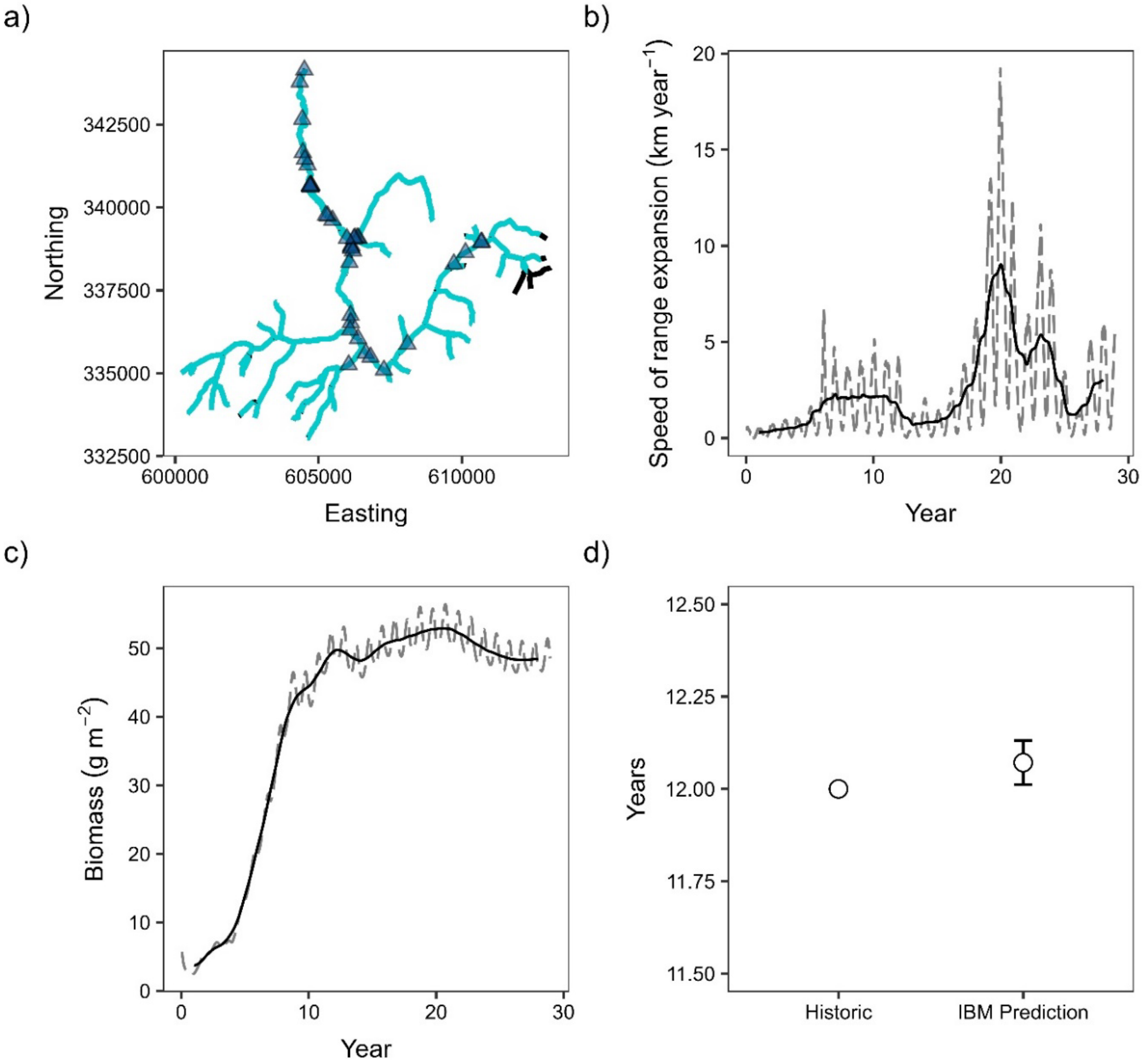

Figure 8.6– Predictions of an individual-based model regarding the spread of American signal crayfish (*Pacifastacus leniusculus*) in the River Glaven catchment (Norfolk, UK) over a 24 year period, showing a) the invaded area at the end of the simulation period (blue lines show invaded area, blue triangles show barriers), b) the total linear expansion rate (TLER) over time (dashed grey line = 20-day rolling average, solid black line = 365 day rolling average) c) the change in daily mean biomass over time (dashed grey line = 20-day rolling average, solid black line = 365 day rolling average, and d) the predicted time taken to pass the barrier at Letheringsett (Easting = 606204, Northing = 338685) compared to the known time from historic observations (error bars show standard deviation).

speed of range expansion, peaking in summer at 19.21 km year^{-1} and falling to a minimum of 0.00 km year^{-1} in winter (values represent 20-day rolling averages to reduce effects of model stochasticity; Fig. 8.6b). The average daily biomass in occupied river sections (i.e., 10 m sections of river used in biomass calculations) rose rapidly over the first 13 years, peaking after 20.7 years at 56.4 g m^{-2} (Fig. 8.6c).

The IBM predicted that the mean time to pass Letheringsett mill (GLA11 in Fig. 8.1) was 12.1 years (SD = 0.10). This prediction was within 0.59% of the known time to reach this point (12 years), meaning the model was deemed to be an appropriate representation of the historical invasion (Fig. 8.6d).

8.3.2 Multi-criteria decision analysis

8.3.2.1 MCDA outcomes

The extent to which the spread of signal crayfish was contained by barrier modifications varied substantially between alternatives (Fig. 8.7a), with the most effective solution limiting the overall invaded river length to 53.77 km (SD = 0.59), compared to 71.54 km (SD = 0.69) in the least effective solution. The AWHA for eel (mean = 11.45 km, range = 9.56 – 13.15 km) was also variable, although results for brook lamprey (AWHA = 3.48 km for all scenarios) and brown trout (mean = 6.45 km, range = 6.39 – 6.49 km) were consistent between alternatives (Fig. 8.7b). Alternatives were available at a variety of costs across the range of potential budgets (mean = £6952.615, range = £0.00 - £9994.27; Fig. 8.7c).

Nine of the ten best-performing alternatives in the MCDA included modifications to one of three large barriers (formerly working mills; GLA12, GLA14, and GLA21 in Fig. 8.1), with the preferred overall solution involving modification to GLA14 only (Table 8.2). For an overall price of £7426.43, this preferred solution restricted signal crayfish to a total invaded length of 54.15 km (SD = 0.63) (Fig. 8.8), while providing 6.49 km of AWHA for brown trout, 3.48 km for brook lamprey, and 12.13 km for European eel. Full rankings and weighted scores are available in Appendix E Table E6.1.

Table 8.2 – Results of a multi-criteria decision analysis to determine to optimal combination of barrier modifications in the river Glaven catchment (Norfolk, UK), showing the 10 highest-ranked alternatives.

		Weighted standardised scores					
Rank	Barriers modified	Invaded length	Trout AWHA	Lamprey AWHA	Eel AWHA	Cost	Score
1	GLA14	0.1917	0.0061	0.0066	0.0230	0.0283	0.2557
2	GLA12, GLA13, GLA31	0.1791	0.0060	0.0066	0.0182	0.0337	0.2436
3	GLA14, GLA21	0.1872	0.0061	0.0066	0.0230	0.0200	0.2430
4	GLA21	0.1035	0.0061	0.0066	0.0246	0.1017	0.2426
5	GLA13, GLA14	0.1954	0.0061	0.0066	0.0183	0.0151	0.2414
6	GLA12, GLA13, GLA30	0.1812	0.0061	0.0066	0.0182	0.0267	0.2387
7	GLA12, GLA14	0.1951	0.0061	0.0066	0.0229	0.0076	0.2383
8	GLA14, GLA15	0.1908	0.0061	0.0066	0.0230	0.0090	0.2356
9	GLA32	0.1899	0.0061	0.0066	0.0236	0.0079	0.2341
10	GLA12, GLA13, GLA21, GLA30	0.1842	0.0061	0.0066	0.0182	0.0184	0.2335

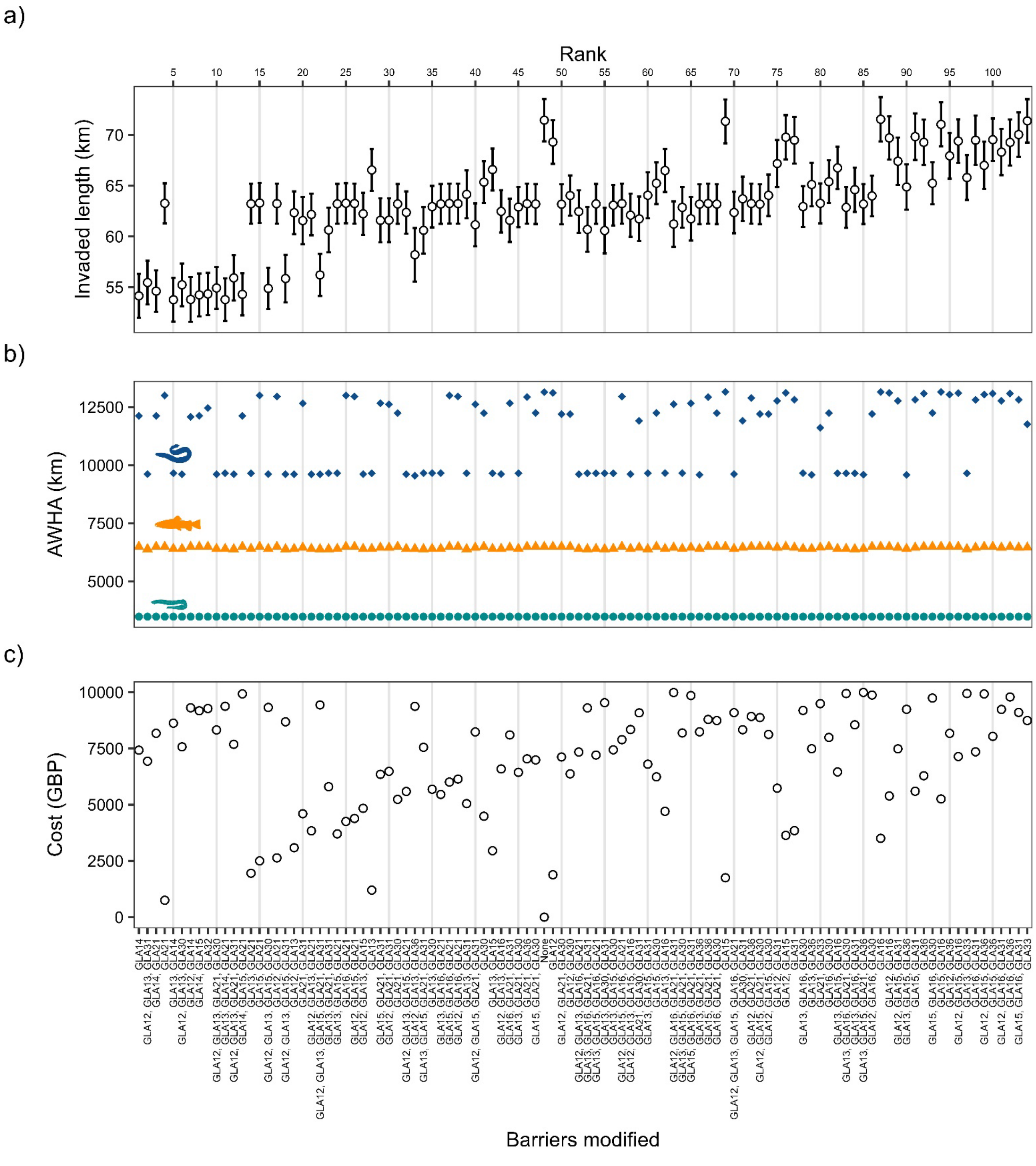

Figure 8.7 – Raw data from criteria assessments conducted as part of a multi-criteria decision analysis (MCDA) aiming to identify optimal containment techniques for American signal crayfish (*Pacifastacus leniusculus*), showing a) river length occupied by signal crayfish in 2033 as predicted by an individual-based model (points = means, error bars = 95% confidence intervals), b) accessibility-weighted habitat availability (AWHA) for native fishes (blue diamonds = European eel [*Anguilla anguilla*], orange triangles = brown trout [*Salmo trutta*], cyan circles = brook lamprey [*Lampetra planeri*]), and c) the total cost associated with different combinations of barrier modifications. Barrier modifications are sorted by their rank in the final MCDA (left to right), starting with the optimal solution.

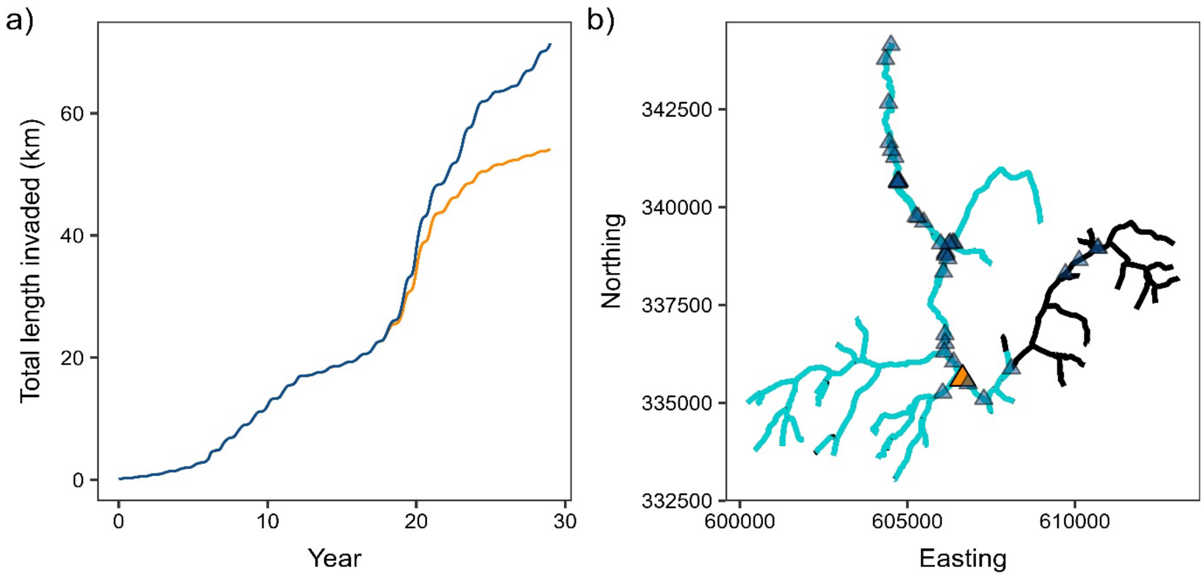

Figure 8.8 – Predictions from an individual-based model showing the performance of the optimal combination of barrier modifications to limit the spread of American signal crayfish in the river Glaven catchment (Norfolk, UK), while minimising costs and impacts on native fishes. The optimal combination was identified using multi-criteria decision analysis, and figures show: a) the total river length invaded over time in the optimal solution (orange line), compared to an alternative with no modifications (blue line), and b) signal crayfish range at the end of the 29-year model simulation (blue lines denote invaded area, blue triangles show unmodified barriers, orange triangles show modified barriers).

8.3.2.3 Sensitivity analysis

Sequential replacement of mean invaded length values by their 95% confidence intervals resulted in a mean change in rank of 13.71 (SD = 6.16; Fig. 8.9a) and 13.81 ranks (SD = 6.19; Fig. 8.9b) for upper and lower confidence intervals, respectively.

The rankings of each alternative after 5- and 10- year model forecasts were not consistent with the rankings after 15-year forecasts (r_s = 0.374 and 0.523, respectively), particularly among the 10 highest-ranked solutions (Fig. 8.10). Full rankings at each time period are provided in Appendix E Table E7.1.

Final ranks were sensitive to the weights applied to each criterion (Appendix E Table E8.1). Adjusted ranks were most similar to the original under the crayfish scenario (r_s = 0.991; Fig. 8.11) but showed low levels of consistency in the equal weights, trout, and lamprey scenarios (r_s = 0.574, 0.571, 0.574, respectively; Fig. 8.11). The 10 highest ranked solutions performed similarly under the crayfish scenario, although performance generally decreased substantially under the alternative weighting scenarios (Table 8.3).

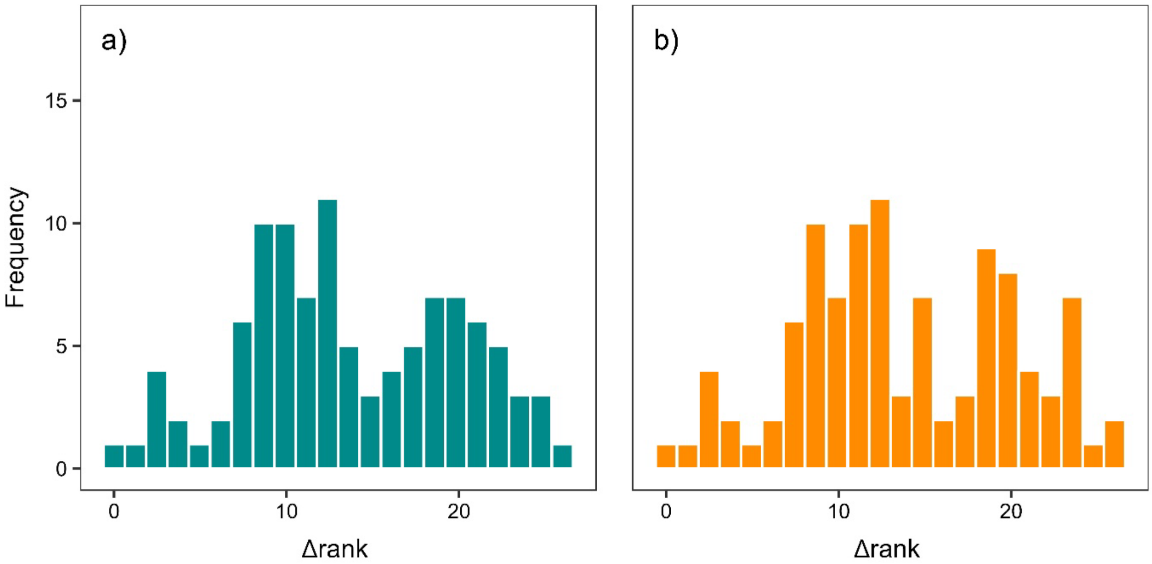

Figure 8.9 – The influence of uncertainty in individual-based model predictions on the results of a multi-criteria decision analysis aiming to identify optimal containment techniques for American signal crayfish (*Pacifastacus leniusculus*), showing the distribution of changes in rank after changing mean predictions to a) upper, and b) lower confidence intervals using a one-at-a-time approach.

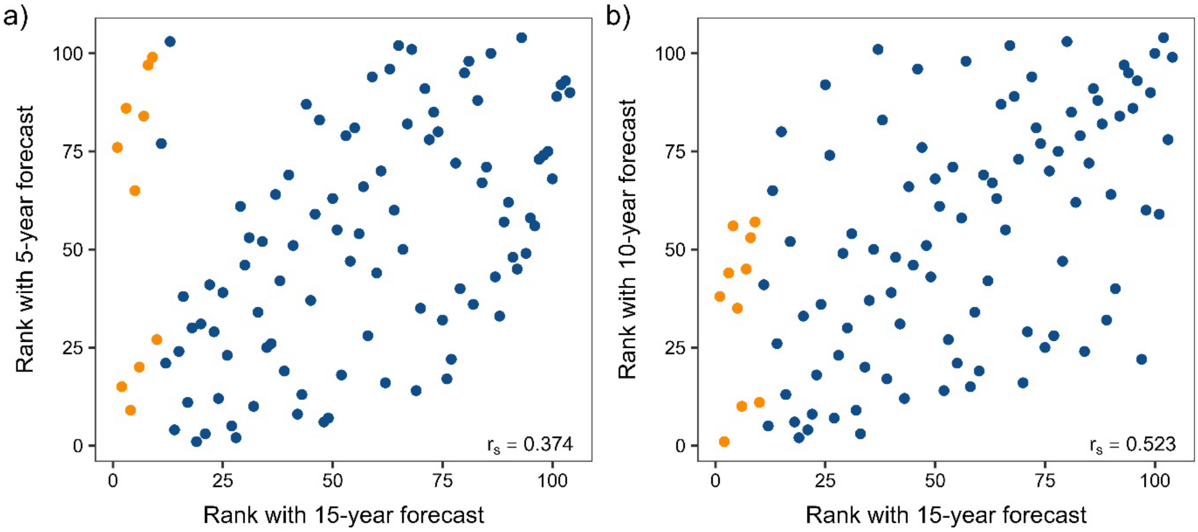

Figure 8.10 – The influence of forecast period on the results of a multi-criteria decision analysis comparing the performance of different combinations of barrier modifications against three criteria (ability to limit the spread of American signal crayfish [*Pacifastacus leniusculus*], impacts on native fishes, and cost). Figures show comparisons of the ranks obtained after 15-year forecasts with those obtained from a) 5-year and b) 10-year forecasts. Orange points show the 10 highest-ranked solutions from the 15-year forecasts.

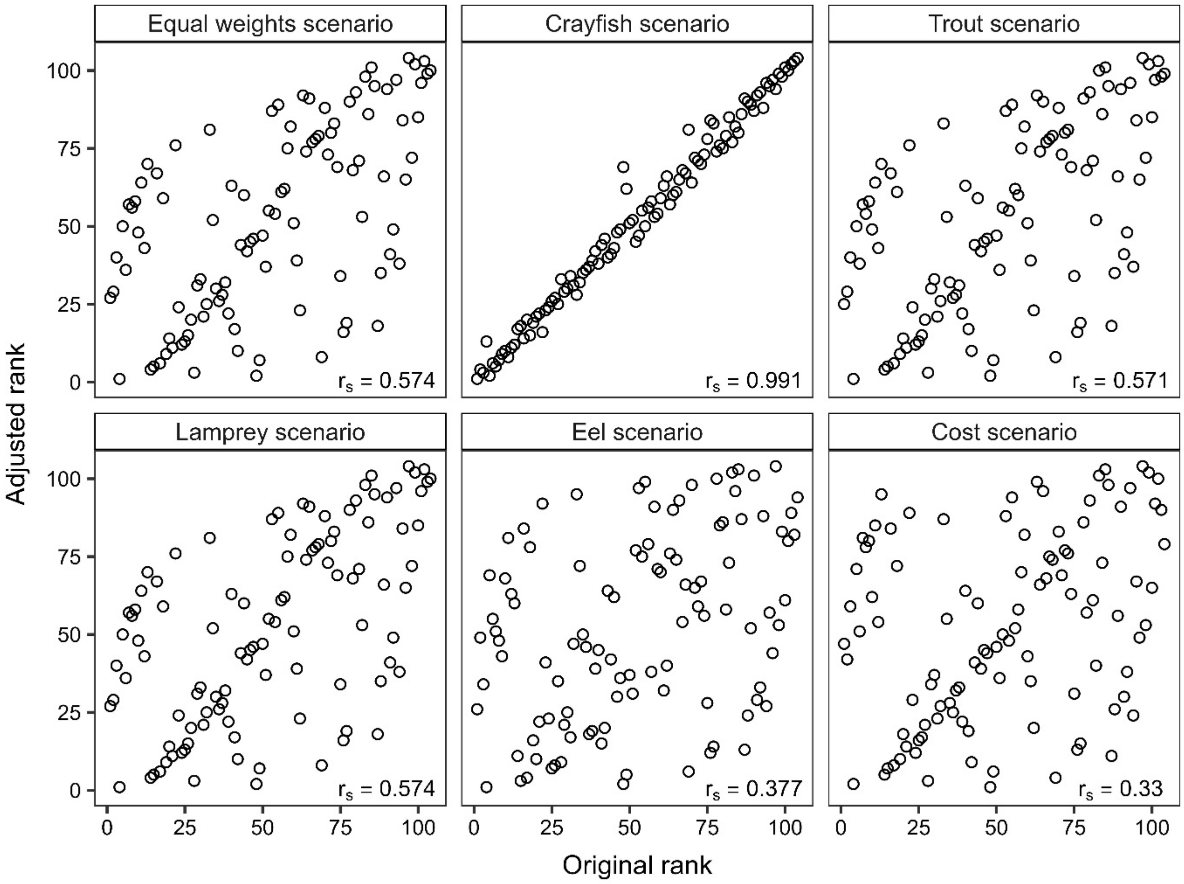

Figure 8.11 – The influence of weights on the results of a multi-criteria decision analysis aiming to identify a combination of barrier modifications that effectively limited the spread of American signal crayfish (*Pacifastacus leniusculus*), while minimising the costs and impacts on native fishes. Figures show a comparison of the ranks obtained using the original weights with the ranks obtained under a variety of weighting scenarios (equal weights; each criteria assigned 60% of the overall weight with equal distribution of the remaining weight). Coefficients (r_s) were obtained from Spearman's rank tests.

Table 8.3 – The sensitivity of ranks obtained during a multi-criteria decision analysis aiming to identify a combination of barrier modifications that could limit the spread of American signal crayfish (*Pacifastacus leniusculus*) while minimising cost and impacts on native fishes, showing the ranks of the 10 originally best-performing alternatives under different weighting scenarios.

	Rank in weighting scenario						
Barriers modified	Original	Equal weights	Crayfish	Trout	Lamprey	Eel	Cost
GLA14	1	27	1	25	27	26	47
GLA12, GLA13, GLA31	2	29	4	29	29	49	42
GLA14, GLA21	3	40	3	40	40	34	59
GLA21	4	1	13	1	1	1	2
GLA13, GLA14	5	50	2	50	50	69	71
GLA12, GLA13, GLA30	6	36	6	38	36	55	51
GLA12, GLA14	7	57	5	57	57	51	81
GLA14, GLA15	8	56	7	54	56	48	78
GLA32	9	58	9	58	58	43	80
GLA12, GLA13, GLA21, GLA30	10	48	10	49	48	68	62

8.4 Discussion

Exclusion barriers are increasingly being used to limit the spread of invasive species in freshwater systems (Jones *et al.*, 2021b), but these structures can also prevent the movements of native fish species. This trade-off has rarely been quantified at large spatio-temporal scales, meaning the role of exclusion barriers in catchment-scale management plans remains unclear. In this study, individual-based modelling of signal crayfish dispersal was combined with MCDA to quantify the trade-off between invasive species containment, native fish movement, and exclusion barrier cost at a catchment scale. The IBM accurately reproduced the invasion history in the river Glaven catchment, and predicted that modifications to existing barriers could slow the secondary range expansion of signal crayfish. However, modifications were costly and reduced the habitat available for European eel and brown trout, but not brook lamprey. MCDA provided a useful framework for considering the relative importance of each variable, and identified an optimal solution involving modifications to a single large mill with high flow velocities (although rankings were sensitive to changes in weighting and uncertainty in IBM predictions). These results demonstrate that exclusion barriers can form an important role in catchment-scale management plans in cases where invasive species containment is a high priority, although explicit consideration of the trade-offs with other conservation goals is essential.

8.4.1 IBM development

The speed of range expansion predicted by the IBM varied substantially over the course of the 29-year model period. This variation is due to the implementation of density-dependent dispersal in the model, whereby periods of rapid range expansion coincide with the invasion of narrow tributaries where high densities are achieved more rapidly. The values predicted by the model may appear high compared to annual invasion rates reported in field studies (range = 0.24 – 5.07 km year-1; Bubb *et al.*, 2005; Peay *et al.*, 2009a; Bernardo *et al.*, 2011; Hudina *et al.*, 2013; Hudina *et al.*, 2017), although this is likely a result of fundamental differences between field studies and the IBM. For example, the model was able to detect all age- and size-classes of crayfish at any location, whereas field studies typically rely on trapping or hand-searching techniques which are not able to detect all individuals (particularly juveniles; Chadwick *et al.*, 2021). These challenges may be particularly pronounced at invasion fronts with low population densities (Stebbing *et al.*, 2014), potentially leading to underestimations of invasion rate in previous studies. Alternatively, these differences may be a result of differences in the metrics used to quantify invasion rate; field studies typically report total linear expansion rates (TLERs) which reflect invasion rates along single unbranching river channels, whereas the metric reported in the IBM captures range expansion occurring in all branches of the dendritic network simultaneously. Therefore, the metric reported by the IBM more closely represents the ‘expansion speed’ metric used to quantify spread in terrestrial systems (Sandvik, 2020), which may explain the comparatively high invasion rates.

The IBM was parameterised with best estimates of crayfish passage based on evidence from the literature. Good agreement was achieved between modelled and observed historic invasion rates in the test catchment, but further work to validate the developed assessment method for predicting crayfish passage at river barriers would be beneficial, especially at a greater diversity of barriers. Indeed, studies of crayfish passage behaviour have typically focussed on sloped weirs (Frings *et al.*, 2013; Rosewarne *et al.*, 2013; Kerr *et al.*, 2021; Chapters 5 and 6), despite the diversity of other infrastructure types present in modern rivers. For example, drop-based barriers (e.g., overshot weirs, sluice gates, elevated culverts) are common in European river systems (Belletti *et al.*, 2020), yet little is known regarding the climbing ability of crayfish (but see Peay & Dunn, 2014), particularly under flowing conditions.

The IBM presented here focuses on active dispersal of signal crayfish, meaning passive movements are not assessed. The importance of passive dispersal for signal crayfish remains unclear, yet drift during high flow periods may be an important component of downstream spread for juveniles (this mechanism is less important for adults as they can remain within refugia; Bubb *et al.*, 2004). Indeed, downstream drift is a well-recognised phenomenon in a wide variety of macro-invertebrate species, and in many cases is a key component of the species' dispersal capability (Bilton *et al.*, 2001). Similarly, the results of Chapter 7 suggest that boats may acts as a vector for passive dispersal, even at local scales. The incorporation of passive dispersal in the IBM would likely lead to faster invasion rates (particularly in the downstream direction), yet additional information is required to determine the spatial and temporal patterns of passive dispersal in signal crayfish. Given the potential importance of passive dispersal as a mechanism of spread, this is recommended as a key focus for future work.

8.4.2 Multi-criteria decision analysis

The MCDA favoured modifications to large barriers with high flow velocities, with nine of the ten most highly ranked solutions including modifications to one of three formerly-working mills (GLA12, GLA14, and GLA21 in Fig. 8.1). Barrier crest velocity is known to be an important determinant of signal crayfish passage success (Frings *et al.*, 2013), and current guidance suggests that flow should be maintained above a threshold value (0.65 m s^{-1}) for continued effectiveness of exclusion barriers (Krieg & Zenker, 2020). Due to the heavily constricted intakes of the mill channels, the minimum flow velocities measured at the barrier crest were comparatively high (GLA12 = 1.385 ms^{-1}, GLA14 = 0.704 ms^{-1}, GLA21 = 1.783 ms^{-1}), meaning these structures were able to block the upstream movements of signal crayfish more effectively, particularly when combined with the barrier modifications (see section 8.2.1.3). Modifications to these larger structures were typically more costly, meaning fewer additional barriers could be modified when these were included. However, the selection of these barriers by the MCDA suggests that resources may be used more effectively by installing fewer, more effective structures, rather than a larger number of less effective barriers.

The optimal alternative identified by the MCDA was not the solution that led to the greatest reduction in invaded length, demonstrating the importance of considering the impacts on native species. Previous studies have focused on quantifying the ability of native species to pass individual exclusion barriers, typically over short experimental periods (Jones *et al.*, 2021b), but the results of this study demonstrate the importance of considering these trade-offs within the context of the catchment-scale barrier network. Indeed, the barrier modifications in this study had minimal impacts on AWHA for brown trout and brook lamprey due to a series of impassable barriers in the lower reaches of the catchment. The addition of overhanging lips is considered to negatively affect passability for these species (SNIFFER, 2010a), meaning assessment of these trade-offs at the level of an individual barrier may have inaccurately predicted substantial reductions in AWHA. Modern rivers are heavily fragmented by river infrastructure (Belletti *et al.*, 2020), and consideration of exclusion barriers within this context is essential for effective implementation (Jones *et al.*, 2021b).

MCDA results were sensitive to variation in the IBM predictions. This variation was driven by stochasticity in model parameters, which leads to a random distribution of physiologically capable and motivated crayfish within the population, and subsequently variation between model runs in the time taken for competent individuals to encounter each barrier. Uncertainty is inevitable in ecological forecasting (Rounsevell *et al.*, 2021), yet Adem Esmail and Geneletti (2018) found that only 6% of studies which utilised MCDA in the field of nature conservation conducted sensitivity analysis relating to the underlying scores. Comprehensive evaluation and reporting of uncertainty is a vital component of informed and transparent decision-making (Milner-Gulland & Shea, 2017; Thompson *et al.*, 2021), and should therefore be a key consideration when applying this approach in the future.

The optimal solution identified by the MCDA varied depending on the time period over which the IBM was used to predict signal crayfish spread. For 5- and 10-year forecasts, the MCDA favoured barriers which were close to the current upstream invasion front, with modifications to GLA12 and GLA13 (the first two structures that would be encountered during upstream range expansion) identified as part of the optimal solution for both (Appendix E Table E7.1). These results support previous studies of crayfish exclusion barriers, which have implicitly assumed that effectiveness is maximised when structures are placed near to the invasion front (Dana *et al.*, 2011; Chucholl *et al.*, 2022). However, modifications to the first upstream barriers were only included in five of the 10 highest-ranked alternatives after a 15-year forecast, likely as a result of long-term changes in invasion dynamics. Over shorter time periods, it is possible that the benefits associated with modifications further upstream were not fully realised, as the invasion front may not have progressed beyond these structures. Similarly, invasion rates are known to recover rapidly once a barrier is passed (Chapter 5), meaning modifications to the first upstream barriers may not prove the most efficient use of resources. Indeed, these results suggest that modifying barriers further upstream can provide comparable reductions in invasion rate, while increasing the overall habitat available for native fishes. These results highlight the importance of considering the long-term catchment-scale effects of exclusion barriers on invasion dynamics, and integrating this information with explicit consideration of other conservation goals. The combined IBM and MCDA approach used in this study provides an effective framework for considering these trade-offs at large spatio-temporal scales, as the quantitative evidence obtained from catchment-scale modelling and barrier assessments can be integrated with value-based information regarding the relative importance of each variable. However, IBMs are computationally intensive, and the expertise required to apply them effectively may limit their widespread use (Mawer *et al.*, 2023).

The final results of the MCDA were also sensitive to variation in the weights chosen. Indeed, the final ranks varied substantially from the original assessment under all alternative weighting scenarios (other than the one favouring crayfish). This sensitivity demonstrates the importance of understanding the meaning and implications of weights, and effectively communicating this to all stakeholders (Adem Esmail & Geneletti, 2018). In this case, the authors were able to discuss the weights to achieve a compromise accepted by all, but this may be more challenging in larger catchments with a greater diversity of stakeholders. Additionally, the criteria included in this MCDA assessment were identified based on the specific management goals in the river Glaven catchment. Conservation priorities are likely to be highly site-specific, meaning careful consideration of the criteria to be assessed is required (Adem Esmail & Geneletti, 2018).

8.4.3 Conclusions

Invasive species are a major threat to global freshwater biodiversity, meaning the prevention of secondary spread is essential to limit the impacts on native ecosystems. Increasingly, exclusion barriers are being used to contain freshwater invasive species, yet the potential non-target effects on native species are rarely considered at large spatio-temporal scales. This study combined an IBM with MCDA to quantify the trade-off between containment of invasive species, native fish migration, and cost at a catchment scale. Barrier modifications successfully limited the spread of signal crayfish over a 15-year period, but were costly and reduced the habitat available for native fishes. MCDA identified a combination of barriers that optimised the trade-off between these variables, but rankings were sensitive to uncertainty in the IBM and variation in weightings. These results suggest that exclusion barriers can be a useful management tool in areas where invasive species containment is a high conservation priority, although explicit consideration of the trade-offs with other conservation is essential.

Chapter 9: Thesis discussion

Invasive species are a major driver of freshwater biodiversity loss (Gallardo *et al.*, 2016; Reid *et al.*, 2019), yet eradication of established populations remains challenging (Simberloff, 2021). In cases where eradication is not feasible, containment (i.e., limiting secondary range expansion) is essential to minimise the impacts on recipient ecosystems (CBD, 2002). In fresh waters, containment is increasingly being achieved through the construction, maintenance, or modification of river infrastructure (e.g., dams, weirs, and culverts), yet the role that these strategies may play in invasive species management remains unclear due to a variety of limitations in the current evidence base (Jones *et al.*, 2021b). Consequently, this thesis aimed to investigate the effectiveness of anthropogenic in-stream infrastructure as a management technique for invasive species. To fully understand the current state of the field, an initial primary objective was defined: 1) to quantitatively review current literature to determine the influence of in-stream infrastructure on invasive species at each stage of the invasion process and to identify research trends, biases, and knowledge gaps. The meta-analysis conducted in pursuit of this initial objective identified a paucity of research regarding the impacts of river infrastructure on the spread of invasive species, and demonstrated that existing evidence is limited by inadequate experimental design, small spatio-temporal scales, and minimal consideration of invasion dynamics.

In this thesis, individual-based modelling was used to address the limitations of previous research due to its ability to simulate complex invasion dynamics over large spatio-temporal scales. The American signal crayfish (*Pacifastacus leniusculus*) was used as a model species for which to formulate the individual-based model (IBM), although additional information was required for model parameterisation. Accordingly, the remainder of this thesis addressed two additional primary objectives: 2) to provide insight into fundamental drivers of signal crayfish barrier passage behaviour and dispersal, and 3) to assess the long-term, catchment-scale effectiveness of exclusion barriers as a method of limiting signal crayfish spread. This chapter discusses the key contributions of this thesis in relation to the primary objectives, before exploring the role that in-stream infrastructure may play in invasive species management and providing suggestions for future work.

9.1 Quantitative review of current literature

The meta-analysis presented in Chapter 2 demonstrated that river infrastructure can facilitate the introduction and establishment of non-native species, suggesting that areas with in-stream structures may act as “invasion hubs” (Muirhead & Macisaac, 2005). The observed increases in rates of introduction are likely due to the increased accessibility of impoundments for anthropogenic activity (Johnson *et al.*, 2008), whereas the greater probability of establishment is likely driven by the high performance of invasive species in disturbed habitats (Marvier *et al.*, 2004). This highlights an important trade-off in the installation of exclusion barriers, whereby the construction of additional infrastructure to prevent the spread of invasive species may actually increase the probability of invasion. Indeed, careful consideration regarding the potential increases in accessibility and habitat disturbance is essential prior to the construction of exclusion barriers. However, the identification of impounded areas as hotspots of invasion may also provide opportunities to improve management efficiency, as targeted interventions in invasion hubs are typically highly effective (Moody & Mack, 1988; Letnic *et al.*, 2015). Additionally, early detection and rapid response is vital for successful eradication (Simberloff, 2009, 2021), and targeted monitoring in high-risk areas (such as those with in-stream infrastructure) is likely to provide a more cost-effective use of limited conservation resources.

Although this thesis attempted to address a number of the biases identified in the meta-analysis by focusing on the spread of invasive species, studying an underrepresented taxonomic group (decapod crustaceans), and assessing the impacts of small structures, the bias towards studies in temperate regions remains a key limitation in the current evidence base. Specifically, the paucity of studies in tropical and subtropical regions is a major challenge, as these areas support the majority of freshwater biodiversity (Balian *et al.*, 2008), and are suffering rapid degradation due to unsustainable resource exploitation (Pelicice *et al.*, 2017). In particular, future construction of large dams is likely to be concentrated in tropical and subtropical regions, especially the emerging economies of south-east Asia, South America, and Africa (Zarfl *et al.*, 2015). Similarly, the frequency of invasions in these regions is likely to increase as rapid globalisation continues (Seebens *et al.*, 2018) and climate change eliminates thermal barriers to invasion (Walther *et al.*, 2009). A more complete understanding of the interaction between invasive species and river infrastructure in these regions is essential for sustainable development, and is strongly recommended as a priority for future research.

9.2 Fundamental drivers of signal crayfish passage behaviour and dispersal

9.2.1 Drivers of barrier passage behaviour

Signal crayfish population density is positively associated with dispersal rate (Galib *et al.*, 2022), likely as a result of fitness costs associated with remaining in high-density areas (Altwegg *et al.*, 2013). Indeed, in Croatian river systems, signal crayfish in the high-density invasion core were found to be smaller (Hudina *et al.*, 2017), more aggressive (Hudina *et al.*, 2015) and in worse condition (Rebrina *et al.*, 2015) than individuals at the low-density invasion front, suggesting there may be a fitness benefit to density-dependent dispersal. However, the experimental results presented in Chapter 5 demonstrated that population density did not affect the motivation or ability of signal crayfish to pass in-stream infrastructure, suggesting that other factors were likely to be driving variation in passage success. Upstream passage success for signal crayfish is highly variable, even between studies with similar barrier designs and flow regimes (e.g., Kerr *et al.*, 2021; Chapters 5 and

6), and numerous factors have been proposed as drivers for the differences (e.g., sex, carapace length, frontal area, muscular force; Frings *et al.*, 2013; Rosewarne *et al.*, 2013). Although the results described in Chapter 5 did not elucidate the factors driving the observed variation in passage success, consideration of the potential drivers prompted the experimental work relating to personality presented in Chapter 6.

The experimental work presented in Chapter 6 demonstrated that signal crayfish exhibit repeatable individual personality traits (boldness and activity), and that these traits formed a behavioural syndrome. These findings add to a growing body of evidence regarding the presence of personality in signal crayfish. For example, Galib *et al.* (2022) found that activity, movement distance, exploration, climbing, and boldness were all repeatable personality traits, with principal components analysis identifying two behavioural syndromes (activity-distance moved and boldness-exploration-climbing). Similarly, Taylor (2016) found that signal crayfish exhibited repeatable activity, foraging voracity, boldness and exploration, and, although not tested explicitly, suggested the presence of an exploration-foraging voracity syndrome. Personality can influence success at any stage of the invasion process (Chapple *et al.*, 2012) and may be an important predictor of overall impact (Juette *et al.*, 2014). For example, bolder and more active individuals may be more likely to encounter transport vectors, and greater levels of exploration within the introduced range may increase the likelihood of finding mates and novel resources (Chapple *et al.*, 2012). Although this is a rapidly accelerating field of research, empirical evidence regarding the importance of personality in invasive species remains rare, and further investigation is encouraged to fully elucidate the role of personality during the invasion process.

Although personality is known to be an important driver of dispersal in a wide variety of taxa (see Spiegel *et al.*, 2017), assessments of personality-dependent barrier passage remain uncommon. Recent studies have demonstrated that higher levels of exploratory behaviour and boldness are associated with increased passage success in native European eel (*Anguilla anguilla*; Mensinger *et al.*, 2021) and brown trout (*Salmo trutta*; Jones *et al.*, 2021a), respectively, but the experimental results presented in Chapter 6 provide evidence for personality-dependent barrier passage behaviour in an invasive species. No relationship was observed between personality and passage success, but bolder individuals were more motivated to pass the experimental barrier. Over longer time periods, increased motivation is likely to lead to higher levels of passage success and may result in spatial sorting of signal crayfish populations (as observed by Hudina *et al.*, 2015), with bolder individuals accumulating upstream of barriers. Given the known positive association between boldness and dispersal rate (Galib *et al.*, 2022), targeted removal of bolder individuals upstream of barriers may substantially decrease the overall invasion rate. Additionally, these results demonstrate the importance of assessing personality when attempting to quantify the effectiveness of exclusion barriers; individuals trapped from the wild for use in experimental or field studies may not be representative of the overall population, as bolder individuals are more likely to encounter and subsequently enter traps (Biro & Dingemanse, 2009). Comprehensive understanding of the factors affecting passage success is essential for effective assessment and application of invasive species exclusion barriers, and therefore further work regarding the importance of personality-dependent passage is recommended for a wider variety of invasive species.

The experiments performed in Chapters 5 and 6 employed a reductionist approach, allowing the respective effects of density and personality to be isolated. While this allowed precise control over potentially confounding variables, it may be argued that flume studies do not accurately replicate natural environments and behaviours (Rice *et al.*, 2010). However, the experiments in this thesis were designed to provide precise information for IBM parameterisation, and carefully controlled flume studies provide valuable reference data for modelling (Rice *et al.*, 2010). Despite this, field studies regarding the effects of density and personality on signal crayfish passage behaviour are encouraged to determine whether the observed relationships are consistent under natural conditions.

9.2.2 Drivers of dispersal

Spatial analysis conducted in Chapter 7 suggested that boating pressure and water temperature were associated with upstream and downstream dispersal of signal crayfish, respectively, although a variety of other abiotic factors (including the density of river infrastructure) did not influence invasion rate. The importance of boating pressure as a driver of local dispersal is particularly interesting, as previous studies have typically considered anthropogenic recreational activities as vectors for long-distance dispersal within (e.g., Kelly *et al.*, 2013) or between catchments (Johnson *et al.*, 2008). Evidence for their importance for local dispersal is rare, although a recent study has suggested that short-distance movements by anglers form ‘invasion superhighways’ which have driven higher invasion rates for bivalves (*Dreissena* spp.) and plants (*Myriophyllum* spp.) in the contiguous USA (Weir *et al.*, 2022). In contrast, water temperature is known to be an important driver of movement dynamics in signal crayfish (Bubb *et al.*, 2004; Johnson *et al.*, 2014). Previous studies have shown that individuals are more active (Johnson *et al.*, 2014) and move greater distances (Bubb *et al.*, 2004) when water temperature is high, but the results presented here suggest that this individual-level variation may have emergent impacts on the overall invasion rate. Water temperatures are likely to increase as a result of climate change (Paul *et al.*, 2019), and the findings presented in Chapter 7 suggest that these changes will result in faster invasion rates for signal crayfish.

It is important to note that the spatial analysis conducted in Chapter 7 relied on sporadic, presence-only data, which may have led to underestimation of the overall invasion rate. Indeed, accurately identifying invasion fronts is challenging due to the low density of individuals (Dragičević *et al.*, 2020), a problem which is exacerbated by the inability of traditional survey techniques (e.g., trapping and hand-surveying) to effectively sample the whole population (Chadwick *et al.*, 2021). Rigorous field studies remain vital for accurate quantification of invasion rate, and modern techniques such as eDNA surveys may provide a more sensitive method of assessing presence and absence (Harper *et al.*, 2018). For example, Greenhalgh *et al.* (2022) surveyed tributaries of the river Wharfe, UK, and found that eDNA-based methods could detect signal crayfish at sites which were deemed unoccupied by hand surveys. Although the underlying data utilised in Chapter 7 may have been limited by the sampling techniques, the large number of records and broad spatial scale allowed insights to be made at a national level. This trade-off between spatial extent and sampling intensity is well-recognised in the adjacent field of citizen science, which commonly accepts the limitations of volunteer-collected data (e.g., sporadic sampling periods, incorrect identification) given its ability to provide insights over broad spatio-temporal scales (Taylor *et al.*, 2019; Robinson *et al.*, 2020).

9.3 Long-term catchment-scale effectiveness of exclusion barriers

9.3.1 Insights into long-term catchment-scale effectiveness of exclusion barriers

The IBM originally assembled by Dr Jim Kerr (Chapter 5) and subsequently developed in Chapter 8 of this thesis provided novel insights into the influence of exclusion barriers on signal crayfish invasion dynamics. The original IBM demonstrated that a partial barrier (passable to 22% of males and 12% of females) could reduce the total length of river invaded by signal crayfish by 2.34 km over a 20-year period. Similarly, the updated IBM described in Chapter 8 demonstrated that low-cost modifications to a single barrier could reduce the invaded length by 17.35 km over a 29-year period compared to a do-nothing scenario. It is important to note that, although no formal statistical comparisons were undertaken, both studies utilised an appropriate control scenario (no barrier and no modifications, respectively). This contrasts with many previous studies aiming to test the effects of exclusion barriers (Jones *et al.*, 2021b; Chapter 2), and provides strong evidence that the observed effects were solely due to the introduction of exclusion barriers. Both models demonstrated that invasion rates were considerably suppressed upon initially encountering the barrier, although invasion rates did recover once the barrier was passed. Previous studies have demonstrated that individual barriers can reduce the probability of upstream movements (Rosewarne *et al.*, 2013; Kerr *et al.*, 2021), but these results provide strong evidence that the observed reductions in passage success can lead to long-term, catchment-scale decreases in invasive range.

The research presented in Chapter 8 builds on previous studies of exclusion barriers by explicitly considering the catchment-scale network of barriers. This was identified by Jones *et al.* (2021b) as a key consideration for the effective application of exclusion barriers, as the location and passability of other structures within the catchment can contribute to invasive species containment. The importance of the catchment context has been extensively studied in the closely related field of barrier removal, where studies typically aim to identify a suite of barrier removals that can maximise habitat availability for native fishes over large spatial scales (McKay *et al.*, 2017). Considering the impacts of removals within the context of the network of barriers leads to substantially more robust conclusions than approaches which consider single mitigation options in isolation, and can reveal solutions unlikely to have been developed by leveraging human intellect alone (Kemp & O'Hanley, 2010; McKay *et al.*, 2017). The results presented in Chapter 8 demonstrated that the existing barrier network in the river Glaven catchment can affect the movements of signal crayfish, highlighting the importance of considering the catchment context when implementing exclusion barriers in real systems.

Identifying suitable locations for exclusion barriers is a key challenge for effective implementation (Jones *et al.*, 2021b), but the combined IBM and multi-criteria decision analysis (MCDA) approach utilised in Chapter 8 allowed optimal locations to be identified by explicitly quantifying the catchment-scale trade-offs between native fishes, invasive species, and cost. Previous studies have typically assumed that modifying or installing exclusion barriers directly upstream of the invasion front is the optimal solution (e.g., Dana *et al.*, 2011; Chucholl *et al.*, 2022), yet these structures were only included in five of the 10 highest-ranked solutions in the MCDA. Indeed, the optimal solution identified by the MCDA (modifications to a large barrier further upstream in the catchment) provided comparable reductions in signal crayfish spread, without decreasing the habitat accessible for European eel and brown trout. This finding emphasises the importance of quantifying the impacts on native species and the costs of installation, and provides a framework for identifying locations for exclusion barrier construction. However, Chapter 8 did not incorporate any assessment of habitat suitability for the native species considered. The quality of the habitat which is blocked by barrier modifications is likely to have a strong influence over the conservation outcomes for these species, and the inclusion of this information is recommended in future studies. Furthermore, the optimal combination of modifications varied when the relative importance of each variable was changed. This finding is comparable to the results of similar studies aiming to optimise dam removal in invaded catchments, which have shown that the optimal combination of removals varies substantially with budget (Milt *et al.*, 2018) and the relative importance assigned to invasive species containment (Cooper *et al.*, 2021). Careful consideration of the importance of each variable is therefore essential when quantifying the trade-offs associated with exclusion barrier construction.

It is important to note that the long-term, catchment-scale efficacy of exclusion barriers is likely to depend on the implementation of effective biosecurity. Indeed, the release of any invasive individuals upstream of an exclusion barrier will likely render it ineffective as a method of containment. However, the results presented in Chapter 2 demonstrated that in-stream infrastructure acts as a hotspot for the introduction and establishment of invasive species, suggesting that there is a high risk of upstream invasion if effective biosecurity is not implemented. A variety of legislation is in place to limit the spread of invasive species (e.g., European Union [EU] Regulation on Invasive Alien Species [EU Regulation 1143/2014]), and numerous campaigns have attempted to improve public awareness of biosecurity (e.g., Check, Clean, Dry in the UK). Additionally, a variety of simple, low-cost biosecurity techniques are available, including broad-spectrum disinfectants (Cuthbert *et al.*, 2018), desiccation (Coughlan *et al.*, 2018), hot water (Anderson *et al.*, 2015), and steam (Bradbeer *et al.*, 2020). However, uptake of these solutions is often low due to a lack of public awareness (Smith *et al.*, 2020) or prioritisation of self-interests (Sutcliffe *et al.*, 2018). Further efforts to improve the effectiveness of current biosecurity measures is therefore required to support the long-term use of exclusion barriers.

9.3.2 Individual-based modelling approach

Although the IBM utilised in Chapters 5 and 8 accurately simulated signal crayfish invasions, there are several interesting opportunities for further development. For example, although boating was identified as a key driver of local dispersal in Chapter 7, it was not implemented in the IBM used in Chapter 8 as there is minimal boating activity in the river Glaven (U. Juta *pers. comm*). Applying the IBM to a catchment with high boating activity could elucidate the mechanisms by which boating accelerates signal crayfish spread, and assess whether navigation is likely to reduce the efficacy of exclusion barriers. Similarly, the variety of management techniques implemented in the IBM could be extended to support the assessment of integrated pest management (IPM) approaches. IPM combines physical, chemical, biological, and cultural control methods, and is increasingly recognised as the optimal strategy for the control of aquatic invasive species (Hubert *et al.*, 2021). Given the ability of the IBM to test management strategies over large spatio-temporal scales, it may prove a useful tool for optimising IPM approaches (e.g., Vinatier *et al.*, 2012).

The IBM approach employed in this thesis allowed long-term, catchment-scale assessments of exclusion barrier effectiveness that likely would not have been possible using field studies (Thompson *et al.*, 2021). However, there are several limitations which may prevent the widespread application of IBMs in invasive species management (Thompson *et al.*, 2021). Firstly, the high degree of complexity means that IBMs are computationally intensive (Grimm & Railsback, 2005) and their development requires time and expertise (Mawer *et al.*, 2023). Secondly, comprehensive autecological data is required for model parameterisation (DeAngelis & Diaz, 2019), which may not be available for species that have been recently introduced. Detailed data are also required to validate model predictions (Bauer & Klaassen, 2013). Finally, IBMs cannot be represented in a concise mathematical framework (Hinkelmann *et al.*, 2011), meaning effective communication to stakeholders is challenging and models are often not reproducible (Grimm *et al.*, 2006). However, steps have been taken to standardise the reporting of IBMs through the development of the Overview, Design concepts and Details (ODD) protocol, which is likely to improve communicability and reproducibility (Grimm *et al.*, 2006; Grimm *et al.*, 2010; Grimm *et al.*, 2020).

9.4 Are barriers an effective management tool for freshwater invasive species?

9.4.1 Effectiveness of exclusion barriers for signal crayfish

Overall, the results presented in this thesis suggest that exclusion barriers may provide a useful tool for slowing the spread of American signal crayfish. However, this contrasts with a recent review which states that exclusion barriers can completely stop crayfish spread (Krieg & Zenker, 2020). While it may be possible to eliminate upstream movements over short time periods, long-term barrier integrity can be compromised by a number of factors. For example, corrosion or algal build-up can increase passability by elevating surface roughness (Frings *et al.*, 2013; Krieg *et al.*, 2021), meaning barrier effectiveness is likely to reduce without regular maintenance. Similarly, signal crayfish have a strong climbing ability (Peay & Dunn, 2014), meaning any accumulation of debris may facilitate successful passage (Krieg *et al.*, 2021). Furthermore, both Krieg *et al.* (2021) and Chucholl *et al.* (2022) observed that crayfish were able to pass otherwise effective barriers during low-flow events. Such events are likely to increase due to climate change (Kay, 2021), meaning long-term effectiveness of exclusion barriers is likely to be limited. Even if the in-stream barrier is effective, signal crayfish can move over land to circumvent impassable structures (Thomas *et al.*, 2019b), meaning complete elimination of terrestrial connectivity is required for long-term viability. Any barrier designs that can address these limitations (i.e., large vertical drops with overhanging lips, elimination of terrestrial passage) are likely to be impassable to native fauna (SNIFFER, 2010b), meaning there are limited cases where such structures can be feasibly deployed. Given the limitations of current exclusion barriers, coupled with the rapid recovery of invasion rate after barrier passage (see Chapters 5 and 8), relying on exclusion barriers to completely stop the spread of signal crayfish over long time periods is unlikely to be successful. Accordingly, it may be more appropriate to consider exclusion barriers as part of an IPM strategy for signal crayfish, providing a useful means of slowing the spread while other techniques are developed or applied. Indeed, a number of novel crayfish control strategies are currently under development (e.g., RNA interference, sterile male release; Manfrin *et al.*, 2019), and slowing the spread of signal crayfish using exclusion barriers may provide the time required for these techniques to become widely applicable. Similarly, reducing the invasion rate of signal crayfish may provide an opportunity to translocate native crayfish to ark sites (Peay & Füreder, 2011). This technique has been widely applied in the UK to protect white-clawed crayfish (*Austropotamobius pallipes*), and has been vital for securing the long-term viability of the population (Souty-Grosset & Reynolds, 2009; Nightingale *et al.*, 2017).

Previous studies have typically focused on the construction of new exclusion barriers, yet the results of Chapter 8 provide strong evidence that modifications to existing structures can slow the spread of signal crayfish. This finding supports two recent field studies, where modifications to dams and bridges (Krieg *et al.*, 2021), as well as culverts (Chucholl *et al.*, 2022) have successfully limited the spread of signal crayfish in Switzerland and Germany, respectively. These modifications are typically low-cost (Krieg *et al.*, 2021), and can be installed at structures which already act as barriers to native fishes, meaning trade-offs with other conservation goals can be minimised. Krieg *et al.* (2021) suggested that modifications should be installed at structures which prevent terrestrial passage (e.g., bridge footings, channels, and walls). However, the MCDA conducted in Chapter 8 favoured large structures with high flow velocities, suggesting these may also be good candidates for modifications. Given the success of low-cost modifications in slowing the spread of signal crayfish, further work is recommended to explore the potential of this approach for other freshwater invasive species.

The experimental work conducted in Chapters 5 and 6 demonstrated that signal crayfish have a greater capacity to pass barriers than previously recognised. Indeed, across the two experiments, 38.1% and 5.4% of crayfish successfully passed upstream against crest velocities of 0.735 ms^{-1} and 0.680 ms^{-1}, respectively. This supports the work of Kerr *et al.* (2021), who found that 14% of crayfish could pass an experimental crump weir with a crest velocity under similar flow conditions, but contradicts the findings of Frings *et al.* (2013), who predicted that crayfish would not be able to pass barriers with crest velocities greater than 0.65 ms^{-1}. Recent guidance on the installation of crayfish exclusion barriers follows the work of Frings *et al.* (2013), suggesting that a minimum crest velocity of 0.65 ms^{-1} should be maintained to prevent crayfish passage. However, the results presented here, coupled with the work of Kerr *et al.* (2021), demonstrate that this velocity is insufficient to completely prevent upstream movements by signal crayfish, meaning current guidelines must be re-evaluated. Additionally, as crayfish were able to pass the crest velocities utilised in this thesis, the flow parameters needed to completely prevent upstream passage remain unknown. This information is vital for effective design of signal crayfish exclusion barriers, and is strongly recommended as a focus for future research.

9.4.2 Overall effectiveness of exclusion barriers

Management of freshwater invasive species follows a stepwise process, whereby preventing introductions is the primary goal, followed by eradication of introduced populations, mitigation to suppress ecological impacts, and containment of secondary range expansion (CBD, 2002; Britton *et al.*, 2023). Exclusion barriers can form a vital part of containment strategies in situations where eradication of introduced populations has failed, and prevention of further dispersal is required to minimise the impacts on recipient ecosystems (Jones *et al.*, 2021b; Britton *et al.*, 2023). Although complete prevention of upstream movements should remain the ultimate goal of exclusion barrier installation, the results of this thesis demonstrate that even partial barriers can slow the spread of invasive species, and thus may contribute to catchment-scale containment strategies. Exclusion barriers are likely to be particularly useful as part of IPM strategies, whereby containment can be combined with other management techniques to maximise the overall effectiveness of control programs (Hubert *et al.*, 2021).

Table 9.1 – Factors that should be considered prior to the installation of invasive exclusion barriers, including some examples of questions that should be addressed by conservation managers.

Consideration	Rationale	Example questions
Species characteristics	Not all species are likely to be affected by exclusion barriers.	Does the species actively disperse upstream? Are there life stages that may not be affected by barriers (e.g., flying insects)?
Barrier effectiveness	Exclusion barriers should only be installed if there is strong evidence that they can prevent the movements of invasive species.	What proportion of individuals are blocked by the exclusion barrier? Is the effectiveness of the barrier consistent across life stages? Have assessments of effectiveness included appropriate control sites? What factors may reduce barrier effectiveness over long time periods?
Current invasive range	Barriers are only likely to be effective if implemented upstream of the current invasion front.	Where is the current upstream invasion front? Have appropriate techniques been used to assess the location of the invasion front? How quickly is the invasion front likely to advance?
Landscape context	Modern rivers are heavily fragmented, and it is likely that other infrastructure is present within the catchment.	What other barriers are present within the catchment? Are they likely to affect the movements of invasive species?
Trade-offs with native species	Exclusion barriers can affect the movements of native species, which often have high conservation value.	What species are present within the catchment? How important is preserving connectivity for native species? Are selective fish passes available?
Trade-offs with other invasion stages	Installation of river infrastructure can facilitate the introduction and establishment of invasive species.	Will the impoundment be large enough to support aquaculture or recreational activities? Will installation of the exclusion barrier cause significant habitat disturbance?
Cost	Conservation projects are typically limited by the availability of funding.	How much will the exclusion barrier cost? Is it an efficient use of resources?
Biosecurity	Exclusion barriers are unlikely to be effective if lax biosecurity measures allow invasive species to be moved upstream.	To what extent is the catchment used for recreational activities such as boating and angling? Are there regular water transfers? Is there an effective biosecurity plan in place?
Policy context	Any conservation management techniques should conform to current legislation.	Is the target invasive species covered by legislation? Is legislation in place to prevent river fragmentation for native species?
Stakeholder engagement	Freshwater systems provide a variety of ecosystem services and are often privately owned, meaning stakeholder engagement is essential.	Who are the stakeholders in the catchment? Are landowners willing to engage with conservation efforts? How might exclusion barrier installation and/or maintenance affect their land?

Although exclusion barriers are likely to form an important part of IPM strategies, it is important to acknowledge that they will not be effective against every species in every situation. The lessons learned from this thesis and previous literature can be distilled into 10 factors that should be considered prior to the installation of an exclusion barrier: 1) species characteristics, 2) barrier effectiveness, 3) current invasive range, 4) landscape context, 5) trade-offs with native species, 6) trade-offs with other invasion stages, 7) cost, 8) biosecurity, 9) policy context, and 10) stakeholder engagement (Table 9.1). Each of these factors could affect the successful application of exclusion barriers, and it is therefore hoped that the information in Table 9.1 will provide a useful starting point for conservation managers contemplating the installation of an invasive species exclusion barrier. Although these considerations represent current understanding, they may change as the field continues to evolve, and there are also likely to be numerous site-specific considerations unique to each project.

9.5 Priorities for future work

A number of potential avenues for further work have been described throughout this thesis, but three topics have emerged as urgent priorities for future research: 1) long-term testing of exclusion barrier efficacy, 2) understanding the role of existing infrastructure in invasive species containment, and 3) further development of selective fish passage to ameliorate impacts on native fauna.

Although evidence for the use of exclusion barriers is rapidly accumulating, there is still a pressing need for further assessment, particularly long-term field tests with rigorous experimental design. Indeed, both the meta-analysis conducted in Chapter 2 and the review conducted by Jones *et al.* (2021b) found that very few studies employ an appropriate control site, substantially limiting the strength of the current evidence base. While the findings presented in Chapters 5 and 8 demonstrated that exclusion barriers could limit the spread of invasive species compared to a control scenario, validation of these results using long-term field studies is essential to fully understand whether exclusion barriers are a viable tool for long-term, catchment-scale management. It is also vitally important that unsuccessful barrier designs are reported, as a publication bias towards successful designs may lead to unrealistic assessments of exclusion barrier efficacy.

Additionally, further work is urgently required to understand the role of existing infrastructure in limiting the spread of invasive species. Typically, previous research has focused on the installation of additional infrastructure (Jones *et al.*, 2021b), yet existing structures are known to prevent upstream migration for a variety of native fish species (Jones *et al.*, 2021a) and may therefore limit the movements of invasive species (Rahel, 2013). Indeed, the IBM developed in Chapter 8 indicated that many of the existing barriers in the river Glaven could limit signal crayfish spread, and the viability of the sea lamprey (*Petromyzon marinus*) control program in the Great Lakes is dependent on a network of 930 pre-existing structures

(Zielinski *et al.*, 2019). Similarly, Rosewarne *et al.* (2013) found that a low-head gauging weir reduced upstream movements of signal crayfish by 45%, and Kerby *et al.* (2005) demonstrated that the upstream dispersal of red swamp crayfish (*Procambarus clarkii*) was limited by both culverts and waterfalls. However, the results of Chapter 7 showed that the density of existing barriers did not affect signal crayfish invasion rate, supporting the results of recent eDNA studies (Ikeda *et al.*, 2019; Robinson *et al.*, 2019). A comprehensive understanding regarding the role of existing barriers is particularly important due to the accelerating rates of dam removal (Mouchliantis, 2022), as the dismantling of infrastructure that prevents the upstream movements of invasive species can facilitate secondary range expansion (e.g., Mahan *et al.*, 2021). Studies aiming to assess the efficacy of existing structures should employ similar experimental design principles as those testing purpose-built exclusion barriers (i.e., long-term assessments with appropriate control sites). The data obtained from these studies could also be used to develop barrier passability assessment tools, similar to those which are widely available for native fishes (Furniss, 2008; SNIFFER, 2010b; Baudoin *et al.*, 2015). For example, the passability assessment protocol described in Chapter 8 can predict whether American signal crayfish of any size are able to pass a structure based on simple physical measurements (e.g., barrier slope and flow). Development of similar assessment protocols for a wider range of invasive species could facilitate rapid quantification of passability for existing barriers, which in turn can be used to inform studies aiming to optimise exclusion barrier construction (e.g., Chapter 8) or infrastructure removal (e.g., Milt *et al.*, 2018; Cooper *et al.*, 2021; Terêncio *et al.*, 2021).

Perhaps the most effective method of resolving the trade-off between invasive species containment and native fish migration is the development of infrastructure that provides selective fish passage (see Rahel & McLaughlin, 2018). The goal of selective fish passage is to allow movements by desirable species while simultaneously blocking the movements of undesirable species (Rahel & McLaughlin, 2018), and this is typically achieved by exploiting morphological (e.g., body size; Hillyard *et al.*, 2010), phenological (e.g., seasonal activity patterns; Zielinski *et al.*, 2019), behavioural (e.g., depth preference; Schultz *et al.*, 2007), or physiological (e.g., jumping ability; Morán-López & Uceda Tolosa, 2017) differences between native and invasive species. There is also potential to exploit differences in sensory capabilities (Rahel & McLaughlin, 2018), as a number of non-physical stimuli can alter the movement patterns of invasive species, including electricity (Johnson *et al.*, 2016), light (Kim & Mandrak, 2017), and sound (Vetter *et al.*, 2017). However, non-physical barriers can also have substantial impacts on native species; Ruebush *et al.* (2012) found that only 2.9% of non-target individuals were able to pass a combined sound-bubble-light barrier in the Chicago Sanitary and Ship Canal. Completely selective fish passage is unlikely to exist within the limitations of current technology (Rahel & McLaughlin, 2018), yet further innovation in this field could provide substantial progress towards resolving the connectivity conundrum.

9.6 Conclusions

Invasive species are already widely recognised as a major threat to global freshwater biodiversity (Britton *et al.*, 2023), and their impacts are only likely to grow as increasing globalisation and climate change facilitate higher rates of transport, introduction, establishment, and spread (Seebens *et al.*, 2021). While prevention remains the most effective method of limiting the impacts of invasive species, the development of effective containment tools is vital for situations where prevention has failed, and eradication is unfeasible due to technological, economic, or ecological constraints (CBD, 2002).

This thesis combined meta-analytical approaches, fine-scale behavioural experiments, national-scale spatial analysis, and long-term catchment-scale modelling to demonstrate that river infrastructure can provide an effective tool for containing the spread of invasive species. However, a wide variety of trade-offs and context dependencies means that the installation of exclusion barriers is unlikely to be the optimal management solution for all species in all situations. Instead, exclusion barriers are perhaps most appropriately employed as part of IPM strategies, where they can be applied flexibly in combination with other control techniques to support coordinated and context-specific management of invasive species.

The research presented in this thesis is of benefit to scientists working in a variety of disciplines (e.g., invasive species management, animal behaviour, sustainable infrastructure design), as well as policy makers and conservation practitioners aiming to conserve freshwater biodiversity in highly modified modern rivers. The main findings of this research have been disseminated to the wider scientific community (see section 9.7), and are already being implemented in real river systems. Ultimately, the changes enacted as a consequence of this research will help to protect invaluable fresh waters from the damaging effects of invasive species, supporting the development of productive and resilient ecosystems that benefit wider society.

9.7 Research outputs

Chapter 2

- Published article
    - Currently in preparation for submission.
- International conferences
    - British Ecological Society Festival of Ecology 2021 – Poster titled ‘River infrastructure can facilitate the introduction and establishment of non-native species’
- National conferences
    - Sustainable Futures CDT Conference 2020 – Poster titled ‘River infrastructure can facilitate the introduction and establishment of non-native species’

Chapter 5

- Published 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*. 60:6. 99-1009. https://doi.org/10.1111/1365-2664.14387
- International conferences
  - British Ecological Society Festival of Ecology 2020 – Poster titled ‘Quantifying the impact of a partial riverine barrier on the dispersal of invasive American signal crayfish (*Pacifastacus leniusculus*) using an individual-based model parameterised with experimental data’ (Runner up - Student Poster Prize).

Chapter 6

- Published article
  - **Daniels, J.A.**, Kemp, P.S. 2022. Personality-dependent passage behaviour of an aquatic invasive species at a barrier to dispersal. *Animal Behaviour*. 192. 63-74. https://doi.org/10.1016/j.anbehav.2022.07.005
- International conferences
  - Association for the Study of Animal Behaviour Easter Meeting 2021 – Talk titled ‘Personality-dependent barrier passage behaviour in invasive American signal crayfish (*Pacifastacus leniusculus*).’

Chapter 7

- International conferences
  - International Conference on Aquatic Invasive Species 2022 – Talk titled ‘Drivers of secondary spread in freshwater invasive species’ (Second Place - Student Presentation Competition).

Chapter 8

- International conferences
  - Symposium for European Freshwater Sciences 2023 – Talk titled ‘The “connectivity conundrum”: River infrastructure as a management technique for invasive species’
- National conferences
  - Sustainable Infrastructure and Cities conference 2023 – Talk titled ‘The “connectivity conundrum”: River infrastructure as a management technique for invasive species’

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Appendix A: Supplementary information for Chapter 2

A.1 Summary of studies included in the meta-analysis

Table A1.1 – Summary of the studies included in a meta-analysis aiming to quantify the impacts of river infrastructure on invasive species at each stage of the invasion process.

Publication	Invasion stage	Country	Barrier type	Head drop (m)	Taxonomic group	Hedge's *g*	Variance
Holmquist *et al.* (1998)	Establishment	Puerto Rico	Dam	38.45	Fish	0.572	0.075
Gehrke *et al.* (2002)	Introduction	Australia	Dam	43	Fish	5.534	1.825
Gehrke *et al.* (2002)	Introduction	Australia	Dam	43	Fish	3.267	0.996
Merritt and Poff (2010)	Establishment	USA	Dam	NA	Plant	-0.556	0.08
Merritt and Poff (2010)	Establishment	USA	Dam	NA	Plant	0.766	0.097
Martinez *et al.* (1994)	Establishment	USA	Dam	15.2	Fish	4.3	1.433
Martinez *et al.* (1994)	Establishment	USA	Dam	15.2	Fish	1.181	0.515
Light (2003)	Establishment	USA	Small Dam	46.25	Macro-invert.	1.062	0.407
Kerby *et al.* (2005)	Spread	USA	Small Barrier	2	Macro-invert.	-0.902	0.09
Vitule *et al.* (2012)	Introduction	Brazil & Paraguay	Dam	196	Fish	0.279	0.056
Vitule *et al.* (2012)	Introduction	Brazil & Paraguay	Dam	196	Fish	1.565	0.067
Poulet (2007)	Introduction	France	Small Weir	4	Fish	1.939	0.348
Poulet (2007)	Introduction	France	Small Weir	4	Fish	1.142	0.26
Mortenson and Weisberg (2010)	Establishment	USA	Dam	84.74	Plant	-1.564	1.667
Mortenson and Weisberg (2010)	Establishment	USA	Dam	84.74	Plant	0.388	0.386
Kirkwood *et al.* (2009)	Establishment	Canada	Dam	48.81	Algae	6.666	0.856
Quist *et al.* (2004)	Establishment	USA	Dam	66.6	Fish	1.018	0.466
Quist *et al.* (2004)	Establishment	USA	Dam	66.6	Fish	1.483	0.525
Quist *et al.* (2005)	Introduction	USA	Dam	95	Fish	4.659	0.93
Quist *et al.* (2005)	Introduction	USA	Dam	95	Fish	8.492	4.272
Alexandre and Almeida (2010)	Establishment	Portugal	Small Dam	NA	Fish	1.235	0.16

Alexandre and Almeida (2010)	Establishment	Portugal	Small Dam	NA	Fish	0.575	0.14
Alexandre and Almeida (2010)	Establishment	Portugal	Small Dam	NA	Fish	0.632	0.141
Bombino *et al.* (2014)	Introduction	Italy	Check Dam	NA	Plant	2.146	0.096
Bombino *et al.* (2014)	Introduction	Italy	Check Dam	NA	Plant	-0.436	0.062
Greet *et al.* (2012)	Establishment	Australia	Dam	55.2	Plant	-0.609	0.024
Greet *et al.* (2012)	Introduction	Australia	Dam	55.2	Plant	-0.823	0.025
Santos *et al.* (2010)	Establishment	Brazil	Dam	39	Fish	3.667	1.013
Santos *et al.* (2010)	Introduction	Brazil	Dam	39	Fish	0.121	0.162
Hoagstrom *et al.* (2007)	Introduction	USA	Dam	59	Fish	1.187	0.671
Jellyman and Harding (2012)	Introduction	New Zealand	Dam	27.25	Fish	3.65	0.201
Jellyman and Harding (2012)	Introduction	New Zealand	Dam	27.25	Fish	0.992	0.086
Głowacki and Penczak (2013)	Establishment	Poland	Dam	16	Fish	0.755	0.811
Głowacki and Penczak (2013)	Establishment	Poland	Dam	16	Fish	-0.189	0.196
Głowacki and Penczak (2013)	Establishment	Poland	Dam	16	Fish	1.044	0.731
Głowacki and Penczak (2013)	Establishment	Poland	Dam	16	Fish	1.842	0.642
Głowacki and Penczak (2013)	Establishment	Poland	Dam	16	Fish	0.755	0.811
Głowacki and Penczak (2013)	Establishment	Poland	Dam	16	Fish	0.755	0.811
Głowacki and Penczak (2013)	Establishment	Poland	Dam	16	Fish	-1.341	0.142
Smith *et al.* (2015)	Establishment	USA	Low-head Dam	5	Macro-invert.	0.014	0.043
Khedkar *et al.* (2014)	Introduction	India	Dam	35.7	Fish	0.612	0.176

Han *et al.* (2008)	Introduction	Japan	Dam	15	Fish	0.297	0.001
Scott *et al.* (2016)	Establishment	Canada	Flood-gate	NA	Fish	-0.182	0.328
Scott *et al.* (2016)	Establishment	Canada	Flood-gate	NA	Fish	-0.17	0.328
Scott *et al.* (2016)	Establishment	Canada	Flood-gate	NA	Fish	1.356	0.401
Scott *et al.* (2016)	Establishment	Canada	Flood-gate	NA	Fish	0.936	0.362
Scott *et al.* (2016)	Introduction	Canada	Flood-gate	NA	Fish	0.343	0.079
Thoni *et al.* (2014)	Introduction	USA	Dam	5	Fish	1.158	0.264
Beatty *et al.* (2009)	Establishment	USA	Low-head Dam	1.59	Fish	2.628	0.103
Beatty et al. (2009)	Establishment	USA	Low-head Dam	1.59	Fish	1.828	0.003
Brun *et al.* (1990)	Establishment	France	Dam	94	Fish	-1.146	0.497
Brun *et al.* (1990)	Establishment	France	Dam	94	Fish	1.68	0.577
Brun *et al.* (1990)	Establishment	France	Dam	94	Fish	-1.866	0.612
Brun *et al.* (1990)	Establishment	France	Dam	94	Fish	-0.741	0.456
Brun *et al.* (1990)	Establishment	France	Dam	94	Fish	1.535	0.552
Brun *et al.* (1990)	Establishment	France	Dam	94	Fish	0.8	0.461
Hasegawa (2017)	Spread	Japan	Low-head Dam	1	Fish	-1.898	0.225
Satake and Ueno (2013)	Introduction	Japan	Dam	16.03	Macro-inv.	0.808	0.367
Satake and Ueno (2013)	Introduction	Japan	Dam	16.03	Macro-invert.	1.423	0.516
Gao *et al.* (2019)	Introduction	China	Dam	181	Fish	2.8	0.845
Liu *et al.* (2019)	Establishment	China	Dam	NA	Fish	0.044	0.067
Liu *et al.* (2019)	Introduction	China	Dam	NA	Fish	0.323	0.068
Franssen and Tobler (2013)	Introduction	USA	Dam	44	Fish	0.672	0.81
Porto *et al.* (1999)	Spread	Canada	Dam	0.6	Fish	0.275	0.039
Porto *et al.* (1999)	Spread	Canada	Dam	0.6	Fish	-0.954	0.741
Rosewarne *et al.* (2013)	Spread	UK	Weir	1.3	Macro-invert.	0.434	0.019
Rosewarne *et al.* (2013)	Spread	UK	Weir	1.3	Macro-invert.	-0.099	0.022
Bestgen and Crist (2000)	Introduction	USA	Dam	153	Fish	0.48	0.139

Zhang *et al.* (2019)	Introduction	China	Dam	168.25	Fish	2.64	0.54
Zogaris *et al.* (2012)	Establishment	Cyprus	Dam	NA	Fish	1.086	0.044
Keefer *et al.* (2013)	Establishment	USA	Dam	77.3	Fish	1.285	0.528
Keefer *et al.* (2013)	Establishment	USA	Dam	77.3	Fish	0.64	0.462
Keefer *et al.* (2013)	Establishment	USA	Dam	77.3	Fish	0.638	0.462
Keefer *et al.* (2013)	Establishment	USA	Dam	77.3	Fish	0.631	0.462
Keefer *et al.* (2013)	Establishment	USA	Dam	77.3	Fish	0.633	0.462
Keefer *et al.* (2013)	Establishment	USA	Dam	77.3	Fish	0.63	0.462
Keefer *et al.* (2013)	Introduction	USA	Dam	77.3	Fish	4.505	1.514
Alexandre *et al.* (2013)	Establishment	Portugal	Dam	55	Fish	1.636	0.207
Alexandre *et al.* (2013)	Establishment	Portugal	Dam	94	Fish	0.476	0.16
Kwak *et al.* (2016)	Establishment	South Korea	Weir	6.9	Fish	1.092	0.434
Kwak *et al.* (2016)	Establishment	South Korea	Weir	6.9	Fish	0.36	0.384
Kwak *et al.* (2016)	Establishment	South Korea	Weir	6.9	Fish	0.102	0.379
Stuck *et al.* (2015)	Establishment	USA	Dam	NA	Fish	1.817	0.363
Linares *et al.* (2018)	Establishment	Brazil	Dam	10.3	Macro-invert.	0.772	0.242
Gottgens (2009)	Establishment	USA	Dam	2.5	Fish	0.584	0.296
Gottgens (2009)	Establishment	USA	Dam	2.5	Fish	1.097	0.327
Gottgens (2009)	Establishment	USA	Dam	2.5	Fish	-0.659	0.299
Gottgens (2009)	Establishment	USA	Dam	2.5	Fish	-1.849	0.405
Gottgens (2009)	Establishment	USA	Dam	2.5	Fish	-1.442	0.358
Gottgens (2009)	Introduction	USA	Dam	2.5	Fish	-0.317	0.288
Gottgens (2009)	Introduction	USA	Dam	2.5	Fish	-2.564	0.517
Clavero and Hermoso (2011)	Establishment	Spain	Dam	NA	Fish	1.103	0.05
Clavero and Hermoso (2011)	Establishment	Spain	Dam	NA	Fish	-0.242	0.034
Clavero and Hermoso (2011)	Establishment	Spain	Dam	NA	Fish	1.178	0.034
Clavero and Hermoso (2011)	Establishment	Spain	Dam	NA	Fish	1.377	0.05

Clavero and Hermoso (2011)	Establishment	Spain	Dam	NA	Fish	0.545	0.076
Clavero and Hermoso (2011)	Establishment	Spain	Dam	NA	Fish	1.087	0.098
Clavero and Hermoso (2011)	Establishment	Spain	Dam	NA	Fish	1.276	0.111
Clavero and Hermoso (2011)	Establishment	Spain	Dam	NA	Fish	-0.149	0.196
Clavero and Hermoso (2011)	Establishment	Spain	Dam	NA	Fish	-0.717	0.666
Gido *et al.* (2002)	Establishment	USA	Dam	47.9	Fish	2.401	0.678
Gido *et al.* (2002)	Establishment	USA	Dam	47.9	Fish	2.096	0.693
Rolls *et al.* (2011)	Establishment	Australia	Dam	40.5	Fish	-0.586	0.341

A.2 Diagnostic plots for meta-analysis

A2.1 Diagnostic plots for introduction

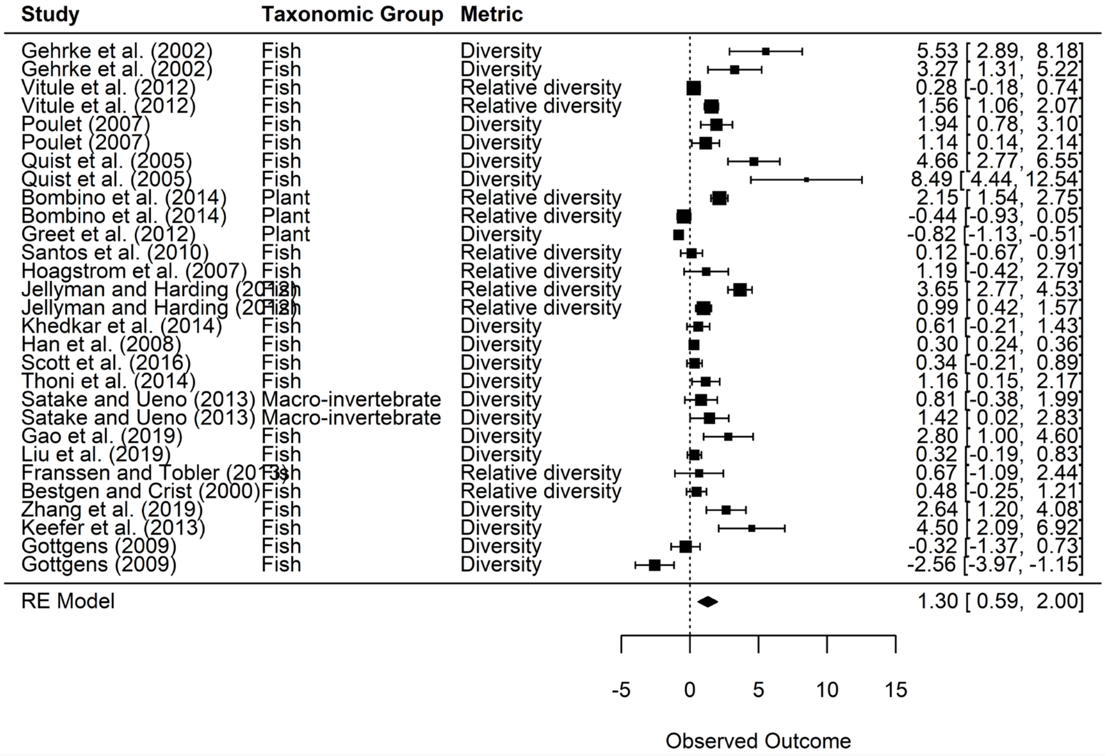


Figure A2.1 – Forest plot showing the effects of in-stream structures on the introduction of non-native species. Points represent weighted effect sizes (Hedge's g), with the size of the point reflecting the weight given. Error bars show 95% confidence intervals.

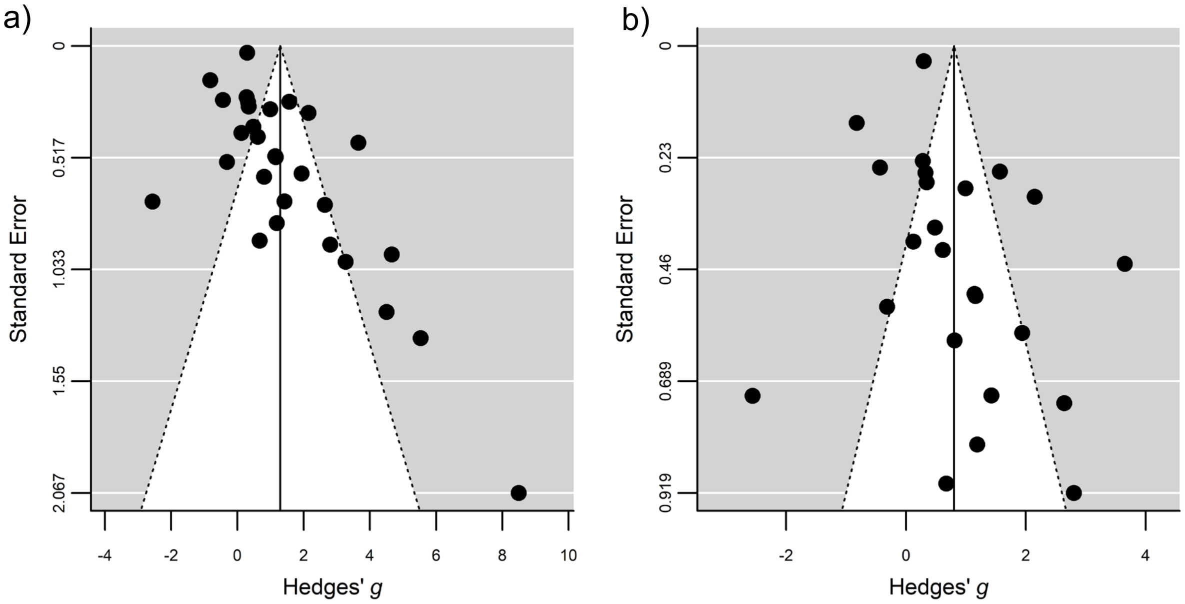


Figure A2.2 – Funnel plot showing the relationship between standard error and effect size (Hedge's *g*) for studies measuring the relationship between in-stream structures and the introduction of invasive species. a) shows the full dataset, and b) shows the dataset after the removal of high variance points.

A2.2 Diagnostic plots for establishment

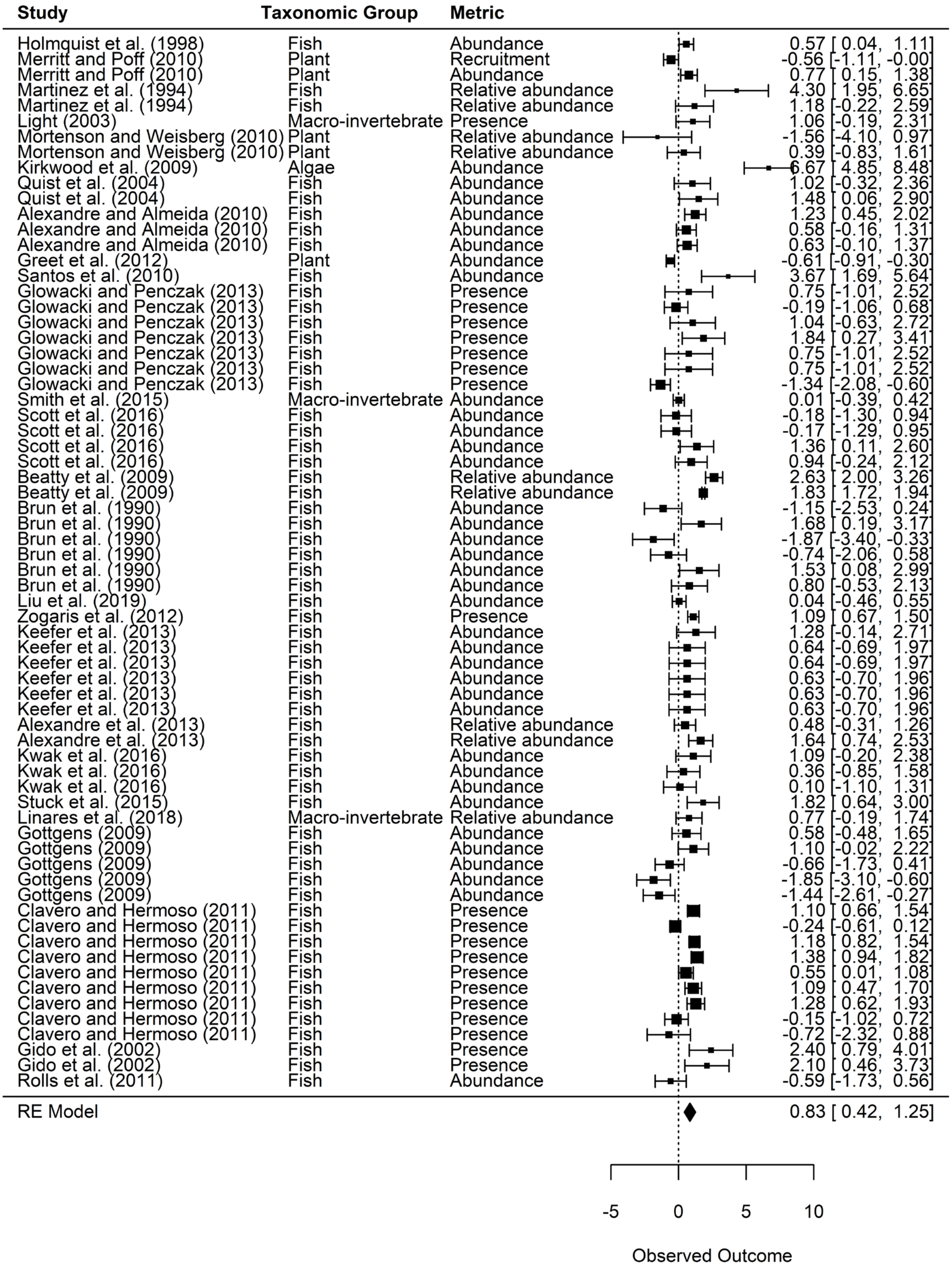


Figure A2.3 – Forest plot showing the effects of in-stream structures on the establishment of non-native species. Points represent weighted effect sizes (Hedge's *g*), with the size of the point reflecting the weight given. Error bars show 95% confidence intervals.

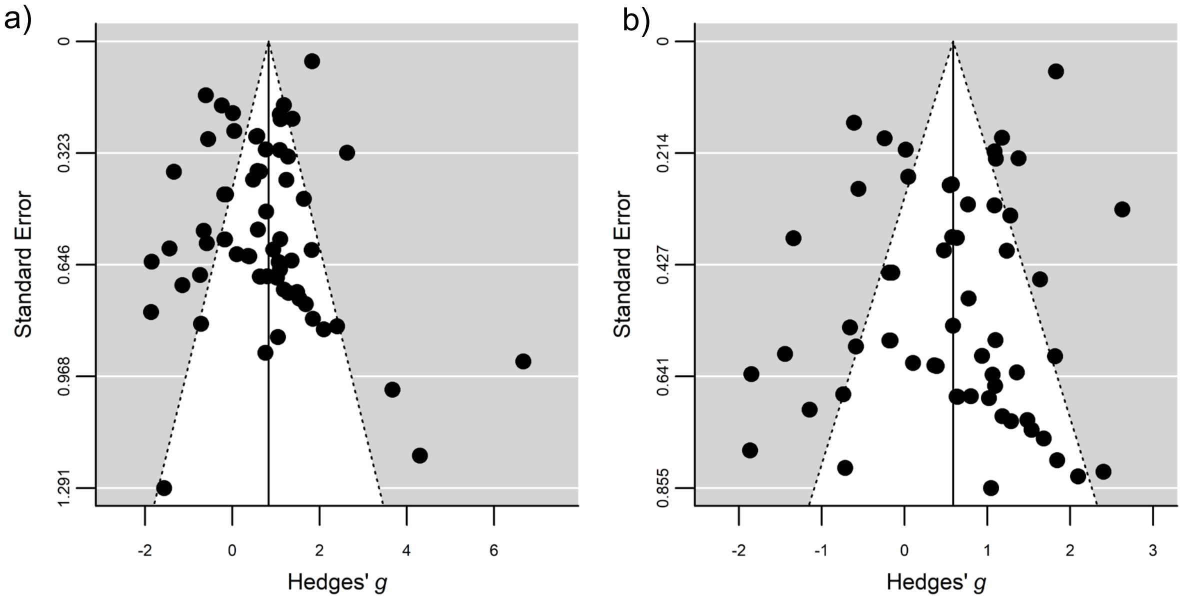
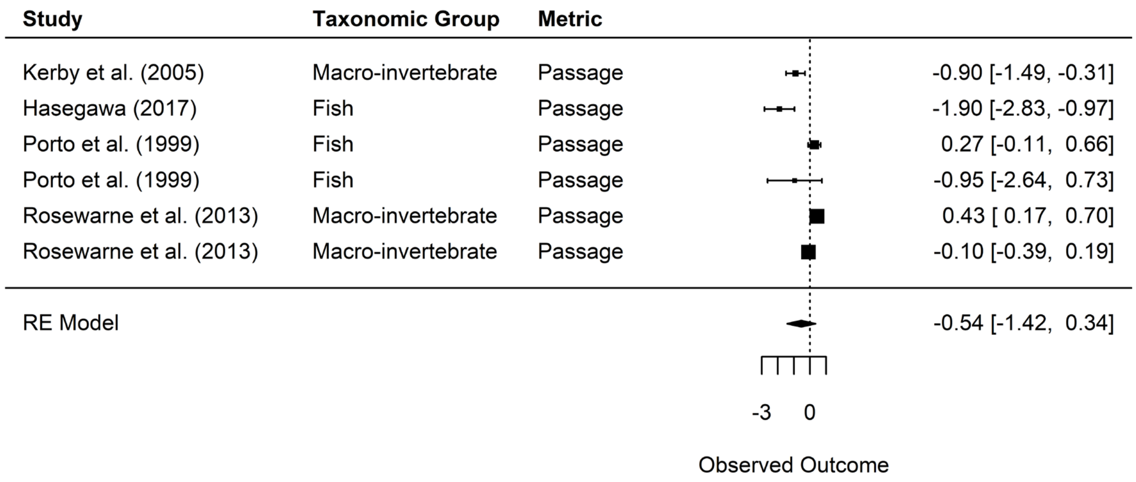


Figure A2.4 – Funnel plot showing the relationship between standard error and effect size (Hedge’s *g*) for studies measuring the relationship between in-stream structures and the establishment of invasive species. a) shows the full dataset, and b) shows the dataset after the removal of high variance points.

A2.3 Diagnostic plots for spread



Study	Taxonomic Group	Metric	
Kerby et al. (2005)	Macro-invertebrate	Passage	-0.90 [-1.49, -0.31]
Hasegawa (2017)	Fish	Passage	-1.90 [-2.83, -0.97]
Porto et al. (1999)	Fish	Passage	0.27 [-0.11, 0.66]
Porto et al. (1999)	Fish	Passage	-0.95 [-2.64, 0.73]
Rosewarne et al. (2013)	Macro-invertebrate	Passage	0.43 [0.17, 0.70]
Rosewarne et al. (2013)	Macro-invertebrate	Passage	-0.10 [-0.39, 0.19]
RE Model			-0.54 [-1.42, 0.34]

Figure A2.5 – Forest plot showing the effects of in-stream structures on the spread of non-native species. Points represent weighted effect sizes (Hedge’s *g*), with the size of the point reflecting the weight given. Error bars show 95% confidence intervals.

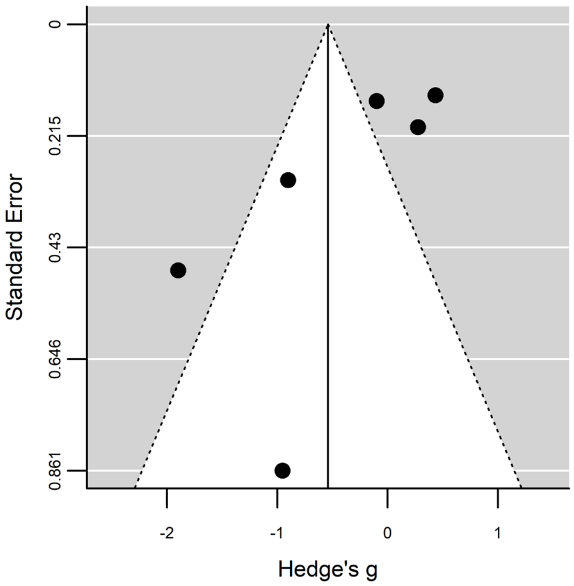


Figure A2.6 – Funnel plot showing the relationship between standard error and effect size (Hedge's *g*) for studies measuring the relationship between in-stream structures and the spread of invasive species.

Appendix B: Supplementary information for Chapter 5

B.1 Experimental evaluation of the effect of density on passage

B.1.1 Morphological characteristics of experimental crayfish

Table B1.1 – Results of statistical tests used to test for differences in morphological metrics between treatments in an experiment designed to test the effects of density on the behaviour of American signal crayfish at a model crump weir.

Metric	Statistical test (test statistic)	Test statistic value	*p*
Mass	Kruskal-Wallis (X^2)	1.913	0.591
Carapace length	Kruskal-Wallis (X^2)	1.292	0.731
Chela length	Kruskal-Wallis (X^2)	2.463	0.482
Proportion of females	One-Way ANOVA (F)	1.379	0.265

B.1.2 Details of experimental setup

A model crump weir (length = 2380 mm, width = 60 mm, height = 340 mm) with a 1:2 upstream slope and a 1:5 downstream slope was installed in an indoor recirculating flume (length = 16 m, width = 0.6 m, depth = 0.8 m) at the University of Southampton Boldrewood Innovation Campus. Screens were placed 1.67 m downstream and 0.4 m upstream of the leading edge and foot of the weir, respectively, to constrain crayfish within the experimental area. The base of the flume was covered with gravel to provide a semi-natural substrate. A removable barrier was also placed at the foot of the weir to create a 1 m^2 acclimation zone (Fig. B1.1a). The effect of density on crayfish passage over the weir was tested under four treatment conditions: 1, 5, 10, and 20 crayfish m^{-2}, representing the range found under natural conditions (Table B1.2). Crayfish density was measured within the acclimation zone, and was adjusted by changing the number of individuals used during each trial.

To track the movements of crayfish within the experimental area, four Passive Integrated Transponder (PIT) antennae (two coils of 2.5 mm^2 stranded copper wire) were placed laterally in the flume, with two antennae in the acclimation zone, one on the downstream face of the weir, and one on the upstream face (Fig. B1.1a). Each antenna was connected to a single multi-antenna half duplex (HDX) reader via an external tuning unit (Oregon RFID) and the system was powered using a 12 V leisure battery. The PIT system was tuned and tested daily. Longitudinal detection distances ranged from 140 mm – 171 mm. Downward facing infrared CCTV cameras (Swann Pro A850) were mounted 0.7 m above the acclimation area, downstream weir face, and weir crest to record crayfish behaviour in case of PIT system failure.

Table B1.2 – Densities of American signal crayfish (*Pacifastacus leniusculus*) reported under natural conditions.

Water Body	**Country**	**Density (crayfish m^{-2})**	**Reference**
River Wharfe	UK	20	Bubb *et al.* (2004)
River Ure	UK	1-2	Bubb *et al.* (2004)
River Wharfe	UK	0-24	Bubb *et al.* (2009)
River Great Ouse	UK	0.8-15.0	Guan and Wiles (1996)
River Great Ouse	UK	2.2-6.1	Guan (2000)
River Mura	Croatia	0.8-1.2	Hudina *et al.* (2011)
Umatilla River	USA	0-15	Wooster *et al.* (2012)
Bookill Gill Beck	UK	25-110.4	(Chadwick *et al.*, 2021)

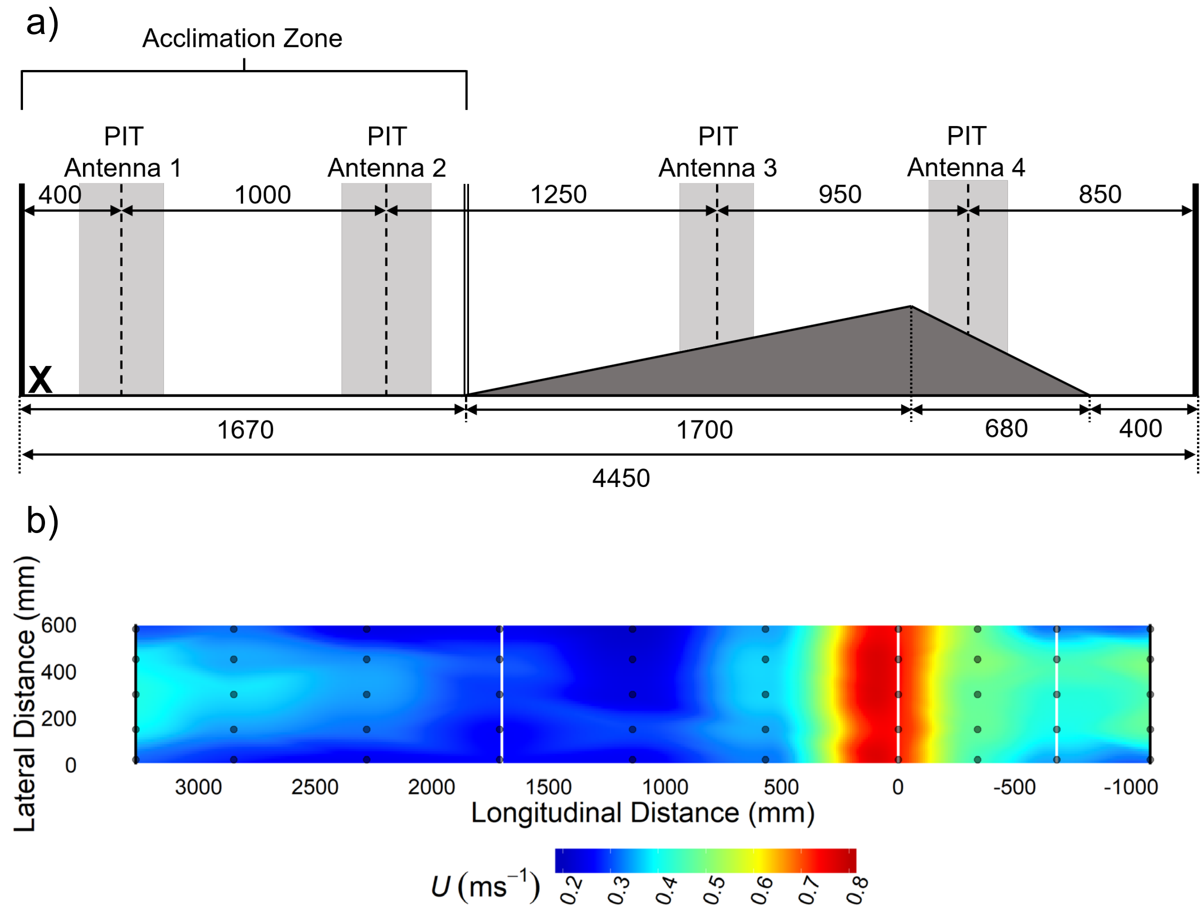


Figure B1.1 – a) Side view of the experimental area showing the model crump weir (dark grey), PIT antennae (dashed lines), PIT antennae detection distances (light grey shaded area), removable barrier at the foot of the weir (double line) and release location of the crayfish (cross). The flow of water is from right to left. b) Plan view flow velocity map of the experimental area used to determine how crayfish density affects movement and passage. Grey circles show measurement locations. From left to right, white lines denote the downstream end, crest and upstream end of the weir.

Discharge was kept constant at 0.065 m^3 s^{-1}, and a sloped overshot weir at the end of the flume was raised to create an upstream and downstream water depth of approximately 440 mm. These conditions were selected to mimic a previous study for which partial barrier passage was recorded (Kerr *et al.*, 2021). Flow velocity was measured using an electromagnetic flow meter (Valeport Model 801; measurements averaged over 10 seconds) at 50 locations in the experimental area, with all measurements taken 20 mm above the substrate (Fig. B1.1b). Water temperature in the flume was monitored throughout the study (mean = 20.7°C, SD = 0.78) and did not differ between treatments (One-way ANOVA: $F_{3,36} = 1.554$, $p = 0.217$).

B.2 ODD description of crayfish dispersal IBM

B.2.1 Purpose and patterns

The purpose of this model is to quantify the impacts of a partial riverine barrier on the longitudinal expansion rates of a high-impact freshwater invasive species (American signal crayfish, *Pacifastacus leniusculus*).

To determine whether the model was sufficient to meet this purpose, the rates of invasion predicted by the model with no barrier present were compared to those measured empirically in field studies. Numerous field studies have measured the longitudinal expansion rates of signal crayfish (Sibley, 2000; Bubb *et al.*, 2005; Peay *et al.*, 2009a; Bernardo *et al.*, 2011; Hudina *et al.*, 2013; Hudina *et al.*, 2017), and the model was considered appropriate if the predicted invasion rates fell within the range measured under natural conditions.

B.2.2 Entities, state variables and scales

Four entities were included in this model: 1) individual crayfish, 2) abundance areas (10m sections of the river for which density and biomass are calculated), 3) breeding areas (100m sections of river used for breeding calculations), and 4) the model environment (controls global variables that change over time). State variables for each entity are described in Table B2.1.

The model reflected a homogeneous single-channel virtual river of predetermined width (2 m) and length (70 km). River depth was discounted, as crayfish are benthic, and density was measured as a function of river area rather than volume. The model time step and duration were one day and 20 years (7300 time steps), respectively.

Table B2.1 – Descriptions of the state variables included in the individual-based model used to predict the longitudinal range expansion of American signal crayfish (*Pacifastacus leniusculus*).

Entity	State Variable	Description
Crayfish	**Model Parameters**	
	Crayfish ID	Unique number assigned to each crayfish.
	Morphometrics	
	Age	Age of each crayfish (days).
	Carapace length	Carapace length of each crayfish (mm).
	Mass	Mass of each crayfish (g).
	Sex	Sex of each crayfish (male or female).
	Movement parameters	
	Location	Location of the crayfish in the current timestep (river m).
	Movement	Total distance to be moved by the crayfish in the current time step (m).
	Upstream/Downstream	Random number between -1 and 1 applied to each crayfish to determine whether they were predetermined to move upstream (positive) or downstream (negative).
	Passer	Random number between 0 and 1 applied to each crayfish to determine their ability to pass a riverine barrier.
	Mortality Parameters	
	Probability of mortality	Probability of mortality for each crayfish.
	Reproduction Parameters	
	Pregnant	Binary indicator of whether the crayfish is pregnant or not.
	Gestation	If pregnant, the number of days the crayfish has been gestating for.
Abundance area	Density	The density of crayfish in the 10 m abundance area (individuals m^{-2}).
	Biomass	The biomass of crayfish in the 10 m section abundance area (g m^{-2}).
Breeding area	Number of males	The number of males present in the 100 m breeding area.
Model Environment	Days since start of the year (DOY)	The number of days since the start of the year at the current timestep.
	Year	Year at the current timestep.

B.2.3 Process overview and scheduling

At each time step (1 day), state variables were updated and seven key processes occurred in the following order:

1. Morphometric calculations
    - Crayfish age and gestation period were incremented by 1 day. Size variables (carapace length and mass), which were derived from crayfish age (section B.2.7.1), were recalculated.
2. Population calculations
    - Crayfish density and biomass were calculated for each abundance area (section B.2.7.2).
3. Movement
    - The distance to be moved by each crayfish was randomly assigned and then adjusted in accordance with local density, seasonal fluctuations, and predisposition to upstream/downstream movement. The location of the crayfish was then updated based on the movement distance (section B.2.7.3).
4. Barrier passage
    - These processes occurred only where updating the location of the crayfish took the individual from downstream of the barrier to upstream. If the value of the "passer" state variable was less than a predefined threshold (sex dependent) the crayfish were able to pass the barrier. If the passer variable exceeded the threshold, crayfish were reflected downstream (section B.2.7.4).
5. Mortality
    - The probability of mortality was calculated based on crayfish size and population density. A random number between 0 and 1 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 the predefined maximum age (7 years) (section B.2.7.5).
6. Reproduction
    - Females became pregnant if it was the breeding season, they were sexually mature and there was an adult male in the same 100 m breeding area (section B.2.7.6).
7. Population expansion
    - The location of the upstream and downstream invasion fronts were calculated, and used to derive the rates of population expansion (section B.2.7.7).

B.2.4 Design concepts

B.2.4.1 Basic principles

This model characterises the interaction between two key global freshwater stressors: invasive species and river infrastructure. These stressors are commonly considered in isolation, but there is increasing recognition that they interact, with river infrastructure providing a partial barrier to the spread of invasive species. Numerous studies have examined barrier passage by invasive species, but this model allows the interactions to be studied in greater detail at a larger spatio-temporal scale, and provides important information on the emergent effects of barriers on invasion dynamics.

B.2.4.2 Emergence

The longitudinal expansion rate of the signal crayfish population emerges largely from the distances moved by each crayfish at each timestep. However, crayfish movement varies between individuals and is dependent on season and density. Hence, longitudinal expansion rates are also partially emergent from processes such as growth, mortality, reproduction and time of year.

B.2.4.3 Adaptation

The behaviour of the crayfish was imposed through empirical rules, meaning they did not make adaptive decisions. Adaptation is reflected in the relationship between movement and population density (i.e., longer movements occur away from high density areas where mortality rates are high), meaning fitness-seeking is implicit in the model.

B.2.4.4 Objectives

Given that the agents in this model do not make adaptive decisions, defining objectives to evaluate decision alternatives was not necessary.

B.2.4.5 Learning

Agents in this model did not make adaptive decisions, and therefore did not change their decision making as a consequence of their experience.

B.2.4.6 Prediction

Agents in this model did not make adaptive decisions, and therefore were not required to predict the future outcomes of decisions.

B.2.4.7 Sensing

It was assumed that crayfish could perfectly sense the population density within their abundance area and the day of the year (DOY). It was also assumed that females could perfectly sense the presence of a male within their breeding area.

B.2.4.8 Interaction

In this model, the only direct interaction between agents was the process of reproduction, whereby adult females became pregnant if an adult male was present in the same breeding area. Indirect interactions (e.g., competition) were modelled through the inclusion of population density, which affected patterns of movement and mortality.

B.2.4.9 Stochasticity

Stochasticity is used at various points to assign the characteristics of the crayfish in the model. The age of the seed crayfish was randomly selected from a normal distribution with a mean of three years and a standard deviation of 0.3, and their sex was assigned randomly (1:1 ratio). Every crayfish generated in the model was assigned a random number between -1 and 1, with negative numbers representing crayfish predisposed to downstream movements, and positive numbers indicating a predisposition to upstream movements. Stochasticity was also employed to determine which crayfish were able to pass the barrier; each individual was assigned a random number between zero and one and was only able to pass if the number was less than a predefined threshold (see section B.2.7.4).

Stochasticity was also incorporated in the calculation of crayfish movement. At each time step, each crayfish was assigned a random number between zero and one, which was used to calculate movement distance (see section B.2.7.3 for details on calculations).

Finally, stochasticity was used to determine the crayfish to be removed from the model at each time step (i.e., mortality). A random number between zero and one was allocated to each agent at each time step, and the agent was removed if it was less than the pre-calculated probability of mortality (see section B.2.7.5).

B.2.4.10 Collectives

Crayfish in this model were assumed to act only as individuals, and no collectives were included (either implicitly or explicitly).

B.2.4.11 Observation

The model includes five main outputs, which are recorded at each time step:

1. The location of the upstream invasion front.
2. The location of the downstream invasion front.
3. The mean biomass within the invaded area (averaged across abundance areas).
4. The total number of crayfish alive in the model.
5. The total number of pregnant crayfish in the model.

The first two outputs were analysed further outside of the model and were used to address the overall purpose of the model (i.e., determining whether the partial barrier reduced the invasion rate). Other outputs were used to assess model performance.

B.2.5 Initialisation

The model started at year 0, day of the year (DOY) 150, with 100 seed crayfish (randomly allocated as either male or female at a 1:1 ratio) released into the river at river km 35. The age of the seed crayfish was randomly selected from a normal distribution with a mean of three years and a standard deviation of 0.3, and the size/mass of the crayfish was calculated from age (as described in section B.2.7.1).

At initialisation, the user was able to define the following parameters (**values used in this study emboldened in brackets**):

- The length of the virtual river in metres (**70,000**).
- River width in meters (**2**).
- The start date of the model in days since start of the year (**DOY 150**).
- The duration of the model in years (**20**).
- The number of seed crayfish at the start of the model (**100**).
- The mean age of the seed crayfish in years (**3**).
- The standard deviation of the age of the seed crayfish (**0.3**).
- The mid-point date of the breeding season in days since start of the year (**DOY 274**) – Derived from Holdich *et al.* (2014).
- The duration of the breeding season around the mid-point date in days (**15**)
    - *With the model settings used, breeding took place at DOY 274 ±15*
- The carapace length (mm) at which crayfish reached sexual maturity (**39**) – Derived from Guan and Wiles (1999).
- The number of days taken for gestation (**223**) - Derived from Holdich *et al.* (2014).
- The release location for the seed crayfish in metres (**35,000**).
- The location of the partial riverine barrier in metres (**upstream = 45,000, downstream = 25,000**).
- Whether to include the barrier in the model (**Yes**)
- Density dependent mortality constant (**0.0071**).

B.2.6 Input data

No external input data was required for this model.

B.2.7 Submodels

B.2.7.1 Morphometric calculations

At each time step, the age of each crayfish was increased by one day, and other morphological parameters were recalculated accordingly. Carapace length (*CL*, mm) of all individuals was calculated as a function of *Age* (years) based on fitting a power law to the age class and length data reported in Guan and Wiles (1999). The relationship between *CL* and age was similar for males and females (Guan & Wiles, 1999), so a single function ($CL = 23.669 \times Age^{0.614}$) was used for all crayfish in the model. *CL* was then used to calculate the wetted mass (*WM*, grams) of each individual using the function $WM = 0.00024 \times CL^{3.05263}$, which was derived from the exponential relationship reported by Guan and Wiles

(1999). *WM* was subsequently converted to dry mass (*DM*, grams) by applying a conversion factor (16.51 %) calculated from (Thompson *et al.*, 2005), who reported the moisture content of a morphologically similar crayfish species (red claw crayfish, *Cherax quadricarinatus*).

B.2.7.2 Population calculations

At each time step, the density (individuals m^{-2}) and biomass (g m^{-2}) of crayfish was calculated for each 10 m abundance area.

B.2.7.3 Movement

At each time step, the distance to be moved by each crayfish was calculated, and the crayfish were moved accordingly. After a thorough assessment of available literature (Bubb *et al.*, 2002; Bubb *et al.*, 2004, 2006a, b; Moorhouse & MacDonald, 2011b; Wutz & Geist, 2013; Johnson *et al.*, 2014; Anastácio *et al.*, 2015), it was decided that the baseline movement parameters for use in the model would be extracted from the comprehensive study undertaken by Bubb *et al.* (2004), who reported log/log fitted inverse power relationships between probability of occurrence (*P*) and movement distance (*MD*, metres) in both the upstream (MD_{u}) and downstream (MD_{d}) directions. The relationships presented by Bubb *et al.* (2004) were rearranged such that MD_{u} and MD_{d} could be calculated for any given *P* (random number between 0 and 1). A correction factor (*c*) was applied to both MD_{u} (c = -13.82 m) and MD_{d} (c = -12.90 m) to ensure the most frequently observed lowest *MD* values were equal to zero. Additionally, *MD* values were halved to reflect the one-day model time step vs. two-day sampling period used by Bubb *et al.* (2004). Finally, the upper extents of MD_{u} and MD_{d} were capped at 90 and 170 m respectively (the maximum recorded movement of signal crayfish distance in 24 hours; Bubb *et al.* (2004)), and values above the upper limit were randomly replaced with values from within the observed range. Thus, baseline movement distances were calculated using Equations B2.1 and B2.2.

$$MD_{\mathrm{u}}\,(0\,,90)\;=\;\left(exp\left(\;\frac{3.845-\ln(P)}{1.464}\;\right)-\;c\right)/\;2 \qquad \text{Equation. B2.1}$$

$$MD_{\mathrm{d}}\,(0\,,170)\;=\left(exp\left(\;\frac{3.161-\ln(P)}{1.236}\;\right)-\;c\right)/\;2 \qquad \text{Equation. B2.2}$$

Pilot model runs indicated that this approach resulted in all crayfish slowly moving downstream, likely due to a bias towards larger movements in this direction. To resolve this, crayfish were predetermined to be either upstream or downstream (1:1 ratio) movers (80% of their movement in one direction) with a small amount of directional inconsistency (20% of their movements in a random direction). This directional consistency is in line with that shown for signal (Bubb *et al.*, 2004) and white-clawed crayfish (Robinson *et al.*, 2000).

Density-dependent dispersal was incorporated in the model through the use of a density dependent scaling factor (DDS_{move}) that was applied to the *MD* values. It was assumed that the data extracted from Bubb *et al.* (2004) represented movement distances of individuals in a system near carrying capacity. Hence, at biomasses above carrying capacity DDS_{move} was equal to one, whereas at biomasses below carrying capacity, DDS_{move} was linearly proportional to biomass (DDS_{move} = biomass / 70.33; Fig. B2.1a).

To incorporate temperature-dependent dispersal, a temperature-dependent scaling factor (TDS_{move}) was applied in the form of a sinusoidal function (Equation B2.3) that varied between 0.1 and 1 at the start and middle of the year respectively (Fig. B2.1b).

$$TDS_{\text{move}} = 0.45 sin\left(2\pi\left(\frac{Julian\ Day}{365}\right) - 0.5\pi\right) + 0.55 \qquad \text{Equation B2.3}$$

Final movement distances (DTD_{move}) at each time step were calculated as a function of DDS_{move} and TDS_{move} using the formula $DTD_{\text{move}} = MD_{(\text{u, d})} \times DDS_{\text{move}} \times TDS_{\text{move}}$.

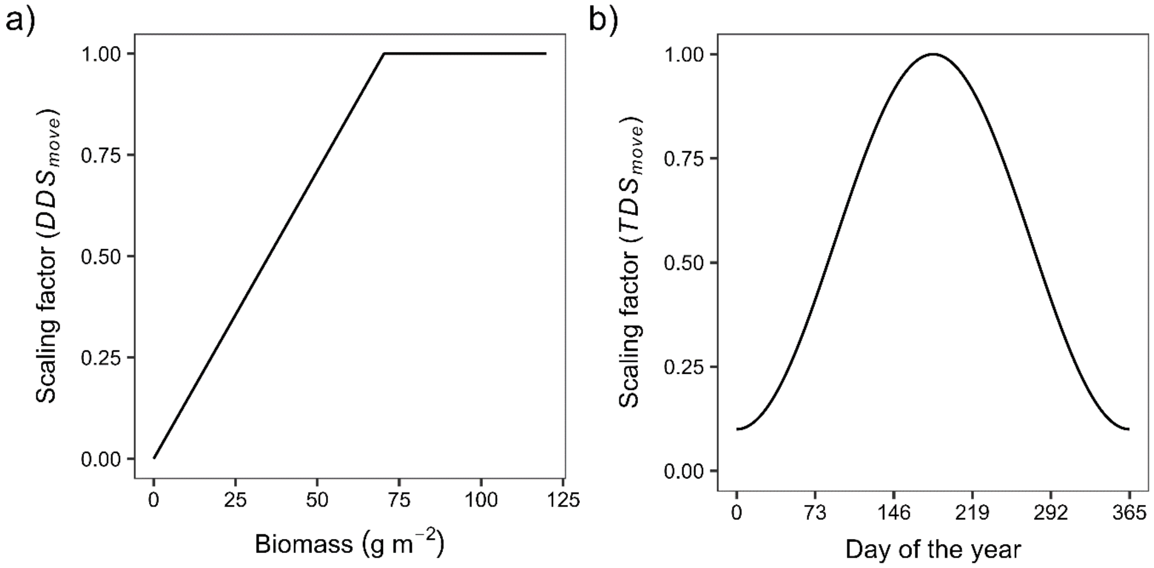


Figure B2.1 – Scaling factors used to implement (a) density-dependent movement and (b) temperature dependent movement of signal crayfish in the individual-based population dispersal model.

B2.7.4 Barrier passage

To mimic the levels of *in situ* upstream barrier passage (males: 22%; females 12%) reported by Rosewarne *et al.* (2013), each crayfish was pre-allocated a random number between 0 and 1, and only crayfish with a number < 0.22 for males and < 0.12 for females were able to ascend the barrier within the model. The same study recorded no difference in downstream passage over a weir compared to through a control reach, hence, in the model, downstream barrier passage was not restricted. For simplicity, it was assumed that changing seasonal discharge did not affect crayfish passage (as recorded by Rosewarne *et al.* (2013)), meaning upstream permeability of the barrier was constant throughout the year. It was also assumed that the influence of temperature on downstream passage recorded by Rosewarne *et al.* (2013) was already sufficiently incorporated into the model through the generic influence temperature has on crayfish movement (section B.2.7.3). Experimental results (described in main text) demonstrated that population density did not influence the ability of crayfish to pass a barrier, and therefore density-dependent passage was not included. Upstream moving crayfish that failed to pass the virtual barrier were reflected back downstream from the barrier a random distance between 0 and 20 m.

B.2.7.5 Mortality

At each time step, the probability of mortality for each crayfish was calculated based on size and population density. Despite a reasonable depth of literature on the population dynamics of signal crayfish, comprehensive mortality estimates for all age and size classes are lacking for this species. Therefore, annual mortality rate (M_a) was calculated as a function of DM using the equation $M_a = -0.26 \times \ln(DM) + 0.91$, sourced from McCoy and Gillooly (2008). This relationship was developed using data from 128 invertebrate species and, although not specific to signal crayfish, it represents a good approximation of the relationship between invertebrate size and survival. To match the one-day time step utilised in the model, M_a was converted to a daily mortality rate (M_d) using the equation $M_d = 1 – (1 – M_a)^{1/365}$.

Signal crayfish mortality is density-dependent, with competition for resources (Momot, 1984) and cannibalism (Houghton *et al.*, 2017) heavily influencing population dynamics. Density dependent mortality (M_{DD}) was incorporated in the model through the use of a scaling factor (DDS_{mort}) that magnifies M_d in high biomass sections ($M_{DD} = M_d \times DDS_{mort}$). The scaling factor was calculated as $DDS_{mort} = 1 + (k * \text{biomass})^{\alpha}$, where k and α are constants (k = 0.01, α = 10). Estimates of biomass for signal crayfish are infrequently reported, but Guan (2000) reported an annual mean biomass of 82 g m^{-2} and 33 g m^{-2} in pool and riffle habitats respectively. Additionally, Chadwick (2019) reported a biomass of 96 g m^{-2} in a British headwater stream. The mean of these reported biomass values (70.33 g m^{-2}) was used as the carrying capacity of the virtual river in the model, and k and α within DDS_{mort} were iteratively refined over multiple model runs to produce a modelled mean river biomass as close to 70.33 g m^{-2} as possible (mean biomass in model after >10 years: 70.25 g m^{-2}). To implement density-dependent mortality in the model, a random number (r) between zero and one was allocated to each agent at each time step, and the agent was removed if r was less than M_{DD}.

Early model runs indicated a small number of very old (12+ years) and thus very large (CL > 100 mm) individuals persisting in the model. Signal crayfish can live for up to 16 years (Holdich *et al.*, 2014), but demographic studies typically have not recorded significant numbers of individuals with CL greater than 69.2 mm (Guan & Wiles, 1996; Guan & Wiles, 1999) to 75 mm (Almeida *et al.*, 2013; Wutz & Geist, 2013). Thus, the morphometrics observed for older individuals in the model were unlikely to be representative of those in the wild, for which growth likely slows after a certain size is reached. For simplicity, crayfish were removed from the model after they reached seven years of age (CL = 78 mm).

B.2.7.6 Reproduction

In the model, females became pregnant if it was the breeding season, they were sexually mature and there was an adult male in the same 100 m breeding section. The breeding period was set between DOY 251 and 289, as mating is known to occur from late September to early October (Holdich *et al.*, 2014). Guan and Wiles (1999) suggested that crayfish can be classified as adults when *CL* exceeds 39 mm, and therefore all individuals with *CL* greater than this threshold were considered sexually mature in the model. Once females became pregnant, the eggs were incubated for a period of 223 days (the median egg incubation time identified by Holdich *et al.*, 2014), and then released at their current location. Fecundity (F) is related to size (Capurro *et al.*, 2015), and therefore the number of eggs released was calculated as a function of *CL* using the formula $F = 0.0436 \times CL^{2.2233}$. Juvenile crayfish were released at the same location as the mother at the end of gestation and were randomly allocated as male or female at a ratio of 1:1.

B.2.7.7 Calculation

The location of the upstream (IF_u) and downstream (IF_d) 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.

The number of crayfish alive, number of crayfish pregnant, and the total crayfish biomass were also calculated and included in the model output.

B.3 Additional information for model validation

To determine the validity of the model, a comprehensive literature search was undertaken to identify upstream, downstream, and total linear expansion rates of signal crayfish reported under natural conditions (Table B3.1).

Table B3.1 – Mean upstream, downstream and total linear expansion [TLER] invasion rates since introduction of American signal crayfish (*Pacifastacus leniusculus*) reported in previous studies and compared to the rates predicted by the individual-based model over a comparable time period.

				Invasion rate (km year^{-1})			
Study	River	Country	Time period (years)	Downstream	Upstream	TLER	U:D ratio
Bernardo *et al.* (2011)	River Maçãs	Portugal	15.5	2.77	1.68	4.45	1:1.65
Bubb *et al.* (2005)	River Wharfe	UK	13	1.80	0.41	2.21	1:4.39
Bubb *et al.* (2005)	River Ure	UK	7	0.18	0.06	0.24	1:3.00
Peay *et al.* (2009a)	Bookill Gill Beck	UK	13	0.26	0.046	0.31	1:5.65
Hudina *et al.* (2013), Hudina *et al.* (2017)	Korana River	Croatia	4	3.63	2.68	6.30	1:1.35
(Sibley, 2000)[1]	Gaddesby Brook	UK	10	0.6	-	-	-
Model	**Model**	**NA**	**10.4**	**1.07**	**0.73**	**1.81**	**1:1.46**

1: Crayfish only introduced to the upper reaches of the brook, so no upstream invasion rates were reported.

B.4 Impacts of a downstream barrier

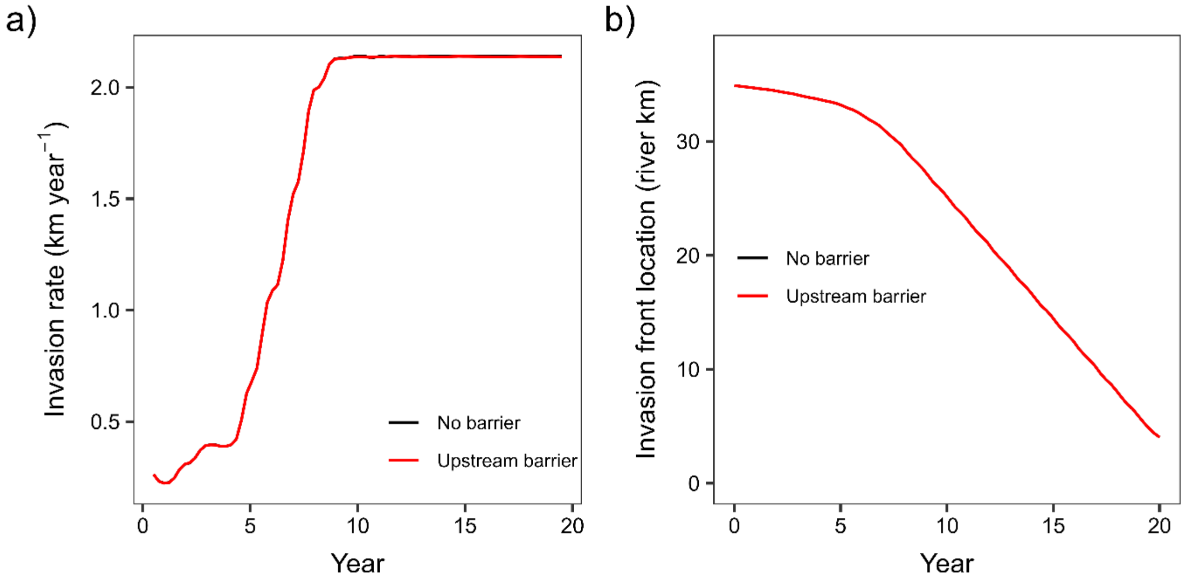


Figure B4.1 - The results of the individual-based population dispersal model for the no barrier and downstream barrier scenario, showing the (a) differences in invasion rate, and (b) location of the invasion front over time.

Appendix C – Supplementary information for Chapter 6

C.1 Repeatability of personality traits

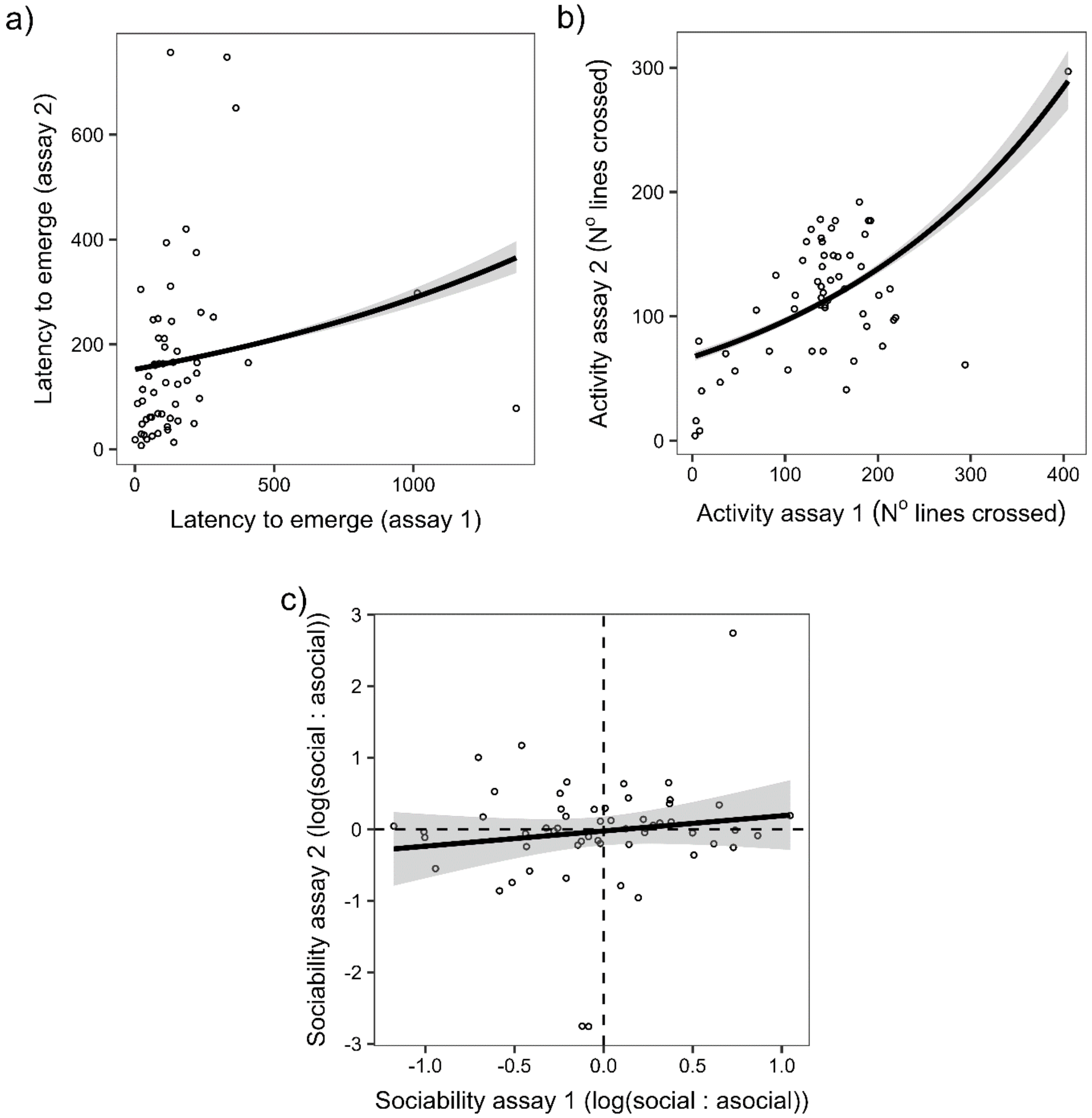


Figure C1.1 – Repeatability of a) boldness, b) activity, and c) sociability in signal crayfish (*Pacifastacus leniusculus*), displayed as the relationship between trait values in the first and second assays. Black lines represent GLM predictions, with grey shaded areas representing 95% confidence intervals.

C.2 Boldness-activity syndrome

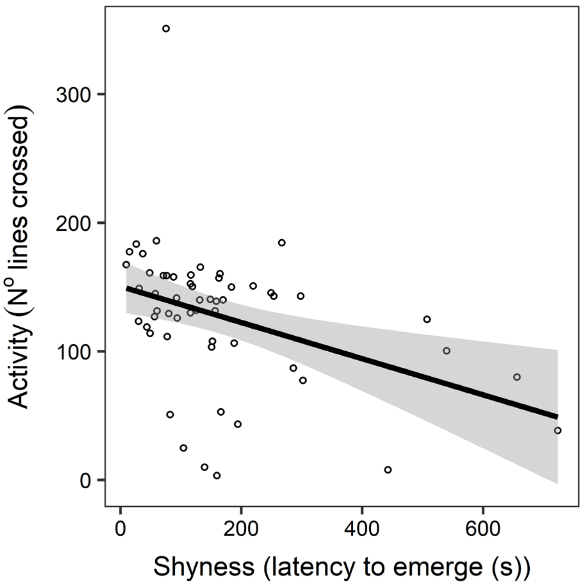


Figure C2.1 – Relationship between boldness and activity of American signal crayfish (*Pacifastacus leniusculus*), indicating the presence of a boldness-activity syndrome. The black line represents GLM predictions, with grey shaded areas representing 95% confidence intervals.

C.3 Time to first attempt

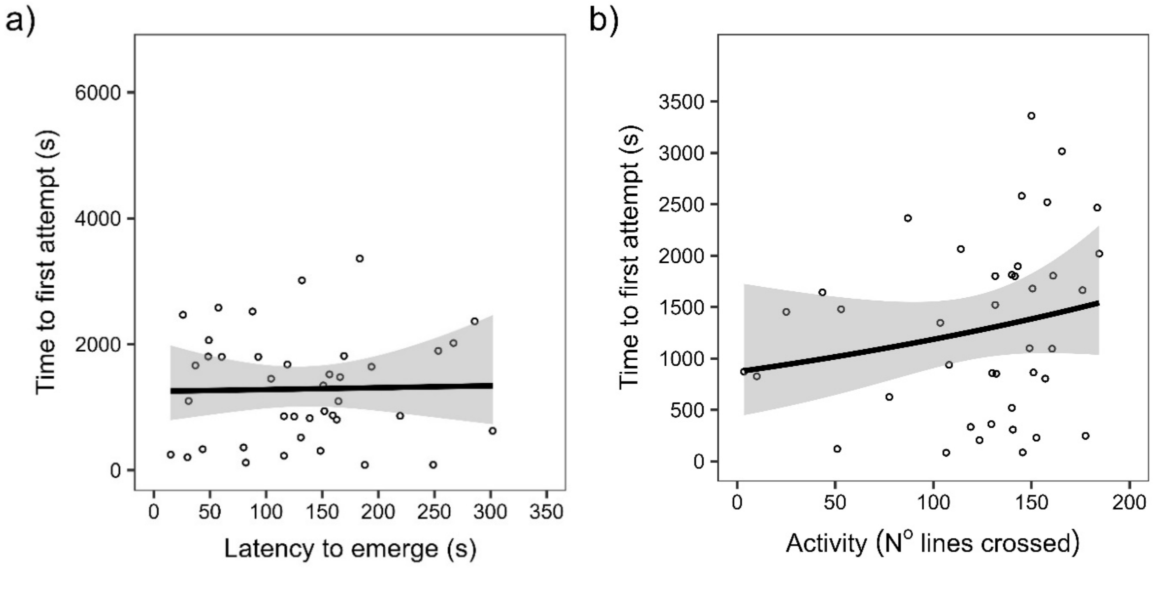


Figure C3.1 – The relationship between a) boldness, and b) activity with the time taken for American signal crayfish (*Pacifastacus leniusculus*) to attempt to pass an experimental in-stream barrier. In these figures, individuals which did not attempt to pass the barrier within the experimental period have been removed.

Appendix D: Supplementary information for Chapter 7

D.1 Keywords for image validation using Google Cloud Vision

D.1.1 Boating

Boat, Watercraft, Boats and boating--Equipment and supplies, Ship, Boating, Canoe, Skiff, Sailboat, Paddle, Oar, Rowing, Watercraft rowing, Canoeing, Kayaking, Kayak, Canoe slalom, Whitewater kayaking, Sea kayak, Longship, Gondola, Dinghy sailing, Sailing, Sail, Windsports, Speedboat, Picnic boat, Tall ship, Full-rigged ship, Windjammer, Barque, Training ship, Carrack, Barquentine, Sloop-of-war, Clipper, Sailing ship, East Indiaman, Galiot, Galleon, Brig, Baltimore clipper, Brigantine, Flagship, Steamboat, Keelboat, Yacht racing, Scow, Dinghy, Yawl, Smack, Sloop, Dhow, Passenger ship, Royal yacht, Cargo ship, Skerry, Feeder ship, Container ship, Royal mail ship, Cruiseferry, Cruise ship, Inflatable boat, Drag boat racing, Powerboating, Hydroplane racing, F1 Powerboat Racing, Personal water craft.

D.1.2 Angling

Recreational fishing, Pole, Fisherman, Casting (fishing), Angling, Fishing rod, Fishing, Fly fishing, Rock fishing.

Appendix E: Supplementary information for Chapter 8

E.1 River Glaven segment map

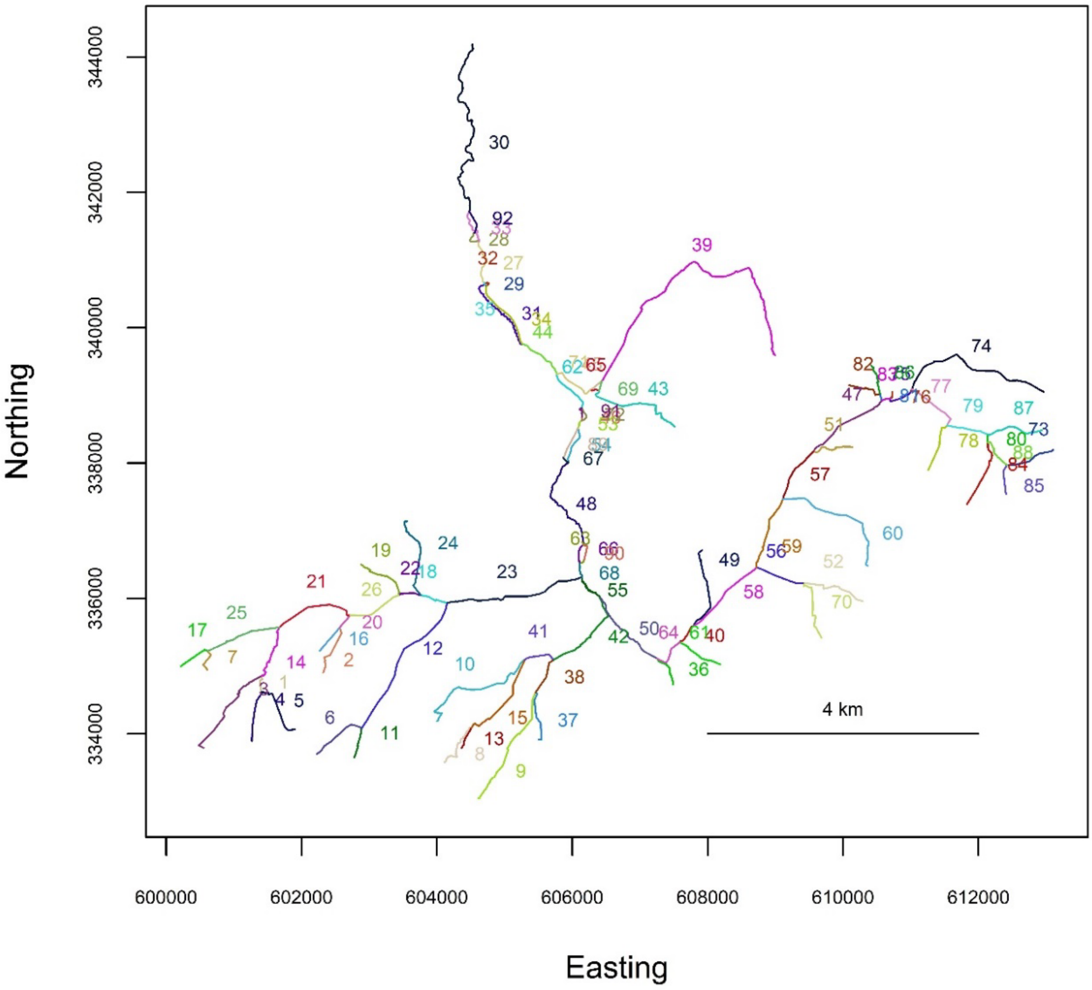


Figure E1.1 – Map of the river Glaven catchment (Norfolk, UK), showing the individual river segments (unbranching sections of river bounded by a confluence or the end of the river network) which acted as sub-units in an individual-based model that predicted the spread of American signal crayfish (*Pacifastacus leniusculus*).

E.2 Super-individual diagnostic plots

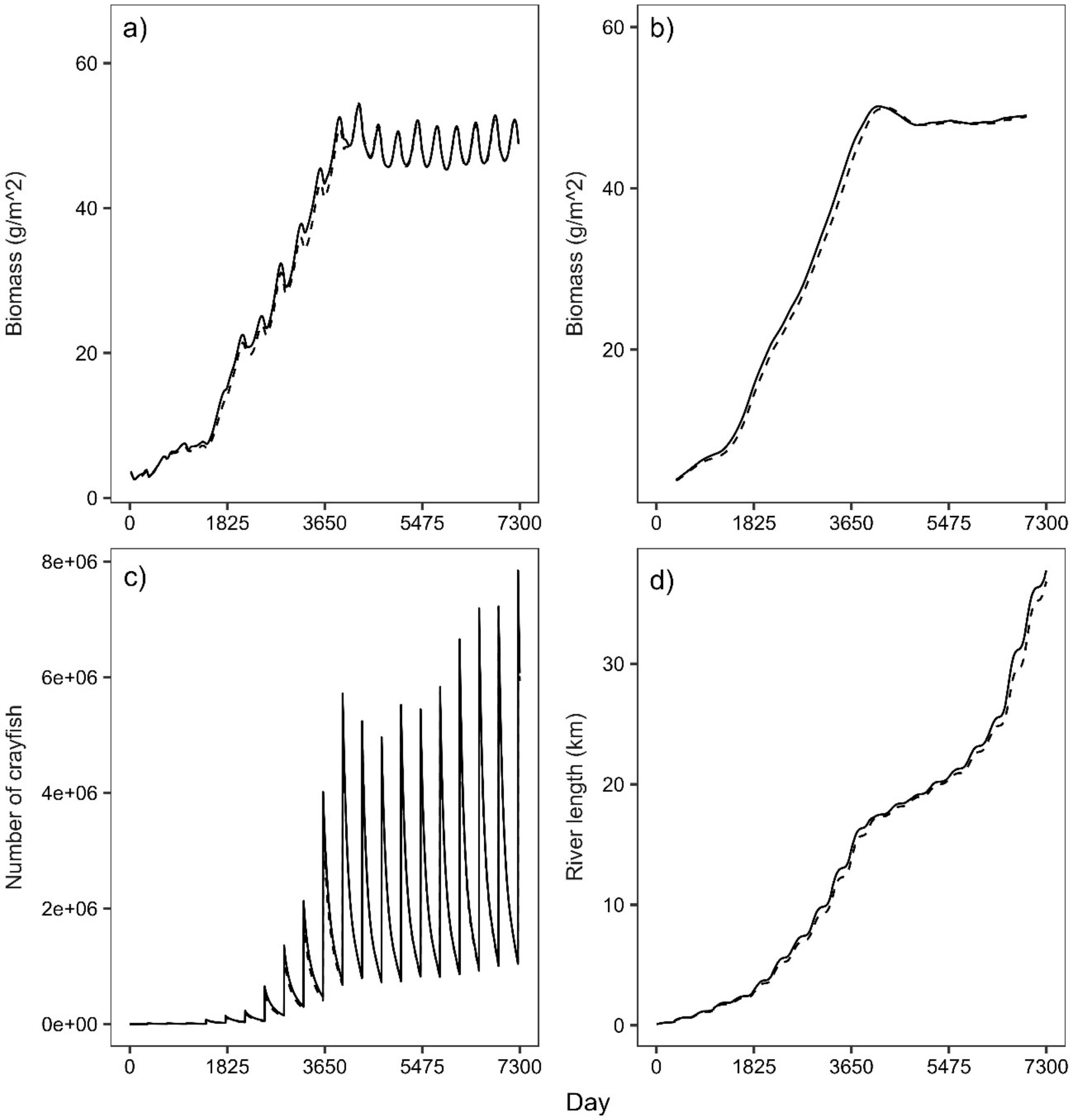


Figure E2.1 - Comparison of the performance of an individual-based model used to predict the spread of American signal crayfish (Pacifastacus leniusculus) over a 20-year period with (solid lines) and without (dashed lines) juveniles being considered as super-individuals (each super-individual representing 6 individuals). Diagnostics shown are a) mean model biomass (rolling average over 20 days), b) mean model biomass (rolling average over 365 days), c) total number of crayfish represented in the model, and d) the total length of river occupied by signal crayfish.

E.3 Flow scaling factor

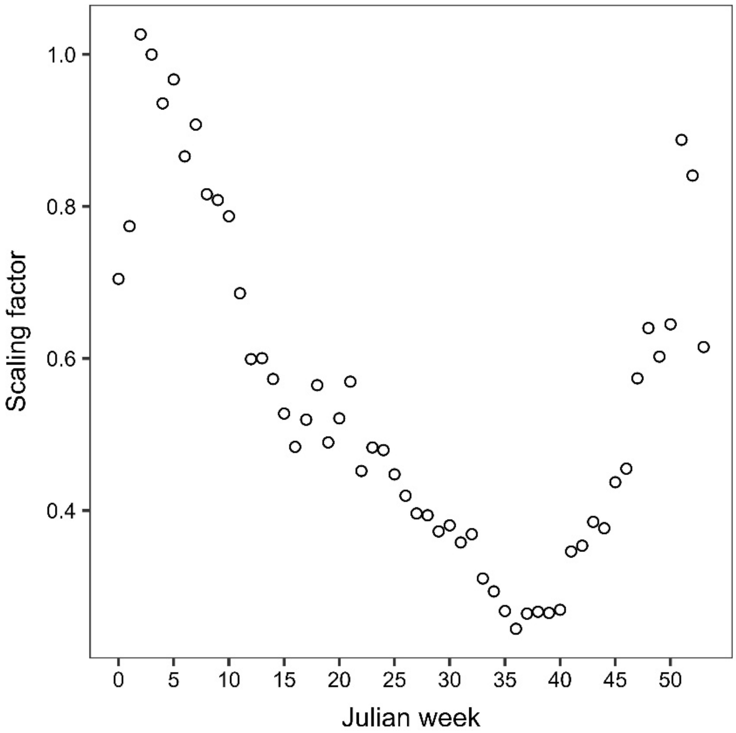


Figure E3.1 – Flow scaling factor used to account for seasonal variation in flow rates in an individual-based model to predict the spread of American signal crayfish (*Pacifastacus leniusculus*).

E.4 Accessibility-weighted habitat availability calculations

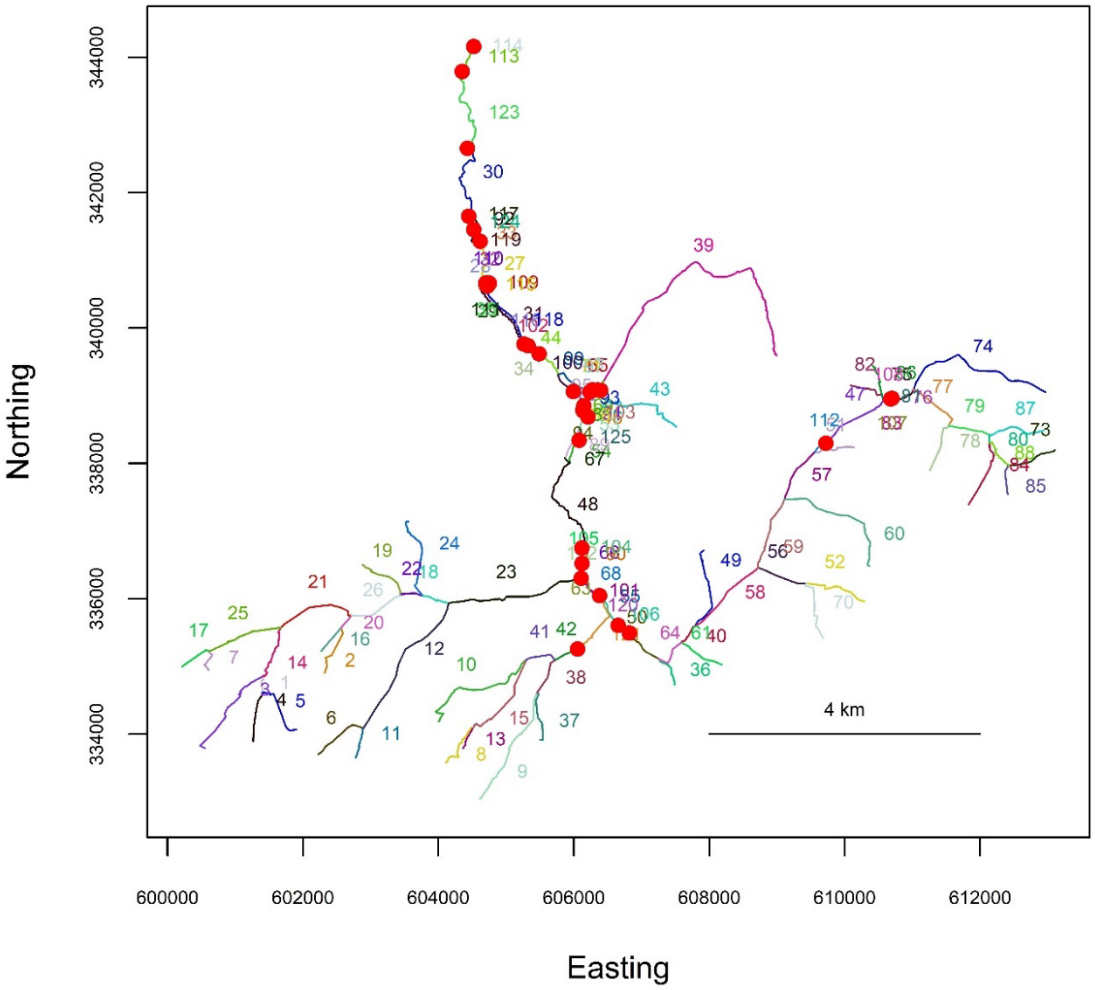


Figure E4.1 - Map of the River Glaven catchment (Norfolk, UK), showing the individual river segments (unbranching sections of river bounded by confluences, barriers (red points) or the end of the river network) which were used to calculate accessibility-weighted habitat availability for three native fish species.

E.5 Value functions

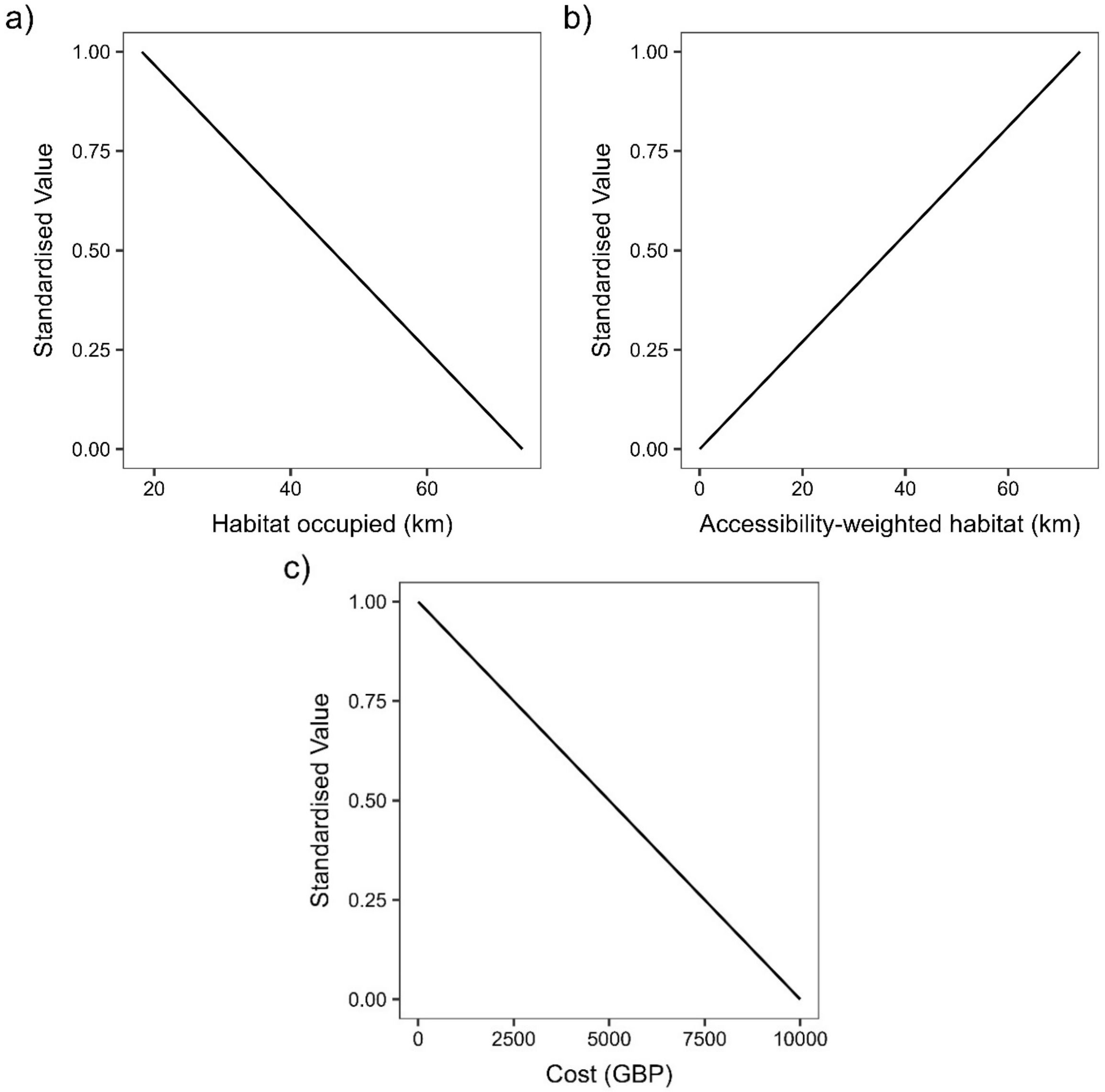


Figure E5.1 – Linear value functions used to standardise raw data from criteria assessments conducted as part of a multi-criteria decision analysis aiming to quantify the trade-offs associated with modifying riverine barriers to limit the upstream spread of American signal crayfish (*Pacifastacus leniusculus*). Criteria assessed and subsequently standardised are: a) length of river habitat occupied by signal crayfish, b) accessibility-weighted habitat availability for native fishes, and c) total cost of the modifications.

E.6 MCDA rankings

Table E6.1 – Ranked results of a multi-criteria decision analysis aiming to identify a combination of barrier modifications in the River Glaven catchment (Norfolk, UK) that limited the spread of invasive American signal crayfish (*Pacifastacus leniusculus*) while minimising cost and impacts on native fish.

		Weighted standardised scores					
Rank	Barriers modified	Invaded length	Trout AWHA	Lamprey AWHA	Eel AWHA	Cost	Score
1	GLA14	0.1917	0.0061	0.0066	0.023	0.0283	0.2557
2	GLA12, GLA13, GLA31	0.1791	0.006	0.0066	0.0182	0.0337	0.2436
3	GLA14, GLA21	0.1872	0.0061	0.0066	0.023	0.02	0.243
4	GLA21	0.1035	0.0061	0.0066	0.0246	0.1017	0.2426
5	GLA13, GLA14	0.1954	0.0061	0.0066	0.0183	0.0151	0.2414
6	GLA12, GLA13, GLA30	0.1812	0.0061	0.0066	0.0182	0.0267	0.2387
7	GLA12, GLA14	0.1951	0.0061	0.0066	0.0229	0.0076	0.2383
8	GLA14, GLA15	0.1908	0.0061	0.0066	0.023	0.009	0.2356
9	GLA32	0.1899	0.0061	0.0066	0.0236	0.0079	0.2341
10	GLA12, GLA13, GLA21, GLA30	0.1842	0.0061	0.0066	0.0182	0.0184	0.2335
11	GLA13, GLA14, GLA21	0.1953	0.0061	0.0066	0.0183	0.0068	0.233
12	GLA12, GLA13, GLA21, GLA31	0.1746	0.006	0.0066	0.0182	0.0254	0.2309
13	GLA14, GLA15, GLA21	0.1902	0.0061	0.0066	0.023	8.00E-04	0.2267
14	GLA13, GLA21	0.1039	0.0061	0.0066	0.0183	0.0885	0.2234
15	GLA15, GLA21	0.1032	0.0061	0.0066	0.0246	0.0825	0.223
16	GLA12, GLA13, GLA15, GLA30	0.1846	0.0061	0.0066	0.0182	0.0074	0.2228
17	GLA12, GLA21	0.1038	0.0061	0.0066	0.0245	0.081	0.2221
18	GLA12, GLA13, GLA15, GLA31	0.1752	0.006	0.0066	0.0182	0.0144	0.2205
19	GLA12, GLA13	0.1124	0.0061	0.0066	0.0182	0.076	0.2193
20	GLA21, GLA31	0.1199	0.0061	0.0066	0.024	0.0594	0.216
21	GLA12, GLA13, GLA21	0.1141	0.0061	0.0066	0.0182	0.0678	0.2127

22	GLA12, GLA13, GLA15, GLA21, GLA31	0.1718	0.006	0.0066	0.0182	0.0062	0.2088
23	GLA13, GLA21, GLA31	0.1289	0.006	0.0066	0.0183	0.0462	0.206
24	GLA13, GLA15, GLA21	0.104	0.0061	0.0066	0.0183	0.0692	0.2042
25	GLA16, GLA21	0.1034	0.0061	0.0066	0.0246	0.0632	0.2039
26	GLA12, GLA15, GLA21	0.1037	0.0061	0.0066	0.0245	0.0617	0.2027
27	GLA12, GLA13, GLA15	0.1134	0.0061	0.0066	0.0182	0.0568	0.2011
28	GLA13	0.0717	0.0061	0.0066	0.0183	0.0968	0.1994
29	GLA15, GLA21, GLA31	0.1197	0.0061	0.0066	0.024	0.0401	0.1965
30	GLA12, GLA21, GLA31	0.1195	0.0061	0.0066	0.0239	0.0387	0.1948
31	GLA21, GLA30	0.1041	0.0061	0.0066	0.0232	0.0524	0.1924
32	GLA12, GLA13, GLA15, GLA21	0.1122	0.0061	0.0066	0.0182	0.0485	0.1915
33	GLA12, GLA13, GLA36	0.1525	0.0061	0.0066	0.0181	0.0069	0.1901
34	GLA13, GLA15, GLA21, GLA31	0.1292	0.006	0.0066	0.0183	0.0269	0.1871
35	GLA13, GLA30	0.1067	0.0061	0.0066	0.0183	0.0474	0.185
36	GLA13, GLA16, GLA21	0.1041	0.0061	0.0066	0.0183	0.05	0.185
37	GLA15, GLA16, GLA21	0.1036	0.0061	0.0066	0.0246	0.0439	0.1849
38	GLA12, GLA16, GLA21	0.1037	0.0061	0.0066	0.0245	0.0424	0.1835
39	GLA13, GLA31	0.0949	0.006	0.0066	0.0183	0.0545	0.1803
40	GLA12, GLA15, GLA21, GLA31	0.1239	0.0061	0.0066	0.0239	0.0194	0.1799
41	GLA30	0.0833	0.0061	0.0066	0.0232	0.0606	0.1798
42	GLA13, GLA15	0.0713	0.0061	0.0066	0.0183	0.0775	0.1797
43	GLA12, GLA13, GLA16	0.1111	0.0061	0.0066	0.0182	0.0375	0.1795

44	GLA16, GLA21, GLA31	0.1197	0.0061	0.0066	0.024	0.0209	0.1773
45	GLA13, GLA21, GLA30	0.107	0.0061	0.0066	0.0183	0.0392	0.1771
46	GLA21, GLA36	0.1039	0.0061	0.0066	0.0245	0.0326	0.1737
47	GLA15, GLA21, GLA30	0.1042	0.0061	0.0066	0.0232	0.0331	0.1732
48	None	0.0242	0.0061	0.0066	0.0249	0.11	0.1719
49	GLA12	0.045	0.0061	0.0066	0.0248	0.0893	0.1718
50	GLA12, GLA21, GLA30	0.1043	0.0061	0.0066	0.0231	0.0316	0.1718
51	GLA12, GLA30	0.096	0.0061	0.0066	0.0231	0.0399	0.1718
52	GLA12, GLA13, GLA16, GLA21	0.1113	0.0061	0.0066	0.0182	0.0292	0.1714
53	GLA13, GLA16, GLA21, GLA31	0.1284	0.006	0.0066	0.0183	0.0076	0.167
54	GLA13, GLA15, GLA16, GLA21	0.104	0.0061	0.0066	0.0183	0.0307	0.1657
55	GLA13, GLA30, GLA31	0.1295	0.006	0.0066	0.0183	0.0051	0.1655
56	GLA13, GLA15, GLA30	0.1053	0.0061	0.0066	0.0183	0.0281	0.1644
57	GLA12, GLA15, GLA16, GLA21	0.1037	0.0061	0.0066	0.0245	0.0232	0.1642
58	GLA12, GLA13, GLA15, GLA16	0.1148	0.0061	0.0066	0.0182	0.0182	0.1639
59	GLA21, GLA30, GLA31	0.1183	0.0061	0.0066	0.0225	0.01	0.1636
60	GLA13, GLA15, GLA31	0.0958	0.006	0.0066	0.0183	0.0352	0.1619
61	GLA15, GLA30	0.0844	0.0061	0.0066	0.0232	0.0414	0.1616
62	GLA13, GLA16	0.0722	0.0061	0.0066	0.0183	0.0582	0.1614
63	GLA12, GLA16, GLA21, GLA31	0.1233	0.0061	0.0066	0.0239	1.00E-04	0.16
64	GLA13, GLA15, GLA21, GLA30	0.1074	0.0061	0.0066	0.0183	0.0199	0.1582
65	GLA15, GLA16, GLA21, GLA31	0.1182	0.0061	0.0066	0.024	0.0016	0.1565

66	GLA13, GLA21, GLA36	0.1043	0.0061	0.0066	0.0182	0.0193	0.1544
67	GLA15, GLA21, GLA36	0.1037	0.0061	0.0066	0.0245	0.0133	0.1542
68	GLA16, GLA21, GLA30	0.1042	0.0061	0.0066	0.0232	0.0138	0.154
69	GLA15	0.0253	0.0061	0.0066	0.0249	0.0907	0.1536
70	GLA12, GLA13, GLA15, GLA16, GLA21	0.1123	0.0061	0.0066	0.0182	0.01	0.1531
71	GLA30, GLA31	0.0991	0.0061	0.0066	0.0225	0.0183	0.1527
72	GLA12, GLA21, GLA36	0.1037	0.0061	0.0066	0.0244	0.0118	0.1526
73	GLA12, GLA15, GLA21, GLA30	0.1043	0.0061	0.0066	0.0231	0.0124	0.1524
74	GLA12, GLA15, GLA30	0.0959	0.0061	0.0066	0.0231	0.0206	0.1523
75	GLA12, GLA31	0.0656	0.0061	0.0066	0.0242	0.0469	0.1494
76	GLA12, GLA15	0.0405	0.0061	0.0066	0.0248	0.07	0.148
77	GLA31	0.0433	0.0061	0.0066	0.0243	0.0677	0.1479
78	GLA13, GLA16, GLA30	0.1066	0.0061	0.0066	0.0183	0.0089	0.1464
79	GLA13, GLA36	0.0856	0.0061	0.0066	0.0182	0.0276	0.144
80	GLA21, GLA33	0.1035	0.0061	0.0066	0.022	0.0055	0.1437
81	GLA16, GLA30	0.0829	0.0061	0.0066	0.0232	0.0221	0.1409
82	GLA13, GLA15, GLA16	0.0697	0.0061	0.0066	0.0183	0.039	0.1396
83	GLA13, GLA16, GLA21, GLA30	0.1073	0.0061	0.0066	0.0183	6.00E-04	0.1389
84	GLA13, GLA16, GLA31	0.0905	0.006	0.0066	0.0183	0.0159	0.1373
85	GLA13, GLA15, GLA21, GLA36	0.1042	0.0061	0.0066	0.0182	1.00E-04	0.135
86	GLA12, GLA16, GLA30	0.0964	0.0061	0.0066	0.0231	0.0013	0.1336
87	GLA16	0.0233	0.0061	0.0066	0.0249	0.0714	0.1324
88	GLA12, GLA16	0.0411	0.0061	0.0066	0.0248	0.0507	0.1294

89	GLA12, GLA15, GLA31	0.0634	0.0061	0.0066	0.0242	0.0276	0.1279
90	GLA13, GLA15, GLA36	0.0879	0.0061	0.0066	0.0182	0.0083	0.127
91	GLA15, GLA31	0.0399	0.0061	0.0066	0.0243	0.0484	0.1253
92	GLA36	0.0454	0.0061	0.0066	0.0248	0.0408	0.1237
93	GLA15, GLA16, GLA30	0.0844	0.0061	0.0066	0.0232	0.0028	0.1231
94	GLA15, GLA16	0.0282	0.0061	0.0066	0.0249	0.0522	0.118
95	GLA12, GLA36	0.0582	0.0061	0.0066	0.0247	0.0201	0.1157
96	GLA12, GLA15, GLA16	0.0442	0.0061	0.0066	0.0248	0.0314	0.1131
97	GLA13, GLA33	0.0789	0.0061	0.0066	0.0183	6.00E-04	0.1104
98	GLA16, GLA31	0.0433	0.0061	0.0066	0.0243	0.0291	0.1094
99	GLA12, GLA15, GLA36	0.0673	0.0061	0.0066	0.0247	8.00E-04	0.1055
100	GLA15, GLA36	0.0428	0.0061	0.0066	0.0248	0.0215	0.1019
101	GLA12, GLA16, GLA31	0.0546	0.0061	0.0066	0.0242	0.0084	0.0999
102	GLA16, GLA36	0.0454	0.0061	0.0066	0.0248	0.0023	0.0852
103	GLA15, GLA16, GLA31	0.0379	0.0061	0.0066	0.0243	0.0098	0.0847
104	GLA33	0.0249	0.0061	0.0066	0.0223	0.0138	0.0737

E.7 Forecast period sensitivity analysis

Table E7.1 – The rank of different alternatives (barrier modifications) after a variety of different time periods, undertaken as part of a sensitivity analysis during a multi-criteria decision analysis aiming to identify the optimal combination of barrier modifications in the river Glaven catchment (Norfolk, UK).

	Ranking after forecast period		
Barriers Modified	5-year	10-year	15-year
GLA14	76	38	1
GLA12, GLA13, GLA31	15	1	2
GLA14, GLA21	86	44	3
GLA21	9	56	4
GLA13, GLA14	65	35	5
GLA12, GLA13, GLA30	20	10	6
GLA12, GLA14	84	45	7
GLA14, GLA15	97	53	8
GLA32	99	57	9
GLA12, GLA13, GLA21, GLA30	27	11	10
GLA13, GLA14, GLA21	77	41	11
GLA12, GLA13, GLA21, GLA31	21	5	12
GLA14, GLA15, GLA21	103	65	13
GLA13, GLA21	4	26	14
GLA15, GLA21	24	80	15
GLA12, GLA13, GLA15, GLA30	38	13	16
GLA12, GLA21	11	52	17
GLA12, GLA13, GLA15, GLA31	30	6	18
GLA12, GLA13	1	2	19
GLA21, GLA31	31	33	20
GLA12, GLA13, GLA21	3	4	21
GLA12, GLA13, GLA15, GLA21, GLA31	41	8	22
GLA13, GLA21, GLA31	29	18	23
GLA13, GLA15, GLA21	12	36	24
GLA16, GLA21	39	92	25
GLA12, GLA15, GLA21	23	74	26
GLA12, GLA13, GLA15	5	7	27
GLA13	2	23	28
GLA15, GLA21, GLA31	61	49	29
GLA12, GLA21, GLA31	46	30	30

GLA21, GLA30	53	54	31
GLA12, GLA13, GLA15, GLA21	10	9	32
GLA12, GLA13, GLA36	34	3	33
GLA13, GLA15, GLA21, GLA31	52	20	34
GLA13, GLA30	25	37	35
GLA13, GLA16, GLA21	26	50	36
GLA15, GLA16, GLA21	64	101	37
GLA12, GLA16, GLA21	42	83	38
GLA13, GLA31	19	17	39
GLA12, GLA15, GLA21, GLA31	69	39	40
GLA30	51	48	41
GLA13, GLA15	8	31	42
GLA12, GLA13, GLA16	13	12	43
GLA16, GLA21, GLA31	87	66	44
GLA13, GLA21, GLA30	37	46	45
GLA21, GLA36	59	96	46
GLA15, GLA21, GLA30	83	76	47
None	6	51	48
GLA12	7	43	49
GLA12, GLA21, GLA30	63	68	50
GLA12, GLA30	55	61	51
GLA12, GLA13, GLA16, GLA21	18	14	52
GLA13, GLA16, GLA21, GLA31	79	27	53
GLA13, GLA15, GLA16, GLA21	47	71	54
GLA13, GLA30, GLA31	81	21	55
GLA13, GLA15, GLA30	54	58	56
GLA12, GLA15, GLA16, GLA21	66	98	57
GLA12, GLA13, GLA15, GLA16	28	15	58
GLA21, GLA30, GLA31	94	34	59
GLA13, GLA15, GLA31	44	19	60
GLA15, GLA30	70	69	61
GLA13, GLA16	16	42	62
GLA12, GLA16, GLA21, GLA31	96	67	63
GLA13, GLA15, GLA21, GLA30	60	63	64
GLA15, GLA16, GLA21, GLA31	102	87	65

GLA13, GLA21, GLA36	50	55	66
GLA15, GLA21, GLA36	82	102	67
GLA16, GLA21, GLA30	101	89	68
GLA15	14	73	69
GLA12, GLA13, GLA15, GLA16, GLA21	35	16	70
GLA30, GLA31	91	29	71
GLA12, GLA21, GLA36	78	94	72
GLA12, GLA15, GLA21, GLA30	85	81	73
GLA12, GLA15, GLA30	80	77	74
GLA12, GLA31	32	25	75
GLA12, GLA15	17	70	76
GLA31	22	28	77
GLA13, GLA16, GLA30	72	75	78
GLA13, GLA36	40	47	79
GLA21, GLA33	95	103	80
GLA16, GLA30	98	85	81
GLA13, GLA15, GLA16	36	62	82
GLA13, GLA16, GLA21, GLA30	88	79	83
GLA13, GLA16, GLA31	67	24	84
GLA13, GLA15, GLA21, GLA36	71	72	85
GLA12, GLA16, GLA30	100	91	86
GLA16	43	88	87
GLA12, GLA16	33	82	88
GLA12, GLA15, GLA31	57	32	89
GLA13, GLA15, GLA36	62	64	90
GLA15, GLA31	48	40	91
GLA36	45	84	92
GLA15, GLA16, GLA30	104	97	93
GLA15, GLA16	49	95	94
GLA12, GLA36	58	86	95
GLA12, GLA15, GLA16	56	93	96
GLA13, GLA33	73	22	97
GLA16, GLA31	74	60	98
GLA12, GLA15, GLA36	75	90	99
GLA15, GLA36	68	100	100

GLA12, GLA16, GLA31	89	59	101
GLA16, GLA36	92	104	102
GLA15, GLA16, GLA31	93	78	103
GLA33	90	99	104

E.8 Weights sensitivity analysis

Table E8.1 – The rank of different alternatives (barrier modifications) under a variety of weighting scenarios, undertaken as part of a sensitivity analysis during a multi-criteria decision analysis aiming to identify the optimal combination of barrier modifications in the river Glaven catchment (Norfolk, UK).

	Rank in weighting scenario						
Barriers modified	Original	Equal weights	Crayfish	Trout	Lamprey	Eel	Cost
GLA14	1	27	1	25	27	26	47
GLA12, GLA13, GLA31	2	29	4	29	29	49	42
GLA14, GLA21	3	40	3	40	40	34	59
GLA21	4	1	13	1	1	1	2
GLA13, GLA14	5	50	2	50	50	69	71
GLA12, GLA13, GLA30	6	36	6	38	36	55	51
GLA12, GLA14	7	57	5	57	57	51	81
GLA14, GLA15	8	56	7	54	56	48	78
GLA32	9	58	9	58	58	43	80
GLA12, GLA13, GLA21, GLA30	10	48	10	49	48	68	62
GLA13, GLA14, GLA21	11	64	8	64	64	81	85
GLA12, GLA13, GLA21, GLA31	12	43	11	43	43	63	54
GLA14, GLA15, GLA21	13	70	12	70	70	60	95
GLA13, GLA21	14	4	17	4	4	11	5
GLA15, GLA21	15	5	18	5	5	3	7
GLA12, GLA13, GLA15, GLA30	16	67	14	67	67	84	84
GLA12, GLA21	17	6	20	6	6	4	8
GLA12, GLA13, GLA15, GLA31	18	59	15	61	59	78	72
GLA12, GLA13	19	9	19	9	9	16	10
GLA21, GLA31	20	14	21	14	14	10	18
GLA12, GLA13, GLA21	21	11	22	11	11	22	14

GLA12, GLA13, GLA15, GLA21, GLA31	22	76	16	76	76	92	89
GLA13, GLA21, GLA31	23	24	23	24	24	41	29
GLA13, GLA15, GLA21	24	12	24	12	12	23	12
GLA16, GLA21	25	13	26	13	13	7	16
GLA12, GLA15, GLA21	26	15	27	15	15	8	17
GLA12, GLA13, GLA15	27	20	25	20	20	35	21
GLA13	28	3	33	3	3	9	3
GLA15, GLA21, GLA31	29	31	29	30	31	21	34
GLA12, GLA21, GLA31	30	33	30	33	33	25	37
GLA21, GLA30	31	21	34	21	21	17	23
GLA12, GLA13, GLA15, GLA21	32	25	31	26	25	47	27
GLA12, GLA13, GLA36	33	81	28	83	81	95	87
GLA13, GLA15, GLA21, GLA31	34	52	32	53	52	72	55
GLA13, GLA30	35	30	35	32	30	50	28
GLA13, GLA16, GLA21	36	26	36	27	26	46	25
GLA15, GLA16, GLA21	37	28	37	28	28	18	32
GLA12, GLA16, GLA21	38	32	39	31	32	19	33
GLA13, GLA31	39	22	42	22	22	39	22
GLA12, GLA15, GLA21, GLA31	40	63	38	63	63	45	64
GLA30	41	17	44	17	17	15	19
GLA13, GLA15	42	10	46	10	10	20	9
GLA12, GLA13, GLA16	43	44	40	44	44	64	41

GLA16, GLA21, GLA31	44	60	41	59	60	42	60
GLA13, GLA21, GLA30	45	42	43	42	42	62	39
GLA21, GLA36	46	45	48	45	45	30	45
GLA15, GLA21, GLA30	47	46	49	46	46	36	44
None	48	2	69	2	2	2	1
GLA12	49	7	62	7	7	5	6
GLA12, GLA21, GLA30	50	47	51	47	47	37	46
GLA12, GLA30	51	37	52	36	37	31	36
GLA12, GLA13, GLA16, GLA21	52	55	45	56	55	77	50
GLA13, GLA16, GLA21, GLA31	53	87	47	87	87	97	88
GLA13, GLA15, GLA16, GLA21	54	54	55	55	54	75	48
GLA13, GLA30, GLA31	55	89	50	89	89	99	94
GLA13, GLA15, GLA30	56	61	56	62	61	79	52
GLA12, GLA15, GLA16, GLA21	57	62	58	60	62	38	58
GLA12, GLA13, GLA15, GLA16	58	75	53	75	75	91	70
GLA21, GLA30, GLA31	59	82	54	82	82	71	82
GLA13, GLA15, GLA31	60	51	59	51	51	70	43
GLA15, GLA30	61	39	63	39	39	32	35
GLA13, GLA16	62	23	66	23	23	40	20
GLA12, GLA16, GLA21, GLA31	63	92	57	92	92	76	99
GLA13, GLA15, GLA21, GLA30	64	74	60	74	74	90	66
GLA15, GLA16, GLA21, GLA31	65	91	61	90	91	74	96

GLA13, GLA21, GLA36	66	77	65	77	77	93	68
GLA15, GLA21, GLA36	67	78	68	78	78	54	75
GLA16, GLA21, GLA30	68	79	67	79	79	66	74
GLA15	69	8	81	8	8	6	4
GLA12, GLA13, GLA15, GLA16, GLA21	70	88	64	88	88	98	83
GLA30, GLA31	71	73	72	73	73	65	69
GLA12, GLA21, GLA36	72	80	71	80	80	59	77
GLA12, GLA15, GLA21, GLA30	73	83	70	81	83	67	76
GLA12, GLA15, GLA30	74	69	73	69	69	56	63
GLA12, GLA31	75	34	78	34	34	28	31
GLA12, GLA15	76	16	84	16	16	12	13
GLA31	77	19	83	19	19	14	15
GLA13, GLA16, GLA30	78	90	74	91	90	100	86
GLA13, GLA36	79	68	76	68	68	85	57
GLA21, GLA33	80	93	75	93	93	86	93
GLA16, GLA30	81	71	79	71	71	58	61
GLA13, GLA15, GLA16	82	53	85	52	53	73	40
GLA13, GLA16, GLA21, GLA30	83	98	77	100	98	102	101
GLA13, GLA16, GLA31	84	86	82	86	86	96	73
GLA13, GLA15, GLA21, GLA36	85	101	80	101	101	103	103
GLA12, GLA16, GLA30	86	95	86	95	95	87	98
GLA16	87	18	91	18	18	13	11
GLA12, GLA16	88	35	90	35	35	24	26

GLA12, GLA15, GLA31	89	66	89	66	66	52	56
GLA13, GLA15, GLA36	90	94	87	94	94	101	91
GLA15, GLA31	91	41	92	41	41	29	30
GLA36	92	49	93	48	49	33	38
GLA15, GLA16, GLA30	93	97	88	96	97	88	97
GLA15, GLA16	94	38	96	37	38	27	24
GLA12, GLA36	95	84	95	84	84	57	67
GLA12, GLA15, GLA16	96	65	97	65	65	44	49
GLA13, GLA33	97	104	94	104	104	104	104
GLA16, GLA31	98	72	99	72	72	53	53
GLA12, GLA15, GLA36	99	102	98	102	102	83	102
GLA15, GLA36	100	85	101	85	85	61	65
GLA12, GLA16, GLA31	101	96	100	97	96	80	92
GLA16, GLA36	102	103	102	103	103	89	100
GLA15, GLA16, GLA31	103	99	103	98	99	82	90
GLA33	104	100	104	99	100	94	79