Modelling and empirical approaches for predicting the invasiveness of alien species

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Abstract

Biological invasions are a pervasive aspect of global change that result from the release of alien species into novel environments. Where an introduced alien establishes a sustainable population, disperses and impacts native species then it is considered as invasive. Predicting the outcomes of alien introductions is critical for conservation management, with predictions of dispersal rates a critical component within this. In riverine ecosystems, dispersal can be inhibited by barriers and unidirectional flow in channels that are primarily linear channels, with establishment, dispersal and colonisation also affected by biological interactions with native biota.

Here, modelling approaches were applied to predicting: (1) invasion outcomes when the species-specific traits are poorly known, but a robust time-series of the dispersal of an invading species is available; (2) optimal scenarios and trade-offs for managing an invasion in a riverine system; and (3) influences of the physical environment on the introduction and invasion. This was followed by empirical approaches that investigated (4) the ecological interactions between analogous invasive and native species; and (5) the probability that an alien invasion could be resisted by the native community.

Individual-based models (IBMs) were used, with approximate Bayesian computation (ABC) successfully applied in Chapter 2 to recreate an ongoing invasion and then predict the range expansion of the species. This model was then used in Chapter 3 to predicting the outcomes for the invasion of different species using a range of management strategies. In these invasion outcomes, the main source of variation in dispersal and establishment rates related to the life history (*r*- to *K*-selected) and dispersal (slow to fast) traits. The final model in Chapter 4 then identified that the complexity of the physical environment also influenced the invasion outcomes in freshwater fish, with the location of the initial introduction and the quality of the invaded area being the two most important factors.

The initial set of empirical approaches in Chapter 5 predicted the trophic impacts of a globally invasive fish on a threatened native fish, with aquaria experiments and experimental ponds predicting that the global invader will substantially impact the trophic ecology of the native species (trophic niche shifts, niche expansion), with the patterns detected in the controlled environments matching those detected in wild, uncontrolled conditions. The second empirical study (Chapter 6) revealed that biological resistance to the Ponto-Caspian invader zebra mussel *Dreissena polymorpha* has been minimal in England, and this was likely to contribute to its invasive success.

In conclusion, these results suggest that a combination of modelling and empirical approaches for predicting the outcomes of biological invasions provide substantially improved understandings of invasion dynamics and processes, leading to more informed policy and practice.

Table of contents

4 Predicting the influence of river network configuration, biological traits and habitat quality interactions on riverine fish invasions………………80

5 Predicting the competitive interactions and trophic niche consequences of a globally invasive fish with threatened native species…………………………………………………………..………....112

List of figures

List of tables

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Author’s declaration

I (VDA) confirm that the research presented within this thesis is my own.

The following research papers were, however, published in collaboration with Stephen C. F. Palmer (SCFP), Demetra Andreou (DA), Phillipa K. Gillingham (PKG), Justin M. J. Travis (JMJT), Emma T. Nolan (EMT), Josie South (JS), Emily R. Winter (ERW) and J. Robert Britton (JRB), with their contributions to each article outlined below.

Dominguez Almela, V., Palmer, S. C. F., Gillingham, P. K., Travis, J. M. J. and Britton, J. R., 2020. Integrating an individual-based model with approximate Bayesian computation to predict the invasion of a freshwater fish provides insights into dispersal and range expansion dynamics. *Biological Invasions,* 22, 1461–1480 https://doi.org/10.1007/s10530-020-02197-6 ***VDA, JRB and PKG conceived the ideas; VDA extracted the data with additional guidance from JRB and PKG; VDA formatted the data and SCFP built the model code; VDA and SCFP analysed the data; and VDA led the writing with assistance from SCFP, PKG, JMJT and JRB (Chapter 2).***

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Dominguez Almela, V., South, J. and Britton, J. R., 2021. Predicting the competitive interactions and trophic niche consequences of a globally invasive fish with threatened native species. *Journal of Animal Ecology*, 90, 2651–2662 https://doi.org/10.1111/1365-2656.13571 ***All authors contributed to the study design; JS and JRB carried out the experiments and collected the data; VDA led analyses and writing, assisted by JS and JRB (Chapter 5).***

Dominguez Almela, V., Nolan, E. T., Winter, E. R. and Britton, J. R., 2022. Dietary contributions of the alien zebra mussel *Dreissena polymorpha* in British freshwater fish suggest low biological resistance to their invasion. *Hydrobiologia* https://doi.org/10.1007/s10750-022-04861-5 ***All authors contributed to the study design. EN, EW and JRB collected the data. VDA led analyses and writing, assisted by EN, EW and JRB. All authors contributed to revising the manuscript and approved its submission (Chapter 6).***

1 Introduction

1.1 Overview

This first chapter outlines the main themes of the thesis: how environmental and biological factors influence the ‘invasiveness’ of alien species (invasiveness: the propensity of an alien species to invade a novel ecosystem). The study’s approaches, and aims and objectives, are then introduced at the end of the chapter. The thesis is presented in an integrated format, whereby material is incorporated in a style suitable for submission and publication in a peer-reviewed journal. Thus, the data chapters (Chapters 2 to 6) are each presented as original and complete pieces of research, either as the actual, published paper, or as a manuscript under review. This format has been chosen as it provides flexibility around the types and numbers of papers included in the thesis. Finally, Chapter 7 discusses the implications of this research and concludes the thesis. A complete list of references is provided at the end of the thesis in order to avoid their replication in the chapters and to improve readability. A note is also provided at the end of this chapter on the impact of the Covid-19 pandemic and associated lockdown periods on the PhD programme.

1.2 Biological invasions: introducing alien species

Biological invasions are considered one of the greatest threats to biodiversity and the fourth highest threat identified to species on the IUCN Red List (Maxwell et al. 2016), especially in freshwater ecosystems (Almeida et al. 2012, Davis and Darling 2017). The introduction of non-native species, intentionally or accidentally, can result in detrimental ecological impacts on native species and their communities (Moyle and Marchetti 2006, Wolter and Röhr 2010, Shi et al. 2016). Hulme et al. (2008) identified six main introduction pathways of alien species (release, escape, contaminant, stowaway, corridor and unaided), with five of them linked to human actions and one being natural diffusion dispersal of the species itself (but following an introduction from one of the other five pathways). Following their introduction, ‘invasiveness’ is the term that tends to be used to describe the propensity of the species to then invade the recipient ecosystem (van Kleunen et al. 2010).

Understanding the invasiveness of alien species is important, as the impacts of species that invade can be severe; these impacts can include genetic introgression, introduction of novel pathogens, habitat degradation and changes in community structure (Maezono et al. 2005, Almeida et al. 2012, Samson et al. 2017). For example, in the Yellowstone Lake of Wyoming, USA, the lake trout *Salvelinus namaycush* was introduced and caused negative effects in aquatic ecosystems by predating native species, resulting in their displacement and extinctions. Impacts were also measured in terrestrial animals such as eagles and bears due to alterations to their diets (Koel et al. 2019). The rainbow trout *Oncorhynchus mykiss* has been widely introduced, including into British freshwaters, where releases for sport angling have continued for many years but with only a small number of established populations to date. However, there is empirical evidence of ecosystem fragmentation and displacement of native salmonid species through competition and predation (Fausch 2007). Many introduced alien species are considered as having high socio-economic value and so have been deliberately introduced into many regions of the world, contributing to the biological homogenisation of ecosystems (Carpio et al. 2019).

The invasiveness of an alien species is elevated when it possesses a suite of characteristics that increase its ability to survive and establish in new environments (Brandner et al. 2013). High reproductive and growth rates, phenotypic plasticity, a generalist diet and/or rapid dispersion are some of the biological traits that potentially contribute to successful colonization of novel environments (Pinder et al. 2005, Moyle and Marchetti 2006, Záhorská and Kováč 2009). Following their introduction into a new environment, the probability of alien species developing an invasion is at least in part determined by complex interactions of the species' traits with the abiotic and biotic components of the receiving environment (Section 1.2). However, the characteristics of the introduction, such as its propagule pressure (the number and frequency of introductions), can also be important (Britton and Gozlan 2013, Blackburn et al. 2015), although it can be a difficult parameter to measure when the introduction is accidental (Copp et al. 2010). For example, zebra mussel *Dreissena* *polymorpha* is a global invader that has been dispersed through their fouling of recreational boats in sufficient numbers for this to constitute an important propagule pressure vector of invasion, although quantifying the actual extent of this is difficult (De Ventura et al. 2016). While fouling species are easy transported across the world, most alien freshwater fish introductions occur through the pathways of aquaculture, sport angling and the ornamental/pet trade (Padilla and Williams 2004, Tuckett et al. 2017, Brosse et al. 2021). For example, the Nile tilapia *Orechromis niloticus* has successfully established across South American freshwaters following their escape from aquaculture facilities (Forneck et al. 2021), with common carp *Cyprinus carpio* considered a global invader, where most introductions occurred from aquaculture (Koehn 2004), although they are increasingly released into the wild for angling. A higher number of unwanted ornamental fish are estimated to be introduced per year in ponds located close to roads or under restoration management (Copp et al. 2005). Carpio et al. (2019) indicated that recreational angling is the second main pathway of introduction of alien species, not only through the deliberate release of alien species to diversify catches (Britton and Nolan 2021), but also through continuous re-stocking by anglers that contributes directly to propagule pressure (Britton et al. 2010a), which can indirectly lead to successful establishment if the species' traits facilitate this (Peoples and Midway 2018). Recently, Jarić et al. (2021) revealed how the use of culturomics analyses and iEcology (e.g. analysis of data mined from the internet) could provide early warning of unwanted introductions or add new monitoring data on an ongoing invasion.

During the first stages of the post-introduction period, the ecosystem status plays an important role in facilitating survival and then establishment of the introduced propagules (Ross et al. 2001, Marchetti et al. 2004). For example, increased anthropogenic disturbances in freshwater ecosystems can increase their vulnerability to invasion, such as habitat alterations (e.g. from impoundment) and nutrient enrichment (e.g. from agricultural run-off or sewage effluents) (Nakano et al. 2015, Shi et al. 2016, Davis and Darling 2017). The construction of reservoirs and impoundments, which have a higher susceptibility to being invaded and colonised by non-native species compared to natural lakes, can facilitate the posterior spread into natural water bodies (Johnson et al. 2008).

Ruiz-Navarro et al. (2020) demonstrated the positive effects of nutrient-enriched waters for invasive topmouth gudgeon *Pseudorasbora parva* (e.g. increased growth and higher trophic niche resulting from increased productivity of the system).

Native species richness can also influence introduction outcomes, with increased numbers of species usually increasing the ‘biological resistance’ to establishment and invasion through competition and/or predation (Alofs and Jackson 2014, Miller et al. 2014; Section 1.3). Also, when the new species is introduced, its ability to adapt to the new conditions is important for establishment and dispersal (Moyle and Marchetti 2006). For example, the golden mussel *Limnoperna fortune* is an invasive species in South Africa that has been successful in invading rivers but tends to fail to establish in isolated lakes where the abiotic conditions differ (e.g. lower dissolved oxygen, higher turbidity and/or elevated nutrient levels) (de Amo et al. 2021). Species that can express their traits in a similar manner to their native range are often successful as they are ‘pre-adapted’ to their new environment (Grabowska and Przybylski 2015, Buoro et al. 2016).

1.3 The invasion pathway and the abiotic and biotic factors affecting dispersal

Following their introduction, to become invasive, the released individuals must survive and then establish a sustainable population that goes on to colonise local habitats before dispersing more widely, with these establishment and dispersal processes being context- and condition-dependent (Allen et al. 2013, Comte and Olden 2018). For dispersal (colonization) and demography (establishment), the biological traits of the invader (such as reproductive rates and probabilities of survival in the new environment) are important, but they must be analysed in combination with other possible biotic/abiotic factors and mechanisms, which also determine the invasion success (Catford et al. 2009).

Although the dispersal process can have different characteristics, in freshwater systems this is usually driven by natural diffusion across the environment, where the individuals gradually colonise new areas (Wilson et al.

2009). The rate of natural diffusion is determined by the connectivity of habitats (Hastings et al. 2005), with this often being more constrained in freshwaters than in terrestrial environments due to minimal connectivity between river basins (Radinger et al. 2017). Riverine dispersal is also usually subject to directional bias due to the effects of flow, with dispersal primarily in a downstream direction as driven by passive drift (Byers and Pringle 2006). However, if upstream dispersal is also detected, then it indicates more active and deliberate dispersal, and opens a new invasion front for further dispersal (Goldberg et al. 2010). The latter can be driven by the invader body size and locomotory capabilities, which may allow overpassing barriers that obstruct smaller individuals (Starrs et al. 2017).

Hydrological connections to other biogeographical areas then potentially allow the natural diffusion of the invader, enabling them to colonise new areas (Gozlan et al. 2010a, de Amo et al. 2021). These movements depend on the connectivity between ecosystems, which can be constrained if natural or artificial barriers are present (Johnson et al. 2008, Morán-López and Uceda Tolosa 2017). The construction of canals to connect different river basins can provide sufficient connectivity to enable alien fish to spread, such as pikeperch *Sander lucioperca* dispersing throughout England via the canal network (Hickley 1986). Artificial barriers can play an important role in preventing the further upstream spread of invasive species, as noted by van der Walt et al. (2016) for Black bass *Micropterus* spp. However, low-head barriers do not always prevent upstream spread, as some fish exhibit leaping capabilities that can overcome them (Morán-López and Uceda Tolosa 2017). For example, the European minnow *Phoxinus phoxinus* can jump up to 27 cm high under summer temperatures, enabling them to move upstream beyond small culverts (Holthe et al. 2005). The use of fish passages in conservation can aid the spread of invasive species (Starrs et al. 2017, Kerr et al. 2021), and studies on the structures' performance have explored ways of preventing this. For example, Newbold et al. (2016) indicated that incorporating high flow velocities in these passes could limit the passage and thus dispersal of the invasive bighead carp *Hypophthalmichthys nobilis* and silver carp *H. molitrix*, but more research is needed on fish swimming performance and behaviour within fish passes and whether there is a need to adapt their design as a result. The dispersal of alien species is not only subject to spatial constrictions but can also vary temporally (Guarnieri et al. 2017). For example, elevated river levels are an important driver of fish dispersal, including escapees from aquaculture facilities during lapses of biosecurity (Rahel and Olden 2008, Davies and Britton 2016, Casimiro et al. 2018). Some of these events are driven (or made more severe) by climate change and can be linked to changes in river flow and water quality (Radinger et al. 2017), such as increased precipatation rates that result in more severe flooding events (Johnson et al. 2008).

As an alien species disperses, its mortality risk can be elevated as it enters the novel habitat - otherwise known as the 'range front' (Thorlacius et al. 2015). Consequenly, individuals at the range front tend to be characterised by behavioural traits grouped together as 'boldness' as they explore and establish populations in the novel environments (Lopez et al. 2012). Indeed, Myles-Gonzalez et al. (2015) revealed that at the invasion front, fish have differing traits (e.g. relating to body size, swimming endurance and/or ability to avoid predation) to those in the established 'core' range. Brandner et al. (2013) suggested that individuals from the invasion front may have lower parasite burdens compared to individuals in the core range, providing fitness advantages as less energy is expended on immune responses to infection. These differences in traits between the populations occur through individuals in both areas investing their energy in different functions, as driven by the contrasting biotic and abiotic pressures of their local environments (Llewellyn et al. 2012, Masson et al. 2018). At the invasion front, it is thus expected that individuals express 'dispersal-enhancing traits' that provide individuals with the highest probability of dispersal success (Phillips et al. 2008, Masson et al. 2018).

Boldness is only one of the many personality-dependent traits associated with invasive species at the dispersal edge (Cote et al. 2010). For example, some species may require very specific conditions to colonise and establish in an area that are associated with their complex reproductive behaviours. For example, bitterling *Rhodeus sericeus* require the presence of freshwater unionid mussels to reproduce and will disperse to suitable areas to accomplish this parasitic relationship. Females lay their eggs within the gills of the mussels and males release sperm close by to fertilise them (Mills and Reynolds 2002, 2003, Damme et al. 2007). Sunbleak *Leucaspius delineatus* exhibit nest guarding, where males protect the offspring, with this leading to a very particular male selection by the female (Gozlan et al. 2003). Sex-specific personality is exhibited by the males of the mosquitofish *Gambusia affinis*, which tend to be quite asocial, enhancing their ability to disperse further from the established population (Michelangeli et al. 2020). These types of behaviours could all add some complexity to the spread and colonisation itself that potentially need consideration when assessing a new introduction of an alien species.

1.4 Importance of ecological interactions between native and invasive species

In the first stages of an invasion, the newly introduced species must establish a sustainable population and, if successful, the bolder individuals will then disperse (Lopez et al. 2012, Allen et al. 2013). Sympatric native species can thus be exposed to aggressive encounters (as competition and predation) with the invader, with these often species-dependent (e.g. life-stage, body size, trophic niche) and density-dependent (Kornis et al. 2014, Brown et al. 2018, Gutmann Roberts and Britton 2018, Grabowska et al. 2019). For example, larger individuals of the introduced mosquitofish *Gambusia affinis* predate on juveniles of least chub *Iotichthys phlegethontis*, with this altering the behaviour of the latter (e.g. longer time spent in refugia) and reduced growth rates (Mills et al. 2004). Invasive gobiid species can induce shifts in the habitat choice of benthic fish species (Van Kessel et al. 2011). Many invasive species exhibit similar negative interactions with the native community (Almeida and Grossman 2012), with additive and synergistic interactions possible in situations where multiple invasive species are present (Balzani et al. 2020). If the same invader was introduced into two habitats of similar characteristics, they can still differ in their invasion outcomes due to context dependencies relating to the native community (Gjelland et al. 2007). In addition, Noonburg and Byers (2005) suggested that in an ecosystem where predators prey on a native species and the invader likewise shows an inclination for the same prey source, the threat of extinction can be apparent for the native species. These individuals are likely to undergo changes due to invasion stress, such as enhancing anti-predator behaviours that can lead to reduced reproductive rates and loss of condition (Howe et al. 1997, Bergstrom and Mensinger 2009, Pardo et al. 2009, Brown et al. 2018).

Invasive species can also access resources more efficiently than some native species, which then supports their traits of fast growth rates and high reproductive investment (Budy et al. 2013, Brandner et al. 2013). Moreover, many successful invaders exhibit high phenotypic plasticity, including in dietary resources, that enable them to assimilate into native food webs, which can result in trophic niche shifts in native species, such as to a more specialised diet that alters the trophic dynamics of the foodweb (Vander Zanden, Casselman and Rasmussen 1999, Bolnick et al. 2010, Britton 2018). Conversely, the integration of an invasive species into a native foodweb can result in the diets of native species becoming more generalised, with species having to exploit a broader range of prey items to maintain their energy intake (Pettitt-Wade et al. 2015). While competitive interactions between native and invasive species are often asymmetric, symmetry is also possible with, for example, interactions between the native crab *Potamonautes loven* and invasive red swamp crayfish *Procambarus clarkii* inducing diet contractions in both crustacean populations (Jackson et al. 2016a).

Alien species that are ecological engineers can also have marked effects on the recipient ecosystem through altering habitat structure and, in some cases, aspects of ecosystem functioning (Emery-Butcher et al. 2020). For example, the globally invasive common carp *Cyprinus carpio* tends to reduce the abundance of aquatic macrophytes and benthic macroinvertebrates in invaded waters, increasing water turbidity through both their foraging activities and through nutrient release that promotes algal growth (Weber and Brown 2009, Maceda-Veiga et al. 2017). Such trophic cascades can thus shift biological, chemical and physical characteristics of the recipient ecosystem (Ricciardi and MacIsaac 2011, Emery-Butcher et al. 2020), and can lead to invasion meltdown effects whereby the modified ecosystem is now more vulnerable to being invaded by another alien species (Simberloff 2006, Britton et al. 2010c). The Ponto-Caspian zebra mussel *Dreissena polymorpha* can also have these cascading effects through their ability to form large colonies that can filter large volumes of water; their reduction of the abundance of phyto- and zooplankton then reduces prey availability for secondary consumers, with the concomitant increased water clarity encouraging macrophyte growth that provides increased refugia for benthic invertebrates (Aldridge et al. 2004). In New Zealand, brown trout *Salmo trutta* not only compete with other fish species or prey upon them, but also can decrease the invertebrate community that can lead to increased algal growth and decreased prey availability for omnivorous native species (McDowall 2003).

Although the ecological consequences of alien species tend to be considered as negative for the recipient ecosystem, there are instances where, arguably, there are positive ecological outcomes for native species, such as increased habitat complexity and novel trophic interactions that are favourable (Rodriguez 2006). For example, the reduced algal dominance and promotion of increased macrophyte growth from zebra mussel invasions can reduce the harmful effects of eutrophication (Kelly and Hawes 2005).

The presence of the new species can provide the native community with a new prey item, which can then inhibit the establishment success of the alien species, resisting its invasion and providing resilience if the population has established (Leprieur et al. 2008, Alofs and Jackson 2014). The extent of biotic resistance in freshwater ecosystems was tested by Britton (2012) using resident common carp *Cyprinus carpio* on introduced topmouth gudgeon *Pseudorasbora parva*, with the results demonstrating that predation-resistance inhibited *P. parva* establishment. This resistance was only able to be overcome through a combination of elevated propagule pressure and the presence of trophic subsidies (Britton et al. 2015). Biotic resistance can also be provided via native parasites and pathogens infecting the alien species that results in increased energy expenditure on immune responses (Lee and Klasing 2004). For example, while alien fishes present in Great Britain are rarely introduced with their native parasites (only 9 % of their invasive parasites have been recorded in Britain), they instead acquire infections of a wide range of native parasites (Sheath et al. 2015).

Consequently, the invasiveness of an alien species is subject to a wide range of abiotic and biotic determinants in the recipient ecosystem, as well as the characteristics of the introduction event (e.g. the propagule pressure) and the species itself, including its adaptive capacity (van Kleunen et al. 2010). This results in the outcomes of introductions of alien species being complex, with multiple factors involved in determining whether an introduced alien species will go on and complete its invasion pathway. Coupling all these factors together is highly challenging, with multiple knowledge gaps as the interactions of these factors can have high context dependency in natural systems. These aspects highlight that predicting the outcome of introductions using empirical approaches alone can be problematic (Blanchet et al. 2009, Thomsen et al. 2011).

1.5 Predictive approaches to biological invasions

The application of predictive approaches to biological invasions is important to increase knowledge of the ecological process itself and manage any associated impact (Samson et al. 2017, Bocedi et al. 2021). In aquatic systems, the development of these tools can be difficult due to lack of reliable data (e.g. spatial information, risk assessments or monitoring) (Bobeldyk et al. 2015), but in recent years there has been considerable effort in this area, with a number of new approaches developed (Sato et al. 2010, Robson 2014, Rogosch and Olden 2021). For the purpose of this thesis, these predictive approaches have been split into two main sections: empirical experiments and theoretical modelling.

1.5.1 Empirical experiments

Increased understanding of biological invasions in freshwater systems can be achieved empirically using simplified representations of the invasion in small (e.g. aquaria/lab facilities) or larger (e.g. mesocosm/wild locations) controlled (or semi-controlled) environments (Britton 2018). The strength of competitive interactions between invasive and native species can be measured in aquaria experiments, such as through co-habitation experiments. This can be achieved by using additive and substitutive treatments that measure the symmetry of competition between the species through measuring specific responses, such as somatic growth rates, and through comparing consumption rates through comparative functional responses (CFRs) to estimate attack and consumption rates (Britton et al. 2019). Personality traits of the invader, such as ‘boldness’, can be tested by recording the behaviour of the fish in specific aquaria situations to generate decision matrix models to predict their intentions to move disperse into new areas (Hirsch et al. 2017). Mesocosm studies can help to investigate the extent of the overlap in trophic niches of the alien and native species, or whether these niches are divergent, indicating considerable differences in resource use (De Santis et al. 2021), with patterns in mesocosms often being representative of patterns in the wild (Tran et al. 2015).

Empirical experiments that test a specific invasion hypothesis can then be applied to estimating and predicting the interactions of the species in the wild (Ricciardi 2003). For example, comparative functional response experiments tend to indicate that high impact invaders tend to have significantly higher consumption rates than trophically analogous native species (Alexander et al. 2014, Dick et al. 2014). However, comparative functional responses (and similar approaches) have been criticised for presenting over-simplifications of the interactions of invasive and native species that occur within more complex systems (e.g. Vonesh et al. 2017). Empirical experiments are rarely able to deal with this high complexity due to the number of treatments that would be required within the experimental design. Correspondingly, if more complex contexts are required for invasion and impact prediction then alternative, complementary approaches are likely to be required.

1.5.2 Theoretical modelling

Models are a simple representation of a specific aspect of the real world and can be used to predict the dispersal and colonization processes of alien species. Posterior model calibration tests how closely the predicted values match real data (Railsback and Grimm 2012), although independent real-world data are often unavailable for many alien species, especially in freshwater ecosystems (Caffrey et al. 2014).

Predictions about the invasiveness of alien species can be based on the behaviour and movements of individuals in a given area within ‘individual-based models’ (‘IBMs’) (Grimm et al. 2006, Railsback and Grimm 2012, Coulon et al. 2015). IBMs allow understanding the system or processes by looking at the responses in the behaviour of the individuals to that system (Wilensky 2001, Railsback and Grimm 2012). IBMs explicitly consider individual organisms (also called “agents”) and attempt to understand how system properties emerge from interactions between agents and their environment (Grimm et al. 2006, Railsback and Grimm 2012), instead of looking at the process itself through variables only. In these models, landscape characteristics and population dynamic parameters need to be specified, with these being the main two sources of uncertainty (Heikkinen et al. 2014). IBMs can simulate different control and eradication strategies that seek the most efficient solution (Lurgi et al. 2016). If the predictions are easy to understand by managers, the output from the model could be accepted for future implementation (Railsback and Grimm 2012).

A principal concern of using IBMs is, however, the complexity that arises from their use of relatively high numbers of parameters that can be difficult to determine *a priori* (Heikkinen et al. 2014, Urban et al. 2016). Whilst this complexity can be considered as important for representing real world scenarios, if the number of the parameters becomes unwieldy, the model can lose credibility and become more difficult to validate (Railsback and Grimm 2012).

Predictive models enable invasion probabilities to be determined for a range of non-native species, according to their ability to disperse, biological traits (e.g. Samson et al. 2017), the characteristics of the communities in the receiving environment (e.g. Fukuda et al. 2013), and the effectiveness of management interventions at minimising their invasion (e.g. Lurgi et al. 2016). Urban et al. (2016) indicated the six biological mechanisms to improve predictive approaches: species-interaction, dispersal, demography, evolution, environment, and physiology. Different combinations of these mechanisms within process-based models are starting to become widely used within theoretical and applied studies. For example, Cheung et al. (2011) explored the factors affecting commercial fisheries using dynamic bioclimatic envelope models with explicit physical and biogeochemical dynamics. Cockrell and Sorte (2013) built a stage-structured population model to study the effect of increased temperature in invasive epibenthic communities. Already built-in software and freeware are available, depending on the final purpose of the study (e.g. Lurgi et al. 2015). For example, Savage and Renton (2014) generated a platform with a general model of biological invasion (GMBI) focused on natural spread of individuals with landscape heterogeneity. Schiffers and Travis (2014) presented ALADYN, which works with spatially structured populations at the individual-level and incorporates genetic traits selection to investigate adaptation.

‘RangeShifter’ is an eco-evolutionary modelling framework that simulates the introduction, spread and invasion success of species. It has been developed to integrate dispersal in three main stages: emigration, dispersion and establishment, and allows modelling at the individual scale using population dynamic information obtained through literature, experiments and/or expert opinion (Bocedi et al. 2014, 2020, 2021). The different versions of ‘RangeShifter’ enable modelling of alien dispersal according to ecological, environmental and management factors that interact in the IBM to influence their natural diffusion. It is spatially explicit and can be run over cell or patch-based models following the researcher’s purposes (e.g. cell-based may be more appropriate for theoretical studies while patch-based would give a better projection of population dynamics and dispersal in applied studies). Modelling at these detailed spatial scales requires having robust data on the range expansion of the species being simulated (Heikkinen et al. 2014).

The general IBM workflow of ‘RangeShifter’ can be divided into two main model steps: (1) population dynamics, where each individual of the population living in a determined cell/patch subjected to demographic density-dependence can reproduce (if mature), grow (if stage-structured) or die; and (2) dispersal dynamics, where each individual can disperse (or not), transfer through the landscape using any of the two main methods available (phenomenological dispersal kernels or mechanistic movement processes) and settle into a suitable new cell/patch (subjected to chosen strategies, behaviours and reaction norms). Both steps take place each year and are repeated until the end of the simulation (Figure 1.1; Bocedi et al. 2014, 2020, 2021). ‘RangeShifter’ is coded in C++ and is now available as an open-source application as well as through an R package (https://rangeshifter.github.io/).

Simulations must rely on information about the dynamics of populations, such as species-specific parameters, sex/stage-dependent information or habitat specific preferences that are going to shape the dispersal behaviour, together with species´ local demography (Jongejans et al. 2008, Bocedi et al. 2014, Lurgi et al. 2015). However, obtaining all the parameters needed for accurate and realistic model simulation can still be a challenging process, even for well-studied species (Heikkinen et al. 2014, Urban et al. 2016).

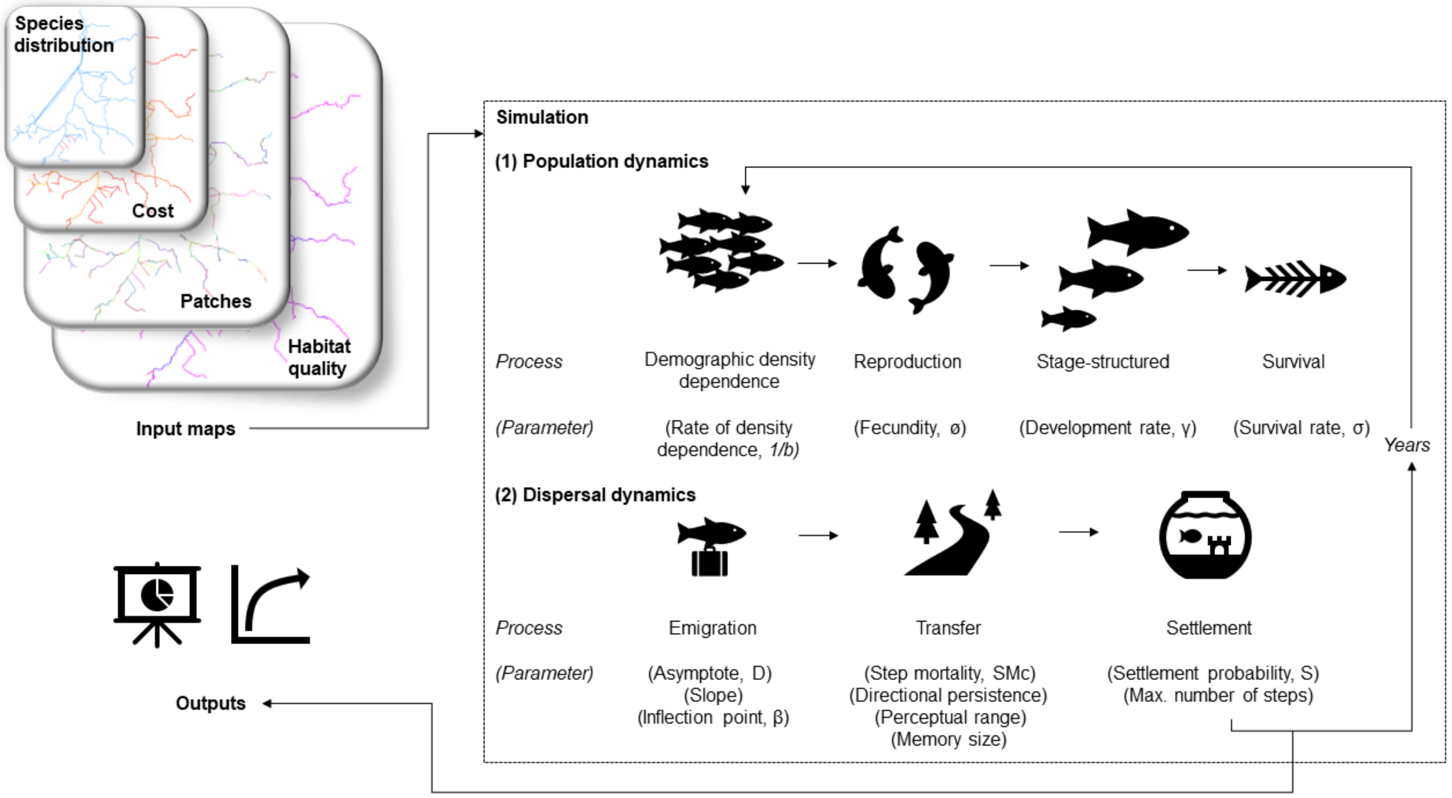


Figure 1.1. Example diagram of the general model workflow using a patch-based model of habitat quality with stochastic movement simulator and initial species distribution

1.6 Management of biological invasions

Although it has been highlighted in Sections 1.2 to 1.4 that there are multiple and interacting biotic and abiotic factors that can influence whether an introduced alien species will develop an invasive population, an additional factor is the extent of the management response (Britton et al. 2010b, Rytwinski et al. 2019). In the management of invasive species, efforts to control an invasion can vary from local to global scales, and strategies include control and containment efforts through to eradication, all with the general aim of reducing the ecological and economic impacts of the invading species (Lintermans 2004, Kopf et al. 2017, Rytwinski et al. 2019). The legislation related to the use and management of invasive species can differ by country (Britton et al. 2011b) and, rather than trying to achieve optimal outcomes for native ecosystems and biota, can be based on economic considerations that actually promote the use of non-native species in aquaculture, as in Brazil (Coelho and Henry 2017, Padial et al. 2017, Junior et al. 2018). These non-uniform management approaches between countries often leads to unwanted introductions that result from legislation clashes with, for example, some states in the USA promoting the introduction of Asian carp species for commercial distribution that leads to escapes from aquaculture facilities and spread into other states where they are strictly prohibited (Kolar et al. 2010).

There are a range of ways in which potentially invasive alien species can be managed. Introduction prevention remains the most effective measure, with investments generally only required on increased surveillance and auditing of major introduction pathways (Pyke et al. 2008). Examination of future potential invasions can be extracted from existing evidence (data, information from literature and/or risk assessments) by horizon scanning in combination with consensus methods (expert knowledge and opinion), and provide estimates of species that may become invasive in a particular area (Roy et al. 2014). Once establishment and spread starts then it becomes more difficult to control or eradicate the species (Vander Zanden and Olden 2008). Invasion risk assessments can help to evaluate an invasion ecologically and economically, as well as highlight possible scenarios of management actions to facilitate decision-making (Roy et al. 2018). An example of a tool used within invasions risk assessments is the ‘Fish Invasiveness Screening Kit’ (‘FISK’), which has been widely used around the world on many alien fish species (e.g. Mastitsky et al. 2010, Simonovic et al. 2013, Mendoza et al. 2015). Risk assessment tools are always evolving and adding new components to improve predictions, for example the Aquatic Species Invasiveness Screening Kit ‘AS-ISK’ is an improved version of ‘FISK’ where climate specific threshold can be included to account for current and future temperatures (Vilizzi et al. 2021).

Following the establishment of an alien species, methods to prevent their dispersal and thus invasion include those that eradicate the population (i.e. remove all of its life-stages). For freshwater fish, eradication methods tend to be chemical based, for example, the application of the ‘rotenone’ pesticide on topmouth gudgeon *Pseudorasbora parva* populations in England (Britton and Brazier 2006, Britton et al. 2010b). However, with rotenone being non-species specific, there is danger of native species also been impacted (Nico and Walsh 2011). Harvesting regimes are also used in combination with other techniques, for example, harvesting in the Mississippi River Basin has been used to help control the abundance of the bighead carp and silver carp, whose densities then decreased by 40 % (Love et al. 2018). Physical removal efforts have also been applied since 2010 in the Mexican Caribbean to control red lionfish *Pterois volitans*, with local campaigns promoting its consumption (Aguilar-Perera 2013).

A further method of controlling invasive species is biological control, where the invaded community is modified to include a higher abundance of natural control agents (Myers et al. 2000, Britton et al. 2011b). This was applied by Davies and Britton (2015) who revealed how the abundances of invasive topmouth gudgeon *Pseudorasbora parva* in England were reduced using a combination of physical removal and biocontrol techniques using the indigenous European perch *Perca fluviatilis* as the control agent that actively predated on *P. parva*. González-Bergonzoni et al. (2020) highlighted the importance of native communities to inhibit invasions, focusing on the rapid spread of the Asian golden mussel *Limnoperna fortune* in South America, where a third of the fish species were predating on the mussel and successfully reduced its density by 70 %. Genetic biocontrol involving male sterilisation has been used to control sea lamprey *Petromyzon marinus* populations in the Great Lakes and has successfully reduced its reproductive potential by 81 % (Bergstedt et al. 2003). While the potential use of an introduced virus to common carp *Cyprinus carpio* in Australia has been reviewed, this has not progressed further as its use required a wider understanding of the effects it would have both on the target and non-target species (McColl et al. 2014).

Independently of the control method chosen, the economic cost of dealing with invasive species is extremely high, being estimated to be at least US$ 1.288 trillion over 1970 and 2017, with an annual mean cost of US$ 26.8 billion globally (Diagne et al. 2021). Understanding management trade-offs is important for estimating the economic impact of an alien species, but most of the available data are associated with economic loss rather than invasion management. These impede expanding our knowledge and easing the decision-making process (Haubrock et al. 2021). Predictions on the invasiveness of alien species are important for understanding the development of invasions for both testing ecological theory (e.g. diffusion theory and invasion hypotheses) and for applied ecology (e.g. understanding impacts on native biodiversity) (Moyle and Marchetti 2006, Catford et al. 2009, Almeida et al. 2012, Tran et al. 2015). The management response to an introduction or invasion could then be incorporated into developing predictions of invasiveness of introduced species based on the factors that increase the probability of invasions occurring (Davis and Darling 2017, Samson et al. 2017). For example, Day et al. (2018) simulated the individual movement and demographics of Eastern brook trout *Salvelinus fontinalis* before, during, and following implementation of control efforts to inform how this species responded to different treatments to managers. A combination of approaches can help disentangle key relationships with the ultimate goal of easing implementation of measures for conservation and management of ecosystems that are subject to a biological invasion (Britton et al. 2011b).

Despite the extent of management efforts that are expended on invasive species, there remains large uncertainties in how alien species respond to management interventions, especially when methods are based on control and containment. The difficulties around predicting their spread or response to management are coupled with the uncertainties around abiotic characteristics of the recipient ecosystem and biotic characteristics of the invader, leaving knowledge gaps that need to be overcome to help understand and manage past, present and future biological invasions.

1.7 Aims and objectives

This chapter has emphasised that while there has been a great deal of effort expended on understanding the mechanistic basis of biological invasions, there remains a great deal of uncertainty in how the biotic and abiotic characteristics of the recipient ecosystem interact with the alien species to determine its establishment success and subsequent dispersal. There also remains considerable uncertainty in how management approaches influence the outcome of invasions. Consequently, there remain important knowledge gaps on the ‘invasiveness’ of alien species, especially in how these different characteristics and management responses interact to influence the outcome of an invasion, including its ecological impact.

Correspondingly, the overall research aim is to predict how the abiotic and biotic characteristics of freshwaters, and the management responses, interact to influence the invasiveness of alien species. In the thesis, invasiveness of the alien fishes is considered as their ability to disperse in the environment and their interactions with the abiotic and biotic components of the receiving ecosystem. Invaded river basins, both theoretical and real-world scenarios, are used as primary study areas. Each data chapter has its own set of aims and objectives, as follows:

Chapter 2: Using an appropriate alien fish model species, develop and calibrate an initial IBM to predict dispersal rates and dynamics according to hydrological connectivity and with no management interventions.

Chapter 3: Parameterise the initial IBM for alien fishes to predict how species traits (*r*- to *K*-selected; low to fast disperser) impact its natural diffusion, and thus their invasiveness, and predict the optimal management scenarios for their population control.

Chapter 4: Parameterise the initial IBM for alien fishes of different traits (*r*- to *K*-selected; low to fast disperser) to predict how the complexity of the river network influenced the invasion dynamics and population growth rates of the invaders.

Chapter 5: Assess the trophic interactions of native and non-native freshwater fishes with similar functional traits through application of comparative functional responses (CFRs) and stable isotopic ecology in field experiments and studies.

Chapter 6: Test the extent of biological resistance to zebra mussel *Dreissena polymorpha* invasion in Great Britain through predictions of their contribution to the diet of native fishes through application of ecological methods in stable isotope analysis.

Chapter 7: Synthesise the main findings of Chapters 2 to 6.

1.8 Consequences of the Covid-19 pandemic on the PhD programme

In the original PhD programme, Chapters 5 and 6 were to be based on empirical data, gained in field studies and aquaria experiments, on the initial model invasive fish species that was used as the basis of the IBM developed in Chapter 2 and used in Chapters 3 and 4, which was the bitterling *Rhodeus sericeus*. However, these field studies and experiments were incomplete when the lockdown periods of the Covid-19 pandemic commenced, and they were unable to be finished subsequently as they were reliant on working with multiple partners where health and safety risk assessments prevented effective joint working. Correspondingly, rather than use these incomplete datasets in the thesis, alternative datasets were used that were originally generated by the supervisory team outside of the PhD programme, but were analysed using the methodologies that would have been applied to the original datasets (had they been able to be completed). The specific details of the approaches used are provided in each chapter.

2 Integrating an individual-based model with approximate Bayesian computation to predict the invasion of a freshwater fish provides insights into dispersal and range expansion dynamics

2.1 Abstract

Short-distance dispersal enables introduced alien species to colonise and invade local habitats following their initial introduction, but is often poorly understood for many freshwater taxa. Knowledge gaps in range expansion of alien species can be overcome using predictive approaches such as individual based models (IBMs), especially if predictions can be improved through fitting to empirical data, but this can be challenging for models having multiple parameters. We therefore estimated the parameters of a model implemented in the ‘RangeShifter’ IBM platform by approximate Bayesian computation (ABC) in order to predict the further invasion of a lowland river (Great Ouse, England) by a small-bodied invasive fish (bitterling *Rhodeus sericeus*). Prior estimates for parameters were obtained from the literature and expert opinion. Model fitting was conducted using a time-series (1983 to 2018) of sampling data at fixed locations and revealed that for 5 of 11 model parameters, the posterior distributions differed markedly from prior assumptions. In particular, sub-adult maximum emigration probability was substantially higher in the posteriors than priors. Simulations of bitterling range expansion predicted that following detection in 1984, their early expansion involved a relatively high population growth rate that stabilised after 5 years. The pattern of bitterling patch occupancy was sigmoidal, with 20 % of the catchment occupied after 20 years, increasing to 80 % after 30 years. Predictions were then for 95 % occupancy after 69 years. The development of this IBM thus successfully simulated the range expansion dynamics of this small-bodied invasive fish, with ABC improving the simulation precision. This combined methodology also highlighted that sub-adult dispersal was more likely to contribute to the rapid colonisation rate than expert opinion suggested. These results emphasise the importance of time-series data for refining IBM parameters generally and increasing our understanding of dispersal behaviour and range expansion dynamics specifically.

2.2 Introduction

Biological invasions are a major aspect of global environmental change, responsible for pervasive changes to native biota and ecosystems (Simberloff et al. 2013, Gámez-Virués et al. 2015). Following the introduction of an alien species into a new range, its invasion success depends, at least in part, on its dispersal dynamics (Byers and Pringle 2006, Havel et al. 2015). In order to make more informed decisions on measures required to control and contain invasive species, managers need information on dispersal dynamics, along with establishment rates and ecological impacts (Gozlan et al. 2010a, Early et al. 2016). The extent of many invasions has proved difficult to predict due to a general lack of knowledge on dispersal dynamics and their relationship with population parameters, especially where the invader lacks data from their native range (Karakuş et al. 2018), so here we demonstrate an analytical method that potentially overcomes these issues.

Predictive approaches that provide realistic representations of real-life invasions and enable scenario testing can develop understanding of the dispersal dynamics of invasive species (Bocedi et al. 2014, Samson et al. 2017). A range of modelling approaches exist for predicting the dynamics of range expansions, including analytical methods such as integro-difference modelling (Gilbert et al. 2014, 2017) and stochastic simulations, including individual-based models (IBMs). IBMs have the benefits of flexibility in model formulation, although they tend to be slower to run during formal model fitting approaches and so can be more challenging to use. However, improvements in computer performance in recent years have helped overcome some of these challenges, resulting in IBMs being increasingly applied to ecological issues (e.g. Hedger et al. 2013a, b, DeAngelis and Grimm 2014, Boyd et al. 2018), with approaches for fitting these models to empirical data now emerging (van der Vaart et al. 2018).

Applications of IBMs to invasive species have included simulations on how population control efforts affect the individual movement and population demographics of Eastern brook trout *Salvelinus fontinalis* (Day et al. 2018) and invasive sea lamprey *Petromyzon marinus* (Madenjian et al. 2003, Neeson et al. 2012). The performance of invasion IBMs can, however, be improved when empirical data are available that enable model fitting and enable the parameters that most strongly influence the predicted patterns to be identified (Phang et al. 2016), but these data are rarely available. For example, although Samson et al. (2017) investigated the spread of invasive round goby *Neogobius melanostomus* using the ‘RangeShifter’ platform (Bocedi et al. 2014), with model parameters developed from stakeholder interaction, scientific literature and inverse modelling approaches, the model could not be calibrated fully due to an absence of empirical data on their invasion. When empirical data are available, the modelling processes can utilise these to derive more robust estimates of model parameters by the application of inverse fitting techniques, such as approximate Bayesian computation (ABC; van der Vaart et al. 2015). ABC enables estimates of model parameters to be refined by combining information from empirical data (such as spatial and temporal distribution data), with prior probabilities derived from literature and/or expert knowledge (van der Vaart et al. 2015). ABC has been used to estimate model parameters within IBMs by Boyd et al. (2018), who developed a generic marine fish bioenergetics IBM for evaluating fish population dynamics. To our knowledge, an ABC process within an IBM has not been applied to modelling the dispersal dynamics of an invading species, despite the importance of estimating their dispersal and population parameters, and how these vary with time since their introduction and establishment (Alford et al. 2009).

The importance of using processes such as ABC to estimate dispersal parameters of invaders is that these parameters strongly influence the invasion process. Whilst introductions of alien species via long-range dispersal events (via transport or through passive dispersal) strongly influence the large-scale rate of range expansion of invaders (e.g. between countries and regions) (Hastings et al. 2005, Wilson et al. 2009), these events are then followed by range infilling via diffusive spread and/or active dispersal (e.g. within the country or region of the introduction) (Gozlan et al. 2010b). Here, diffusion theory suggests that there will be a symmetrical, radial expansion from the area of introduction (Skellam 1951), with the rate of expansion dependent on the interaction of the dispersal ability and reproductive rate of the population (Fraser et al. 2015). It will also be influenced by factors including spatial heterogeneity, temporal variability and biotic resistance from native species (Hastings et al. 2005). This dispersal of the alien species at the ‘leading edge’ of their invasion range is important for understanding the rate at which habitats in the new region are colonised (Wilson et al. 2009) and the population parameters that are driving this.

Within fluvial environments, dispersal events are also likely to be subject to directional bias, given the ease of downstream movement by individuals via passive drift (Byers and Pringle 2006). If upstream colonisation is to be achieved, then active dispersal is important, especially if obstacles are to be overcome that can impede movement (Vitule et al. 2012). This makes it especially important to understand the processes driving active dispersal at the upstream leading edge of the invasion range. Tracking the natural dispersion of invasive fishes in rivers can be difficult when anthropogenic activities occur, such as unregulated secondary release (stocking) events by anglers to increase angling opportunity, as these releases are likely to result in more rapid colonisation rates than possible by natural processes alone (Antognazza et al. 2016). However, these activities are less apparent when the invader has low recreational and socio-economic value, such as in many small-bodied alien fishes (especially if the species is rarely used as bait fish by anglers), meaning their colonisation rates are primarily due to natural dispersal alone (Davies et al. 2013, Davies and Britton 2016).

The aim of this study was to thus incorporate an ABC process into an IBM for simulating the 30 year invasion of an alien, small-bodied fish in a river basin, including identifying the population parameters that most strongly influenced their rates of dispersion, and then predicting their future range expansion. The model invader was bitterling *Rhodeus sericeus* and the modelled river basin was the Great Ouse in Eastern England, with the model developed on the ‘RangeShifter’ IBM platform. In the Great Ouse, bitterling has undergone a natural range expansion since the 1980s, with the species not considered to have been subject to multiple releases due to their low recreational and socio-economic value.

2.3 Materials and methods

2.3.1 Study species and river system

The bitterling is a freshwater fish of the Cyprinidae family that was introduced into Britain in the 1920s, probably for ornamental reasons (Davies et al. 2004, Damme et al. 2007). A small-bodied (< 70 mm) littoral species, it shares many life history traits with other small-bodied invasive fishes, such as a limited lifespan (< 4 years) and early sexual maturity (in the second or third year of life). It has no angling or aquaculture value, so is considered as rarely subject to secondary stocking events for fishery interests (Davies et al. 2004). Unlike other small-bodied invaders, however, its reproduction involves a parasitic relationship with freshwater mussels, where females lay their eggs within the mussel gills (Mills and Reynolds 2002, 2003, Damme et al. 2007). The presence of eggs in gills can impact mussel performance through decreased ventilation, food intake and growth (Reichard et al. 2006). The quality of individual mussels as hosts also reduces with increased parasitism due to gill damage (Mills et al. 2005, Reichard et al. 2007, Smith 2017), suggesting some density-dependent regulation of bitterling reproduction.

The River Great Ouse rises in central England and flows in a generally north-easterly direction before entering the North Sea, and drains a catchment of approximately 8380 km^2. In its lower reaches, the river flows through areas of low-lying land of low gradient (fenland). In these fenland areas, the river channel is characterised by anthropogenic alteration for land drainage and flood relief, including the presence of artificial drainage ditches and pumping stations (Mostert 2017). The bitterling is believed to have been introduced into its tributary, the River Cam, in the mid-1970s (Davies et al. 2004), although the reason for its release (such as whether it was accidental or intentional) is not known.

2.3.1.1 Bitterling time-series data in the Great Ouse

The Environment Agency (the public regulatory body for inland fisheries in England) and its predecessors commenced monitoring of the fish assemblage of the Great Ouse catchment in 1984; this monitoring involves sampling up to 72 sites approximately every 3 years using a consistent seine netting methodology (Bayley and Herendeen 2000). In the initial surveys of the mid-1980s, bitterling was captured only in a series of small channels that connect to the River Cam (Figure 2.1). Surveys completed up to 2017 provide data that enables their spread throughout much of the lower catchment to be tracked. The minimum data available for each of these surveys are the site location, date of sampling, and the number of bitterling captured (Environment Agency 2018). Due to the relatively large mesh size of the seine nets used, the majority of captured bitterling were 55 to 70 mm in length, i.e. mature adults of generally 2 or 3 years old, with smaller individuals unrepresented in catches. It was this data time-series that was used to estimate key parameters of the IBM (Environment Agency 2018).

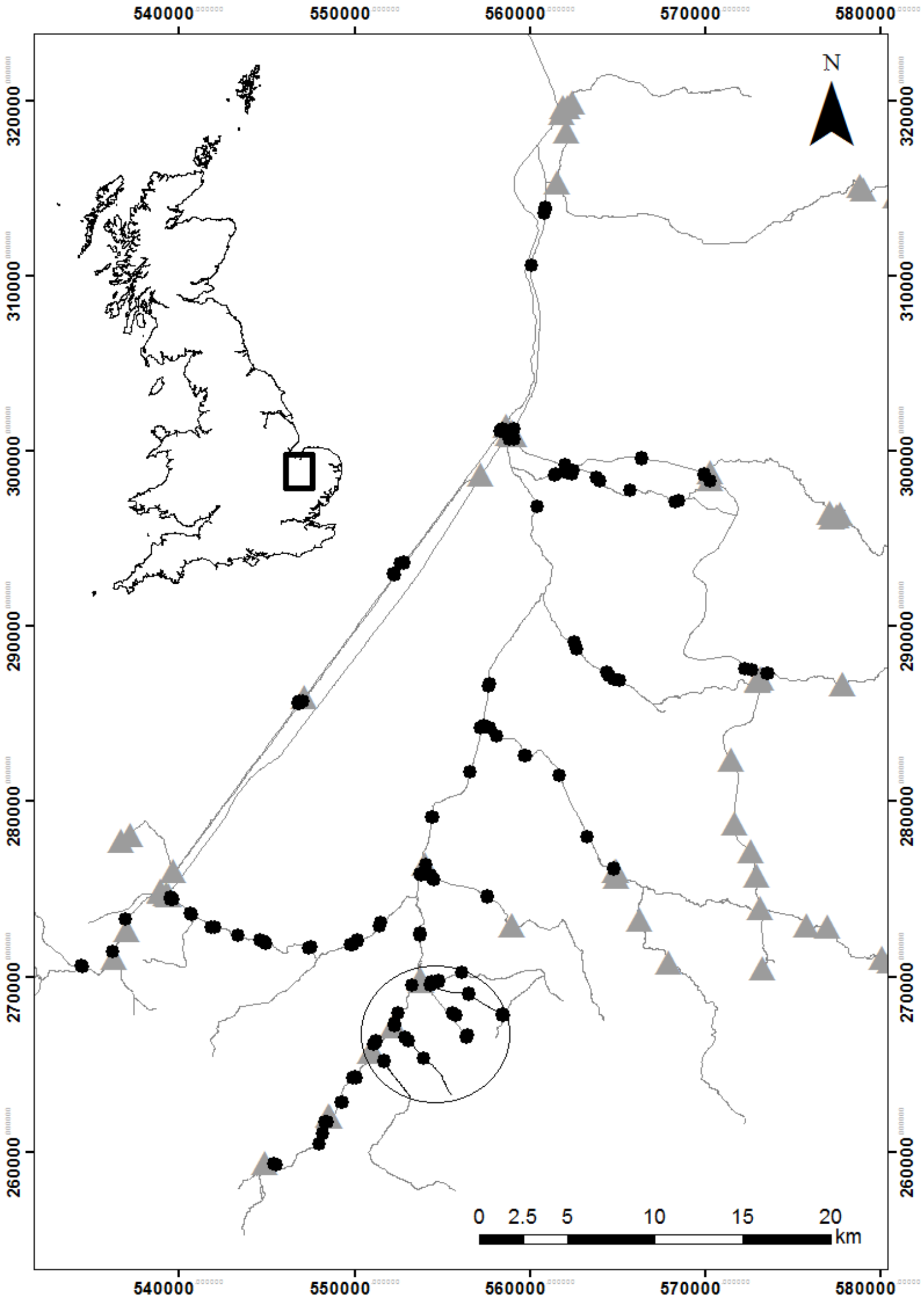


Figure 2.1. The lower catchment of the Great Ouse river in eastern England, showing bitterling sampling sites (black circles) and potential barriers to their upstream dispersal within the catchment (grey triangle; weirs, locks, pumping stations, sluices and aqueducts). The river channel is in light grey, other than the area where bitterling were initially captured in 1984 (indicated by a black open circle). Co-ordinates are of the Ordnance Survey national grid, and the inset figure shows the location of the catchment by a black square. © Crown copyright and database rights 2018 Ordnance Survey (100025252)

2.3.2 IBM development to model bitterling range expansion

The platform ‘RangeShifter’ was used to develop the IBM, as it allows the development of spatially explicit IBMs in which the three key dispersal phases of emigration, transfer and settlement are represented independently (Bocedi et al. 2014, Samson et al. 2017). A customised version of ‘RangeShifter v2.0’ was used, which incorporated code to estimate model parameters by ABC given suitable high-level observed data. Development of the IBM required the following steps: mapping the catchment (including splitting the continuous river stretches into discrete sub-population patches), collating data on bitterling demography, dispersal and range expansion in the Great Ouse catchment, setting the prior distributions of parameters to be estimated, model fitting by ABC and finally, simulation of future spread. Fitting the ABC was examined by using the customised version of ‘RangeShifter’, with the simulation of future bittering spread then completed in ‘RangeShifter v1.1’ (Bocedi et al. 2014) using the final set of parameter samples from the ABC.

2.3.2.1 Mapping the cacthment

The initial catchment layers were extracted as tiles of geographic mark-up language from Ordnance Survey data (Ordnance Survey 2018) and converted into a shapefile using ‘QGIS 2.14.20’. Following removal of minor drainage channels in which fish were assumed not to be present, it was converted to a raster format at a resolution of 50 m using ‘ArcGIS 10.3.1’. However, as the channel width throughout most of the catchment was substantially less than 50 m, each river cell was assigned a quality score using the mean channel width of the features enclosed by each cell. Thus, we created a raster of habitat quality, with this quality measure based on our assumption that sections of greater river width would have larger and more heterogeneous littoral areas that provided enhanced habitat quality for bitterling.

The catchment was then divided into a series of non-overlapping contiguous patches, where a patch comprised of a set of cells that delimited an area of river. Although the Great Ouse is a continuous and linear system, the use of patches assumed that each patch delimited the range of a reasonably self-contained sub-population, which was connected to neighbouring sub-populations by dispersal. The delimitations were made in a consistent manner, in which confluences, weirs and other anthropogenic features were used to delimit patches where they were present (Figure 2.1); elsewhere, patches were based on segmentation in the Ordnance Survey data which in turn was based on stream width (n = 272, mean length = 2420 m, SD = 1270 m). The variation in patch length had a minimum effect in the model, as patches of contrasting length were well-mixed locally throughout the catchment.

2.3.2.2 Bitterling development stages and population parameters

Three stages of bitterling development were defined in the model, 'juveniles', 'sub-adults' and 'adults'. Juveniles were the fish that initially develop inside the mussel gills before emergence and were less than one year old (0 + , young-of-the-year). Sub-adults were fish between 1 and 2 years old that were primarily immature and so not considered as reproductively active. Finally, adults were fish of 2 + years old and were considered as mature fish, capable of reproduction. This enabled each of the stages to be treated separately within the modelled dispersal process (Bocedi et al. 2014).

For each year in the simulation, the probabilities of juveniles developing into sub-adults, sub-adults developing into adults, and adults reproducing were set to unity, i.e. the event occurred if the individual survived. Reproduction was modelled using a transition matrix for each of the three stages defined above (Caswell 2001), with the parameters being survival, development to the next stage and fecundity (Table 2.1). The latter was set as the number of offspring per female that survive to one year old at quasi-zero population density, and was subject to density-dependence (lower rates for higher population densities; Neubert and Caswell 2000). Survival by stage was also assumed to be density-dependent, and was weighted such that juveniles had no effect on later stages, and sub-adults had only 10 % of the effect on adults as adults had on each other and on sub-adults. The density-dependence attributed to the two previous parameters was due to the negative effect that a large number of parasitizing bitterling eggs can have on the quality of mussel gills, where mussel performance is reduced and bitterling would not be able to reproduce again on those mussels with reduced fitness (Mills et al. 2005, Reichard et al. 2007, Smith 2017).

Table 2.1. Demographic and dispersal parameters used in the bitterling IBM implemented in ‘RangeShifter’. ABC* in the ‘Value’ column denotes parameters that were estimated by approximate Bayesian computation

Model parameters	Stage-structure	Density-dependence	Value
Population dynamics parameters			
Number of reproductive seasons/year	Adults	No	1
Proportion of males	Whole population	No	50 %
Rate of density dependence (***1/b***)	Whole population	No	ABC*
Probability of reproducing	Adults	No	1
Fecundity (**ø**)	Adults	Yes	ABC*
Survival rate (**σ**)	Juveniles	Yes	ABC*
	Sub-adults	Yes	ABC*
	Adults	Yes	ABC*
Development rate (**γ**)	Juveniles	No	1
	Sub-adults	No	1
	Adults	No	0
Emigration parameters			
Asymptote (**D**)	Juveniles	No	0
	Sub-adults	Yes	ABC*

	Adults	Yes	ABC*
Slope	Whole population	No	10.0
Inflection point (**β**)	Juveniles	No	0
	Sub-adults	Yes	ABC*
	Adults	Yes	ABC*
Transfer parameters			
Directional persistence	Whole population	No	1.5
Perceptual range	Whole population	No	50 m
Memory size (no. of cells)	Whole population	No	2
Step mortality probability (**SMc**)	Whole population	No	ABC*
Settlement parameters			
Settlement probability (**S**)	Whole population	No	ABC*
Max. no. of steps	Whole population	No	100

2.3.2.3 *Dispersal parameters*

In 'RangeShifter', dispersal is modelled in three phases: emigration, transfer and settlement, so that dependencies can be added to each phase separately (Bocedi et al. 2014). Emigration was set to zero for juveniles, which stay within mussel gills for a proportion of their first year of life. For older stages, emigration was low if density was below a certain inflection point and higher if density was above the inflection point. We assumed that the dispersal probability of the sub-adults would be low due to high mortality risks at this life stage, and therefore the adult fish would be the main dispersers. The transfer of individuals was modelled using the stochastic movement simulator (SMS). This models how the individual moves on a cell-by-cell basis, as determined by relative costs (in the sense of the least cost path approach) and a tendency to maintain a correlated path (directional persistence) (Palmer et al. 2011, Coulon et al. 2015, Samson et al. 2017). Our habitat quality raster was incorporated, so that a dispersing individual would be more likely to move into the wider of two branches when reaching a confluence. A per-step mortality constant was applied so that individuals would not move indefinitely if they did not find a suitable patch for settlement. Finally, settlement probability in a non-natal patch was considered as density-independent, but less than 1.0 (Table 2.1).

2.3.2.4 *Estimation of parameters by ABC*

Prior distributions of the eleven parameters to be estimated by ABC (Table 2.1) were generated using information extracted from the literature and expert opinion. Given that bitterling life history traits have not been studied extensively, information extracted from literature was mainly based on the parasitic relationship between mussels and bitterling, so that the model should incorporate some density dependence in fecundity to account for this (Mills et al. 2005, Reichard et al. 2007, Smith 2017). Otherwise, priors were based on author opinion from their experience of working on other small-bodied invasive cyprinid fish, such as *Pseudorasbora parva* (e.g. Britton et al. 2007, 2008, 2010; Figures 2.2, 2.3 and 2.4; Table A1.1). A total of 250,000 parameter combinations was sampled independently from the prior distributions and, for each of the parameter combinations, five replicate simulations were run. These simulations were initiated using the bitterling distribution in 1984 (using 1983 as year of starting simulation; Figure 2.1), and finishing in 2018. Predicted patch-level presence and pre-reproduction sub-population sizes averaged over the five replicates for each simulation were compared with observed presence data and fish density estimates. A distance metric was computed to determine how close the predictions of the model given the sampled parameters were to the actual time-series of range expansion. We adapted the distance metric ρ of van der Vaart et al. (2015) by introducing a weighting for each observed value, so that the model fit for the ith sample set becomes

$$\rho(i) = \sqrt{\sum_j w_j \left(\frac{m_{i,j} - D_j}{sd(m_j)}\right)^2}$$

where D_j is the observed value for empirical data point j given weight w_j, $m_{i,j}$ is the corresponding predicted value from the model for parameter sample set i and the standard deviation $sd(m_j)$ is a scaling factor to allow for the observed data points to be made at different scales (sub-population count up to many thousands, presence constrained to lie between zero and one). We used 620 observed data points. These comprised 394 presence/absence observations and 226 sub-population estimates. We down-weighted 220 of the presence/absence observations (56 %) for which we had assumed absence (e.g. that a patch was not occupied in the years immediately preceding the first observation of bitterling within it); weightings were reduced from 1.0 by 0.1 in successive years from the actual observation up to a maximum reduction of 0.5. A ranking of the 250,000 distance metrics was then generated and the best-fitting 250 retained to provide the posterior probability distributions. These 250 samples provided the credible intervals for the estimated parameters based on the observed range expansion data, enabling comparison of prior versus posterior distributions (Csillery et al. 2010).

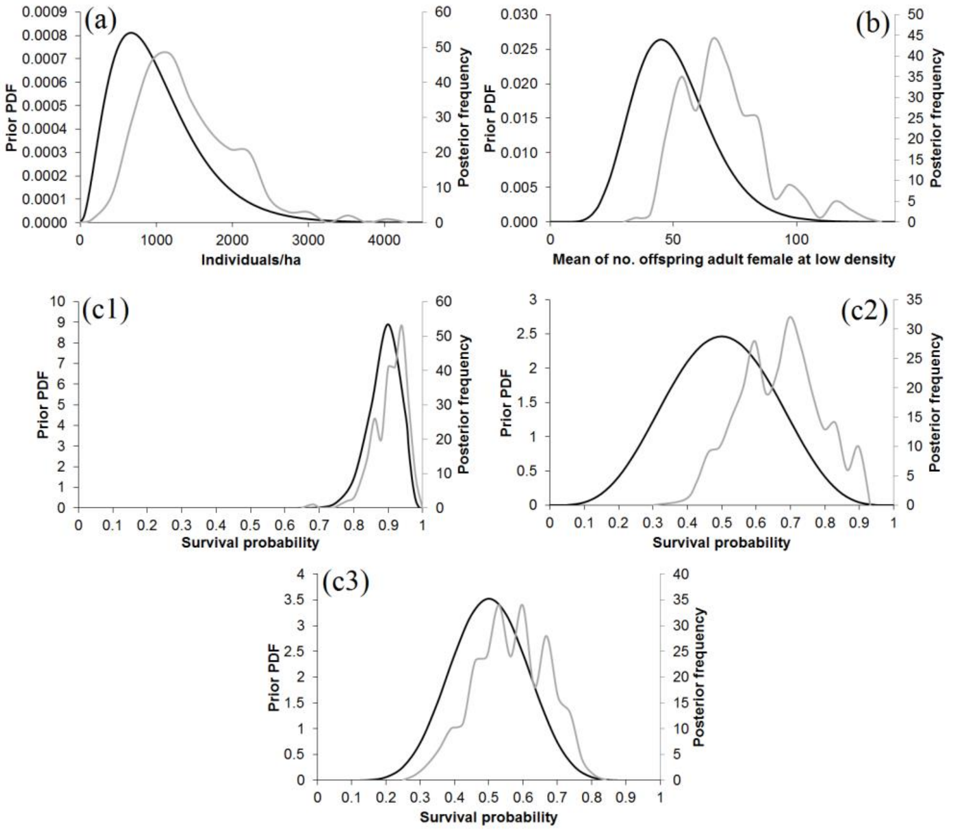


Figure 2.2. Prior (black) and posterior (grey) distributions of the demographic parameters: (a) rate of density dependence (*1/b*), (b) fecundity (ø), (c) stage-dependent survival rates (c1 juveniles, c2 sub-adults, c3 adults). *PDF* probability density function

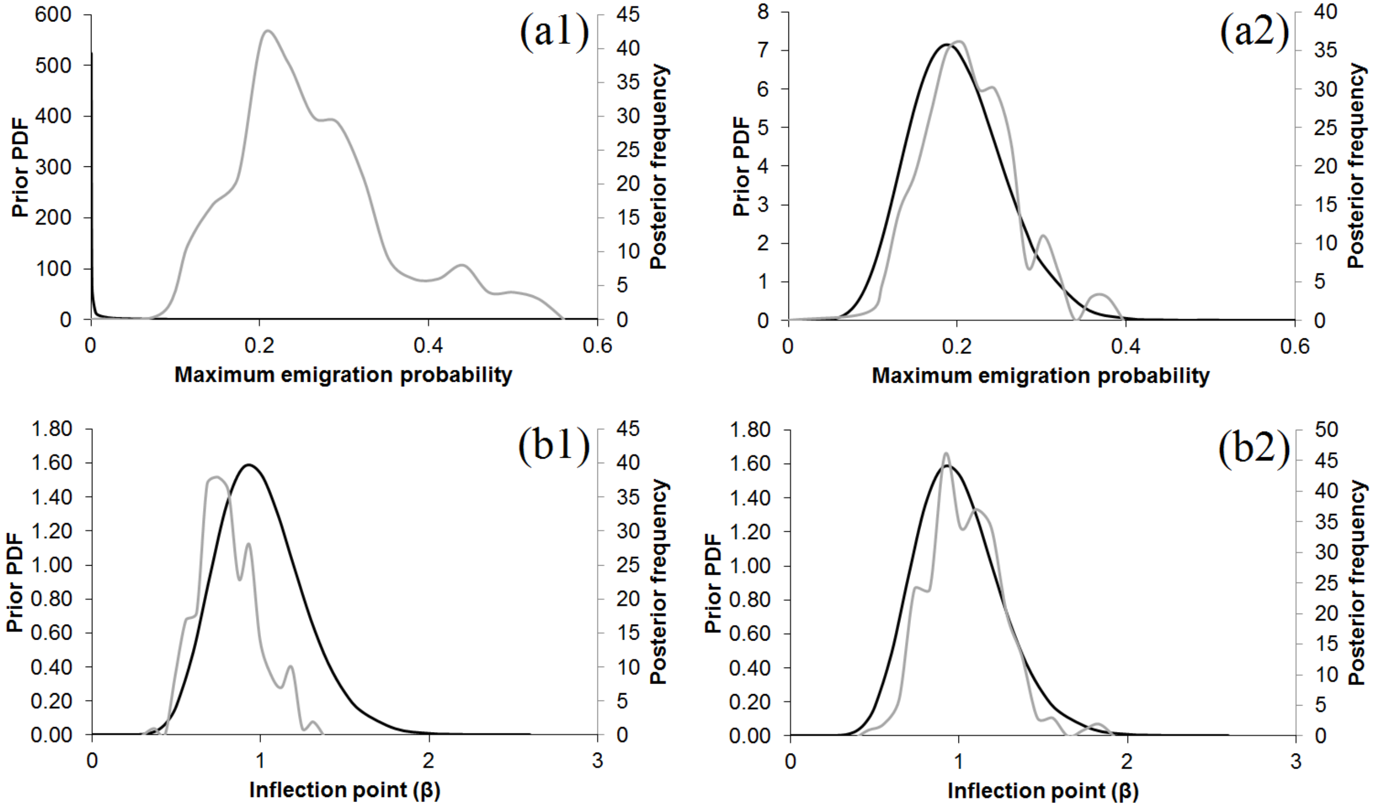


Figure 2.3. Prior (black) and posterior (grey) distributions of the density-dependent emigration model: (a) stage-dependent asymptote (a1 sub-adults, a2 adults), (b) stage-dependent inflection point (b1 sub-adults, b2 adults). *PDF* probability density function

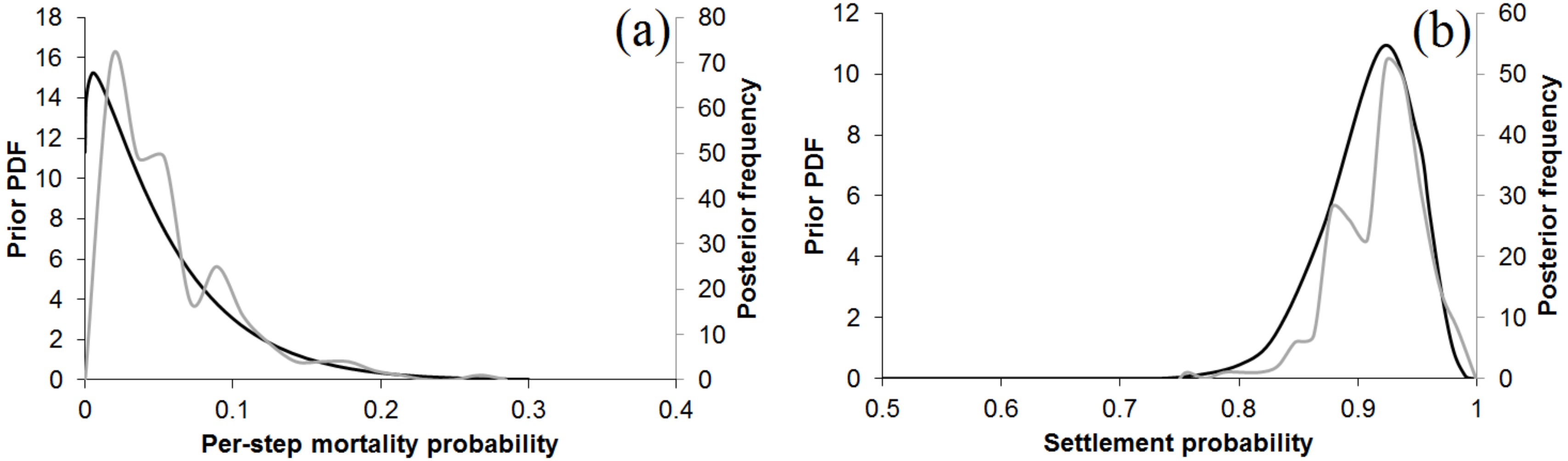


Figure 2.4. Prior (black) and posterior (grey) distributions of the transfer and settlement phase parameters: (a) step mortality probability (SMc), (b) settlement probability (S). *PDF* probability density function

2.3.2.5 Goodness-of-fit

We estimated the goodness-of-fit of the model in two ways: (1) predicted presence/absence was averaged over all 250 parameter sets and a single goodness-of-fit statistic was calculated on the basis of one set of predictions encompassing parameter uncertainty, and (2) owing to parameter uncertainty, a goodness-of-fit statistic for each parameter set was calculated and then an average statistic and uncertainty was determined around it. In both cases, the true skill statistic (TSS) was used, which has been recommended for evaluating the accuracy of species distribution models (Allouche et al. 2006). The TSS takes a value from −1 to +1, where zero equates to a fit no better than random and +1 indicates a perfect fit.

2.3.2.6 Prediction of future range expansion

Following this model-fitting process, prediction of the future expansion of bitterling was simulated, starting from their initial detection in samples in 1984 (using 1983 as year of starting simulation) and running for the next 100 years. The starting point of 1983 was used instead of the most recent observed distribution (2018), as ‘RangeShifter’ requires all patches to be initialised at the same density. Thus, had 2018 been used as the starting point, then simulations would have been based on that year’s mean patch density and ignoring the high spatio-temporal variance in population sizes at the range front, thereby altering the patterns of density-dependent emigration and settlement in the years following initialisation.

All the parameters used during this simulation were set up as in the posterior distribution, i.e. 250 simulations were run which would give predictions allowing for model parameter uncertainty. Standard error and confidence intervals for 90 % and 95 % of patch occupancy from the 250 predictions were also calculated. Those percentages correspond to when the catchment is considered to be fully colonised. The bootstrapping resampling technique was used for this purpose, as the data did not meet parametric assumptions (Mooney and Duval 1993, DiCiccio and Efron 1996, O’Hagana and Stevens 2003). All statistical analyses were conducted using ‘R 3.5.1’ (R Core Team 2018).

The data used to develop and calibrate the model are available from the Environment Agency (2018).

2.4 Results

2.4.1 Model fitting

The posterior distributions for six of the parameters were similar to their priors, i.e. the empirical data provided little additional information upon which to reduce parameter uncertainty. For the other five, however, there were varying degrees of difference between posterior and prior (Figures 2.2, 2.3 and 2.4). For rate of density dependence (*1/b*), sub-adult survival and adult maximum emigration probability, the posterior estimates were somewhat higher than priors. For per-step mortality probability, posterior estimates were lower than priors. Most notably, for sub-adult maximum emigration probability, there was a substantial difference between the relatively high maximum emigration probability posterior estimates and the prior assumption of extremely low probability. These five posterior distributions showed some tendency to be inter-correlated, especially sub-adult maximum emigration probability, for which low values tended to be associated with high values of *1/b* and low values of per-step mortality probability (Table A1.2).

The goodness-of-fit of the model as calculated by method 1 yielded a TSS value of 0.759, and method 2 yielded a mean TSS value of 0.728 (90 % confidence interval 0.685 to 0.765). The applied goodness-of-fit revealed that the model presented here was able to reproduce the observed pattern of colonisation of the catchment with a relatively high degree of accuracy. Moreover, a more accurate fit to the observed pattern was obtained if the 250 samples of our posterior distribution were treated as a collective whole than as individual predictions.

2.4.2 Simulating bitterling range expansion

From the initial records of bitterling presence in 1984, their predicted early spread matched relatively well with the observed time-series occupancy (Figure 2.5a), although the model was unable to replicate the period of near stasis in the sampled data between about 1992 and 2007. Maps of model deviance of bitterling presence at the patch level that were averaged over the whole modelled period and for the decade of near stasis (Figures A1.1 and A1.2) both demonstrated spatially correlated patterns, which suggested some potential influence of spatio-temporal variation in sampling effort and possibly also the effect of a sluice acting as a barrier in the south-western part of the catchment. Predicted patch occupancy showed a sigmoidal pattern; while it took 20 years for bitterling to occupy 20 % of the catchment, they are then predicted to only require a further 30 years to achieve 80 % occupancy (2030) (Figure 2.5b). With 95 % confidence, it was predicted that 90 % of the patches would be occupied after 61 to 63 years (2044 to 2046) and 95 % occupied after 69 to 71 years (2052 to 2054) (Figure 2.6; Table 2.2).

Table 2.2. Predicted mean year at which 90 % and 95 % patch occupancy of the Great Ouse catchment will be attained, together with predicted numbers of sub-adult and adult bitterling at that time. Standard error (SE) and 95 % confidence intervals (CI) were calculated by the adjusted bootstrap percentile method across all 250 simulations from the posterior parameter distribution

	Patch occupancy	**Year**	**Number of sub-adults (thousands)**	**Number of adults (thousands)**
Mean	90 %	62.3	109	102
	95 %	70.1	110	103
SE	90 %	0.259	4	3
	95 %	0.281	4	3
CI	90 %	(61.8, 62.8)	(102,117)	(96,109)
	95 %	(69.5, 70.6)	(103, 118)	(97, 111)

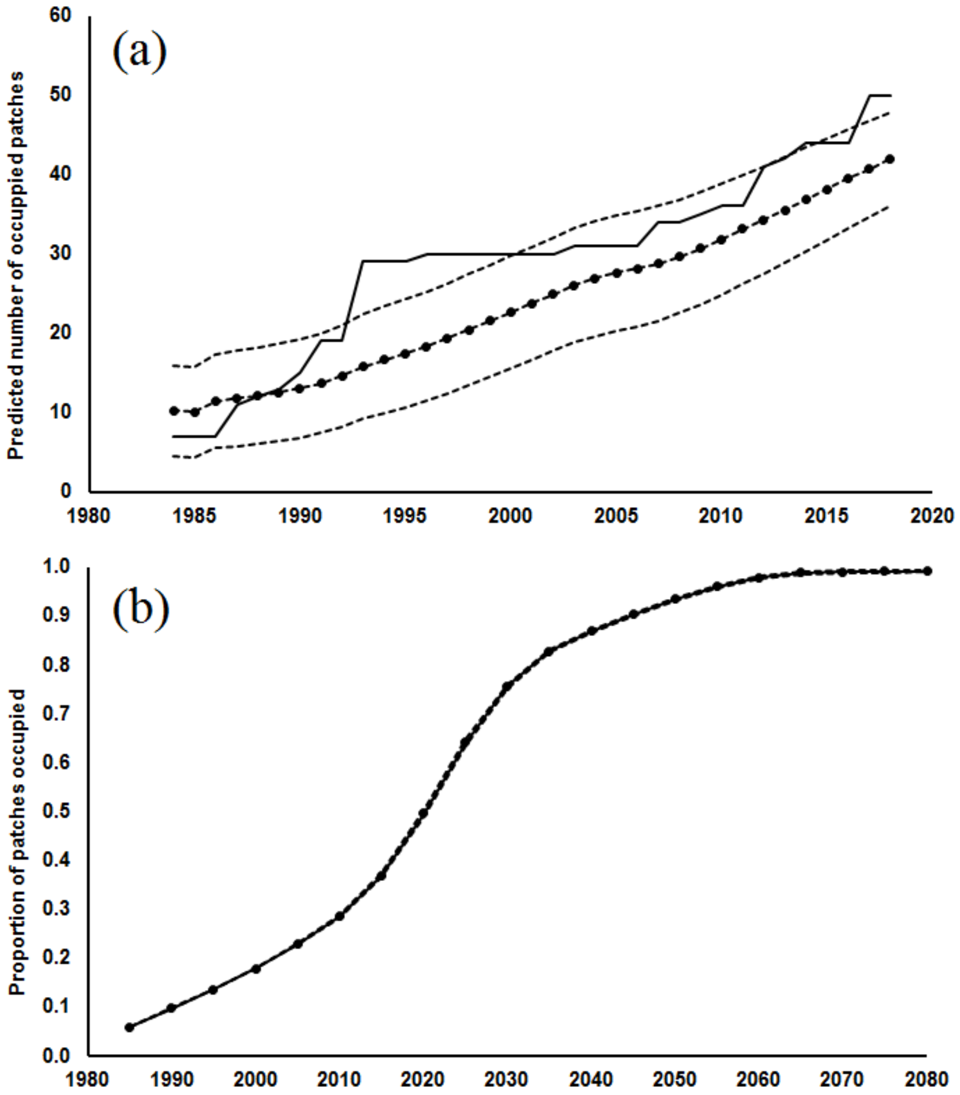


Figure 2.5. (a) Comparison between the observed number of occupied patches (black continuous line; sampled by seine-netting) and the mean occupancy of the same patches from 250 predictions using the posterior parameter distributions (Dotted-dashed line), (b) predicted patch occupancy over 100 years of the whole catchment using the 250 parameter sets of the posterior distribution (Dotted-continuous line). Upper and lower 95 % confidence limits for the mean of 250 posterior predictions are shown with dashed lines on both figures

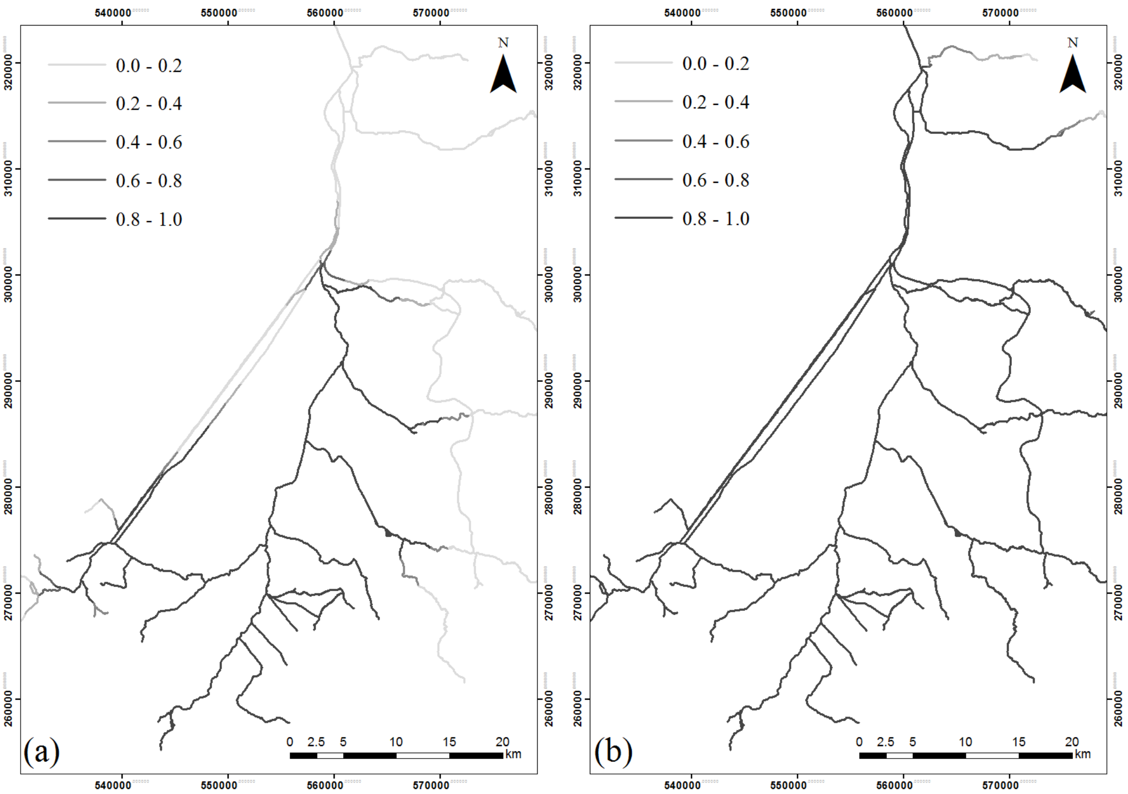


Figure 2.6. (a) Predicted current distribution (2018) and (b) predicted occupancy (by 2045) of the catchment with 95 % confidence. Grey-scale: probability of occupancy ranging from low (light grey) to high (dark grey). Crown copyright and database rights 2018 Ordnance Survey (100025252)

2.5 Discussion

We have demonstrated how approximate Bayesian computation can be applied to estimate the parameters of a mechanistic simulation model for predicting the future spread of an invading alien species. Our prior knowledge of some of the model parameters was imprecise, but by combining that knowledge with observed data on the spread of the case-study species to date, and with estimates of its local population density, we were able to refine the parameter estimates and, just as crucially, allow for inter-correlations between them. The refined parameter estimates enabled predictions of future occupancy of the catchment to be made with a relatively high degree of precision. The model revealed a sigmoidal pattern in temporal patch occupancy by bitterling in the catchment, with predictions of 95 % patch occupancy after 69 years. The implications of this model are now discussed in relation to the insights gained on bitterling dispersal by the model, the performance of the model in predicting the temporal and spatial pattern of bitterling dispersal, and finally how the model provides important insights into invasion management.

2.5.1 Model insights into bitterling dispersal

Our prior distributions of model parameters were mainly based on expert opinion of the ecology of small-bodied cyprinid fishes, as bitterling population biology is relatively data poor because of their negligible fishery value and interest. The only exception was that their mode of reproduction involves parasitism of mussels, resulting in some density dependence in recruitment (e.g. Mills et al. 2005, Reichard et al. 2007, Smith 2017). That the prior bitterling population biology data were limited was not unusual, as low value aquatic species often lack empirical data on their populations (Karakuş et al. 2018, Tarkan et al. 2018). Thus, when these species are introduced into a new region, whether intentionally or accidentally (Gozlan et al. 2010a), the data available for predicting their invasiveness are often limited (Top et al. 2018), resulting in poorly informed model parameters (Heikkinen et al. 2014, Urban et al. 2016) and final models with high uncertainty (Parry et al. 2013). We showed that monitoring programmes can provide dispersal time series that, when coupled with ABC methods, can help overcome this lack of prior data, enabling more robust predictions of the dispersal dynamics and future invasiveness of the modelled species (Neeson et al. 2012, Barros et al. 2016, Samson et al. 2017).

The ABC routine thus enabled the values of the data-poor model parameters to be predicted in a more robust manner (van der Vaart et al. 2015, 2016). Comparison of the prior versus posterior distributions of these parameters revealed that some posteriors differed little from their priors, suggesting that expert opinion appropriately informed the model priors. There were, however, five model parameters that were strongly informed by the dispersal time series and thus were poorly informed by expert opinion. Of these, the relatively high posterior estimates of maximum emigration probability of sub-adult bitterling (D) were particularly interesting. The prior distribution of D for sub-adults was based on the assumption that the dispersal probability of the sub-adults would be low, due to high mortality risks at this life stage. This assumption was formed due to the combination of asocial, individual fish often being the dispersers at the invasion front (Cote et al. 2010) and smaller-bodied individuals having higher predation risks (Nilsson and Brönmark 2000). Thus, small-bodied, sub-adult bitterling were assumed to be relatively sedentary to maximise their survival, and any that did disperse would have a high probability of predation. Indeed, in invasive round goby *Neogobius melanostomus*, upstream-directed range expansion was led by the movement of larger bodied individuals of high trophic positions, rather than juveniles that were leaving high density areas due to, for example, high competition (Brandner et al. 2013). However, when we used low emigration rates of sub-adults, patch occupancy did not match the observed occupancy time series. Instead, the ABC component of the IBM showed that there should be dispersive behaviours by both sub-adults and adults driving this bitterling invasion. In part, this may be due to an artefact of ‘RangeShifter’, whereby an individual which has dispersed may not do so again. If the model allowed dispersal by adults only, then there would inevitably be a delay of two years between the colonisation of a patch and the production of the next wave of dispersers. We could compensate by making patches longer, but that would result in reduced spatial precision.

The age-specific dispersal preferences of bitterling detected by our model have also been detected in other fishes (Frank 1992, Stiver et al. 2007). For example, high levels of gene flow in *Lethrinus nebulosus* were assumed to result from high adult dispersal, yet models indicated that it was larval dispersal, not adult, that caused the gene flow patterns (Berry et al. 2012). Correspondingly, the use of ABC provided an important insight into bitterling stage-specific dispersal and suggests some counter-intuitive dispersal patterns at the invasion front that warrant further empirical investigation.

2.5.2 Predictions of the bitterling dispersal pattern

The comparison of simulated versus actual time series data enabled the future development of bitterling invasion to be predicted by the IBM with relatively high confidence. In periods of rapid range expansion, individuals at the range front often show rapid population growth, facilitated by individuals investing heavily in somatic growth and reproduction when density dependence process are rarely apparent (Britton and Gozlan 2013). For example, in *N. melanostomus*, individuals at the invasion front gained dispersal advantages by attaining large body sizes relatively quickly, facilitated by low competition (Brandner et al. 2013). With 20 % occupancy of the catchment after 20 years, the somewhat higher colonisation rates thereafter were likely to be due to the population gaining sufficient distribution that it was then able to increase its occupancy of the catchment relatively quickly in both upstream and downstream directions, i.e. it had reached a level beyond which dispersal into a larger number of sites was possible in a relatively short timeframe. However, there was a period of relative stasis in the observed rate of colonisation lasting about 10 years, which the model was unable to capture. Environmental factors acting on key dispersal processes and parameters may have been important in this and would require further exploration in future model development. At present, however, we lack a detailed understanding of the effects of environmental factors on demographic and (especially) dispersion rates, and such relationships have yet to be incorporated into ‘RangeShifter’. Notwithstanding, environmental factors such as water temperature and flow rates in the first summer of life are recognised as important determinants of annual recruitment rates in other riverine cyprinid fishes in England and so might also be important in bitterling population dynamics (Nunn et al. 2007, Beardsley and Britton 2012).

While the IBM was able to provide a series of important insights into how bitterling, as a model small-bodied invasive fish, might disperse through a lowland river catchment, it was also apparent that issues remain with the model that could potentially be improved. The ABC routine could, for example, be refined, especially with regard to the need for the averaging of predicted values over a number of replicates to allow for 'RangeShifter' being a stochastic model (Bocedi et al. 2014). This makes it more difficult for the model to capture the wide variation in adult population densities observed at many of the sampling sites in the years immediately following colonisation. Also, the manner in which the river environment was represented could be improved. For example, the River Great Ouse has a relatively linear river channel whose primary purpose is the flood and drainage management of the surrounding agricultural land. Whilst its separation into a series of patches in the model that accounted for the presence of artificial barriers (weirs, locks, etc.), in the areas away from these barriers, the patches were based mainly on size (2 to 3 km of river length). This was mainly to assist the modelling process and underlying assumptions. This meant, however, that patch delimitation was based on modelling requirements rather than on knowledge of bitterling population demographics and dispersal abilities. For this to be overcome would, however, require data on the individual movements of bitterling across different stages, something that remains technically difficult due to their small body sizes that makes the use of some common telemetry methods highly challenging (e.g. Klinard et al. 2018). Nevertheless, the relatively accurate predictions of the bitterling dispersal pattern were similar to the empirical data. This suggests that the model has high applied utility for simulating the outcome of, for example, management interventions that aim to inhibit their invasion.

2.5.3 Implications for invasion management

The results of this study have highlighted that IBMs have high utility for gaining knowledge on the dispersal processes of aquatic invaders that are difficult to obtain from empirical data collection alone and can be used to help develop more informed management practices (Sakai et al. 2001, Grimm et al. 2006, Samson et al. 2017). Indeed, even without completing any further simulations, the IBM results suggest there were two opportunities for management interventions to have been implemented on the Great Ouse that could have inhibited the bitterling invasion. The first would have been immediately following their initial detection in a very restricted spatial area in 1984, as management interventions are easier and more effective when the extent of invasion is limited (Pyke et al. 2008, Britton et al. 2011b). The second opportunity would have been the 20-year period of low colonisation rates, although this would have been more difficult than previously due to the greater spatial extent of catchment occupancy. It is, however, acknowledged that eradicating or even controlling populations of invasive fishes in open systems is highly challenging (Britton et al. 2011b, Davies and Britton 2015). Management interventions on this scale also usually require rapid implementation (Pyke et al. 2008), supported by robust invasion risk assessment processes (Copp et al. 2009). Management interventions are then usually only implemented on those invaders assessed as relatively high risk (Britton et al. 2011b). Correspondingly, the lack of initial management interventions in 1984 were likely to have resulted from the paucity of invasion assessment tools available at that time, coupled with no predictive assessment of the potential extent of their invasion. Given the extent of their range today, even if invasion risk assessments suggest some population control is required, it would most likely be prohibitively expensive and/or have a low likelihood of success (Britton et al. 2011b).

2.6 Conclusions

A relatively complex IBM was developed here that enabled key invasion processes, such as dispersal, to be incorporated into model fitting using an ABC regime. The model revealed that whilst a range of different combinations of parameter values fitted the observed time series data, nevertheless, it delivered some important predictions into the dispersal dynamics of bitterling. Thus, the approach delivered novel insights into the ecological behaviours and dynamics of this invader, with the model improving our ability to predict, and ultimately manage, successful invasive species.

3 Predicting the outcomes of management strategies for controlling invasive river fishes using individual-based models

3.1 Abstract

The effects of biological invasions on native biodiversity have resulted in a range of policy and management initiatives to minimize their impacts. Although management options for invasive species include eradication and population control, empirical knowledge is limited on how different management strategies affect invasion outcomes. An individual-based model (IBM) was developed to predict how different removal (‘culling’) strategies affected the abundance and spatial distribution of a virtual, small-bodied, *r*-selected alien fish (based on bitterling, *Rhodeus sericeus*) across three types of virtual river catchments (low/intermediate/high branching tributary configurations). It was then applied to nine virtual species of varying life-history traits (*r*- to *K*-selected) and dispersal abilities (slow/intermediate/fast) to identify trade-offs between the management effort applied in the strategies (as culling rate and the number of patches it was applied to) and their predicted effects. It was also applied to a real-world example, bitterling in the River Great Ouse, England. The IBM predicted that removal efforts were more effective when applied to recently colonized patches. Increasing the cull rate (proportion of individuals removed per patch), and its spatial extent was effective at controlling the invasive population; when both were relatively high, population eradication was predicted. The characteristics of the nine virtual species were the main source of variation in their predicted abundance and spatial distribution. No species were eradicated at cull rates below 70 %. Eradication at higher cull rates depended on dispersal ability; slow dispersers required lower rates than fast dispersers, and the latter rapidly recolonized at low cull rates. The trade-offs between management effort and the outcomes of the invasion were, generally, optimal when intermediate effort was applied to intermediate numbers of patches. In the Great Ouse, model predictions were that management interventions could restrict bitterling distribution by 2045 to 21 % of the catchment (versus 90 % occupancy without management). Synthesis and application. This IBM predicted how management efforts can be optimized against invasive fishes, providing a strong complement to risk

assessments. We demonstrated that for a range of species' characteristics, culling can control and even eradicate invasive fish, but only if consistent and relatively high effort is applied.

3.2 Introduction

Biological invasions are an important component of global change (Simberloff et al. 2013), which have resulted in the application of a range of policy and management initiatives to minimize their impacts (Larson et al. 2011). Optimising population control efforts within management programs remains highly challenging, and considerable uncertainty remains in how to apply limited staff and financial resources to population control measures, especially as to how these measures should be applied spatially and temporally (Maguire 2004).

Following the introduction of a new species, the probability of an invasive population developing depends on the interactions of a range of biotic and abiotic factors, including the species' dispersal abilities and life-history traits, and the environmental conditions encountered (Catford et al. 2009). Dispersal rates are important and are influenced by habitat connectivity (Hastings et al. 2005), which is often more constrained in freshwaters than in terrestrial environments (Gozlan et al. 2010a, Radinger et al. 2017). Management responses also influence invasion probabilities (Britton et al. 2011c), and their effectiveness generally increases when they occur soon after introduction, when the species is spatially constrained and of relatively low abundance (Rytwinski et al. 2019).

Effective strategies for controlling invasive species must consider two important aspects. First, the most efficient, cost-effective and safe means of removing individuals from a local population must be determined, which will vary by the invader's life stage and the ambient environmental conditions (Buhle et al. 2005). Second, the timing and location of the control measure needs determining. For example, in invasive plant management, there is debate about whether efforts should be focused at the range front, where the invader is of low abundance and patchy in distribution, or at the invasion core, where populations are established and usually more abundant (e.g. Hastings et al. 2006, Januchowski-Hartley et al. 2011). Invader dispersal rates and abundances can also be affected by habitat complexity, with terrestrial invaders generally spreading more easily in unfragmented than fragmented landscapes (Dewhirst and Lutscher 2009). Therefore, understanding the ease with which invaders spread in different environmental configurations needs consideration within management planning (Lurgi et al. 2016).

In managing freshwater invaders, the utility of individual-based models (IBMs) to predict rates of establishment and spread has recently been highlighted (Dominguez Almela et al. 2020), along with comparisons of the methods for controlling and/or eradicating local populations (Rytwinski et al. 2019). There is, however, less known on how invader dispersal rates affect the long-term efficacy of population control, especially at large spatial scales and in open, linear systems. In rivers, while controlling invasive fish can be a management priority, their removal usually relies on capture methods (e.g. nets, traps, electro-fishing; Rytwinski et al. 2019). Although these are effective at capturing (and culling) fish species across most of their size range (Davies and Britton 2015), they are unlikely to remove all the population, and surviving individuals can then potentially compensate for losses (Berry et al. 2012). This can result in culled populations rapidly recovering to their previous abundances and management objectives not being met (Davies and Britton 2015, Dominguez Almela et al. 2020).

Here, our aim was to develop an IBM to predict the effects of management control strategies on invasive river fishes. We applied it within factorial experiments to ‘virtual’ invasive fish with a range of life-history traits in river networks of varying spatial complexity to predict how different culling strategies affected fish spread and abundance. The objectives were to predict: (a) how altering the application of culling (rate/location/timing/life stage) affected the abundance and spatial distribution of an initial invasive fish, based on the demographic characteristics of bitterling *Rhodeus sericeus*, a small-bodied invasive fish (Dominguez Almela et al. 2020); (b) how invader abundances and distributions varied across nine virtual invasive fish differing in life-history traits and dispersal abilities; and (c) the trade-offs between management effort (cull rate and the number of patches culled) and the predicted invader abundances and distributions to optimize management responses. The final model was then applied to a real-world scenario to predict how management interventions could have constrained the real-world invasion of bitterling in the River Great Ouse, Eastern England (Dominguez Almela et al. 2020).

3.3 Materials and methods

3.3.1 Model configuration and virtual species

The model was implemented in a customized version of the individual-based spatially explicit modelling platform ‘RangeShifter’ (Bocedi et al. 2014, 2020), incorporating a new module for managing invasive species. River catchments of an overall mean extent of 74.5 ha and of three basic types were created using ‘ArcGIS Pro’, where the configuration varied by the extent of its tributary branching: high branching (12 tributaries), moderate branching (eight tributaries) and low branching (four tributaries). Each catchment type was replicated three times in slightly different configurations (Figure 3.1). All catchments were created in raster format at 50 m resolution, and each cell was assigned a habitat quality score proportional to stream width (Dominguez Almela et al. 2020). Catchments comprised a mean of 298 (SD: ±20) cells divided into a similar number of non-overlapping patches (mean = 44.9 patches/catchment, SD = ±0.3), which were delineated manually such that no patch overlapped a confluence. The ratio of good to poor quality habitat sections was similar in all configurations; in the main stem, it was kept consistent at 1:1, and in the tributaries, the ratio was maintained across replicates within the branching groups (low/moderate/high) at an overall mean of 8:15.

The initial virtual fish, whose demographic and dispersal parameters were drawn from bitterling (cf. Dominguez Almela et al. 2020), had the characteristics of an alien fish that followed a stage-structured population dynamic: juveniles (<1 year old), subadults (1–2 years) and adults (over 2 years). Its population parameters (Table 3.2; Table A2.1) were also similar to other small-bodied, invasive, pest fish species, such as topmouth gudgeon *Pseudorasbora parva* (Britton and Gozlan 2013). It was set to reproduce once per year, exhibit density-dependent fecundity and have a sex ratio at birth of 1M:1F. Its survival probability was also density dependent, applied and weighted per stage, so the effect of subadults on the survival of adults was 10 % of the effect of adults on each other and on subadults (Dominguez Almela et al. 2020). After reproduction, juveniles, subadults and adults could disperse according to a density-dependent emigration probability, limited to one dispersal event per lifetime. Movement from the natal patch during the transfer phase of dispersal was modelled by the stochastic movement simulator (SMS; Palmer et al. 2011), which simulates movement from cell to cell on the basis of perceived costs within a limited perceptual range and a tendency to follow a correlated path (directional persistence). A relative cost of movement map was derived from the habitat map, such that perceived costs were inversely related to habitat quality; thus, upon reaching a confluence, a disperser would more likely move into the wider of the two streams available. Individuals could settle in any non-natal patch subject to an inverse density-dependent settlement probability (Table 3.2; Table A2.1).

For all model simulations, initial populations were established in 10 patches (including in tributaries) at the upstream end of the catchment (Figure 3.1). These were mainly in first and second order streams, the rationale being that this enabled the invasion front to spread mainly downstream into streams of higher order (Kim et al. 2021), although the direction of individual movement was stochastic in the model and could occur in either direction unless the fish was in a terminal patch. Propagule pressure by the random addition of further individuals into the system was not considered in the model. Each simulation (a single combination of culling parameters and catchment; Table 3.1) was run for 30 years and replicated five times. A ‘control’ simulation was run for each catchment in which no management was applied.

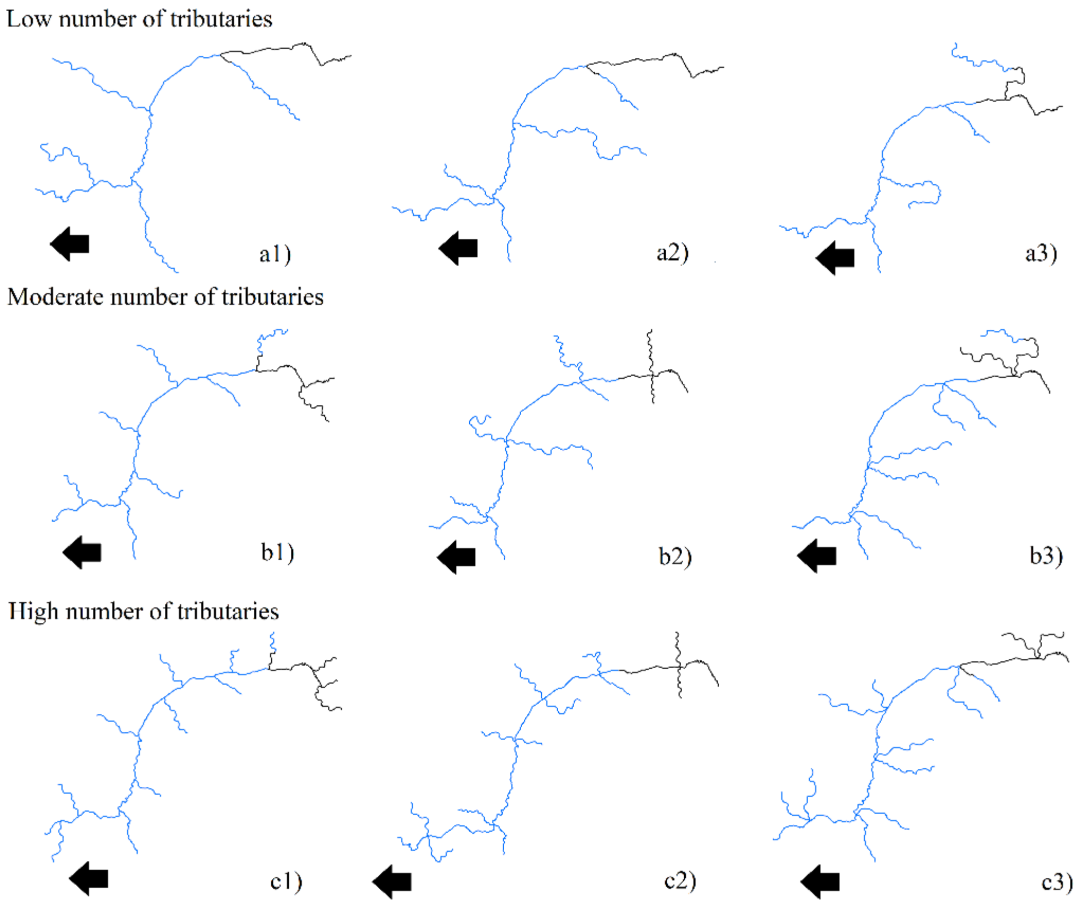


Figure 3.1. Virtual catchments having a low number of tributaries (a1–3), medium (b1–3) and high (c1–3). Grey thick lines highlight the initialized patches in the upper areas of the catchment, and the arrows indicate the direction of flow along the main stem

Table 3.1**.** Factorial design of simulated management experiments. Factors: number of patches culled (N); maximum culling rate (CR); specific culling strategy (SCS)

Experiment 1									
N	4	8	12	16	20	24			
CR	0.9	0.8	0.7	0.6	0.5	0.4	0.3	0.2	
Experiment 2									
SCS	CR=0.9 N=5	CR=0.8 N=9	CR=0.7 N=14	CR=0.6 N=18	CR=0.5 N=23	CR=0.4 N=28	CR=0.3 N=32	CR=0.2 N=37	CR=0.1 N=41
Variation of species	3 strongly *K*-selected species (1 'fast-disperser', 1 'intermediate-disperser', 1 'slow-disperser')								
	3 with similar demographic traits as for experiment 1 (1 'fast-disperser', 1 'intermediate-disperser', 1 'slow-disperser')								
	3 strongly *r*-selected species (1 'fast-disperser', 1 'intermediate-disperser', 1 'slow-disperser')								
Experiment 3									

SCS	CR=0.9 N=5	CR=0.8 N=9	CR=0.7 N=14	CR=0.6 N=18	CR=0.5 N=23	CR=0.4 N=28	CR=0.3 N=32	CR=0.2 N=37	CR=0.1 N=41

Table 3.2**.** The model parameters of the nine virtual species used in Experiment 2. See Table A2.1 for parameters common to all species. *Species 5 was the same as the single species used in Experiment 1 (and in preliminary experiments 0a, 0b in Supplementary Information). ***1/b* is the rate of density dependence, i.e. the rate at which mean fecundity decreases with increasing local density

Parameter	**Strongly *K*-selected species**	**Intermediate demography**	**Strongly *r*-selected species**
Fast disperser	**Species 1**	**Species 2**	**Species 3**
Fecundity	30	63.77	180
*1/b*** (inds/ha)	823.73	1750.96	4942.34
Survival probability in juveniles	1	0.93	0.8
Survival probability in sub-adults	1	0.89	0.2
Survival probability in adults	0.5	0.4	0.1
Max. emigration probability in juveniles	0.4	0.4	0.4
Max. emigration probability in sub-adults	0.7	0.7	0.7
Max. emigration probability in adults	0.9	0.9	0.9

Max. settlement probability	0.6	0.6	0.6
Per-step mortality	0.01	0.01	0.01
Intermediate dispersal	**Species 4**	**Species 5***	**Species 6**
Fecundity	30	63.77	180
1/b (inds/ha)	823.73	1750.96	4942.34
Survival probability in juveniles	1	0.93	0.8
Survival probability in sub-adults	1	0.89	0.2
Survival probability in adults	0.5	0.4	0.1
Max. emigration probability in juveniles	0.1	0.1	0.1
Max. emigration probability in sub-adults	0.18	0.18	0.18
Max. emigration probability in adults	0.18	0.18	0.18
Max. settlement probability	0.84	0.84	0.84
Per-step mortality	0.01	0.01	0.01
Slow disperser	**Species 7**	**Species 8**	**Species 9**

Fecundity	30	63.77	180
1/b (inds/ha)	823.73	1750.96	4942.34
Survival probability in juveniles	1	0.93	0.8
Survival probability in sub-adults	1	0.89	0.2
Survival probability in adults	0.5	0.4	0.1
Max. emigration probability in juveniles	0.01	0.01	0.01
Max. emigration probability in sub-adults	0.05	0.05	0.05
Max. emigration probability in adults	0.14	0.14	0.14
Max. settlement probability	1	1	1
Per-step mortality	0.01	0.01	0.01

3.3.2 Experimental designs

The management of the modelled populations took the form of an annual cull, the format of which was controlled by a series of variable parameters. A specified number of patches was selected each year for culling in which individuals were subjected independently to a mortality probability determined as a stage-dependent logistic function of density and subject to a maximum culling rate. This means that the proportion of individuals removed from a patch per year (the 'cull rate') would depend on its density, and low invader numbers would translate into low removals, reflecting the difficulties of catching those individuals when the population is very low. In contrast, if the density was high, the logistic function would result in removal of a higher proportion of individuals up to a pre-defined maximum. Both the culling rate and the number of patches selected were kept constant across years. We modelled the cull as occurring after dispersal and its spatial application as biased towards recently colonized patches based on results from preliminary experiments (see Appendix A2.1–A2.3). Then, the first experiment assessed the interaction of culling rate and number of patches culled by varying the cull rate on an initial virtual species across different numbers of patches (Experiment 1; Table 3.1). The second experiment varied the demographic (as type of demographic species, SpType) and dispersal (as type of dispersal species, SpDispType) characteristics of the model alien species that was being managed (Experiment 2; Table 3.1). Finally, in the third experiment, we applied the model to a real case study using bitterling as the model species and the Great Ouse as the model catchment, following the study by Dominguez Almela et al. (2020).

3.3.2.1 Experiment 1: Interaction of culling and management effort

Six levels of the maximum number of patches culled (N), ranging from low to high numbers (4 to 24) of patches culled per year, were tested against eight levels of maximum cull rate (CR, 0.2–0.9; Table 3.1). The cull was applied to all three life stages simultaneously. The experiment was run for all nine catchments (432 parameter combinations).

Following the model simulations, the results of Experiment 1 were analysed using two population-level summary statistics that were extracted from the model output data:

(1) Rate of population increase (P_1):

$$P_1 = \frac{Nind_{t+n} - Nind_t}{n},$$

where $Nind_t$ is the total number of individuals across the catchment at time t and n is the number of years during which there was active growth. The simulated population when no culling was applied was used to determine n, the number of years of approximately constant growth before the population growth trajectory began to decline.

(2) Rate of change in patch occupancy (Q_1):

$$Q_1 = \frac{NOccupPatches_{t+n} - NOccupPatches_t}{n},$$

where $NOccupPatches_t$ is the number of occupied patches at time t and n is the number of years for the period of active growth as above.

3.3.2.2 Experiment 2: Trade-off between the number of patches culled and the cull rate within each patch across a range of species

This experiment evaluated a potential resource-limited trade-off between the maximum number of patches culled and the maximum cull rate within each patch across a further eight contrasting virtual species (specific culling strategy; SCS), to identify whether patterns detected in the initial species were common across species with contrasting life-history traits and dispersal abilities (Table 3.1). It was based on the assumption that the total management resource (finance, man-power) was fixed annually, and so managing more patches in a year would result in reduced effort per patch, reducing the effects of the culling on the invader. For example, culling all patches would spread resources thinly across the whole catchment, so the lowest maximum cull rate (CR = 0.1) would have to be applied per patch in each year in this scenario (Table 3.1). The initial virtual species (Experiment 1) was the reference species, having intermediate demographic traits and dispersal abilities, and eight additional virtual species were developed that varied by their: (a) demographic traits and/or (b) dispersal traits. (a) ranged from being more intensely *r*-selected (i.e. higher fecundity, lower survival) to being more intensely *K*-selected (lower fecundity, higher survival). (b) Varied from being better dispersers by increasing stage-dependent maximum emigration probabilities (more dispersers per generation) and decreasing maximum settlement probability (more likely to keep moving), to poorer dispersers by decreasing stage-dependent maximum emigration probabilities (fewer dispersers per generation) and increasing maximum settlement probability (less likely to keep moving; Table 3.2). The experiment was applied to all nine catchments (729 parameter combinations).

As there was substantial variation between population trajectories in the experimental predictions, fixing a specific year as the basis for calculating the rate of population increase (P_1) and change in patch occupancy (Q_1) was inappropriate. Therefore, for each replicate simulation trajectory, the rate of population increase in the first decade (*P*10) was calculated, using:

$$P10 = \frac{pop[year = 10] - pop[year = 1]}{10}$$

where *pop*[*year*=10] is the number of individuals at year 10 and *pop*[*year*=1] is the number of individuals at year 1, and similarly for years 6–15 inclusive to give *P*15; 11–20 (*P*20), 16–25 (*P*25) and 21–30 (*P*30). Finally, the maximum mean annual increase in population size achieved was determined as:

$$P_2 \ = \ max(P10, P15, P20, P25, P30)$$

The same approach was used to calculate the maximum decadal rate of change in patch occupancy (Q_2):

$$Q10 = \frac{NOccupPatches[year = 10] - NOccupPatches[year = 1]}{10}$$

where *Q*10 is the rate of change in patch occupancy for the years 1–10 inclusive, *NOccupPatches*[*year*=10] is the no. of occupied patches at year 10 and *NOccupPatches*[*year*=1] is the no. of occupied patches at year 1, etc.

3.3.2.3 Experiment 3: Case study on specific management to control bitterling in the Great Ouse

The predictive performance of our approach was evaluated using bitterling as the model invader and the River Great Ouse in Eastern England as the model river basin. The map of the catchment (including its division into 272 patches) and the key model parameters were taken from the study by Dominguez Almela et al. (2020), where the parameter estimates used were from their posterior distributions obtained by approximate Bayesian computation. The full posterior parameter distributions (from 250 simulations) were used to determine the level of culling needed for reducing the bitterling spatial range, using the culling scenarios applied in Experiment 2 (SCS; Table 3.1), giving a total of 2,250 parameter combinations. The simulations started in 1983 when the species was first recorded in fisheries monitoring surveys (Dominguez Almela et al. 2020) and ran for 100 years, producing five replicates per set of parameter combinations. Values of rate of population increase (P_2) and change in patch occupancy (Q_2) were calculated, with the mean of each set of five replicates providing a single prediction for each posterior parameter combination per SCS, allowing the confidence intervals for variation only between posterior parameter sets.

3.3.3 Statistical analyses

For both P_n and Q_n, factorial linear models for each experiment were fitted using ‘R 3.6.3’ (R Core Team 2020) to partition the variance in the response variable. The models incorporated, as appropriate, the management scenarios that were applied (N, CR and SCS), the three sets of river catchments (low, medium and high branching; B, ID) and species (SpID, SpType and SpDispType) (Table 3.1). The effect of the factor(s) that had the greatest influence on model outcomes was investigated further using posterior marginal means analyses (package ‘*emmeans*’; Lenth 2020).

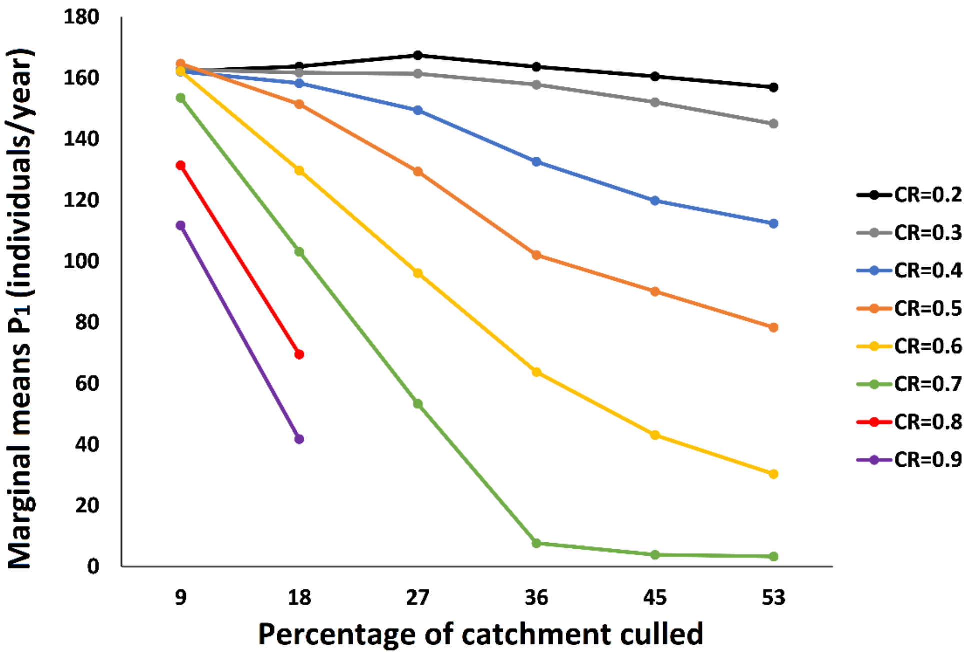
3.4 Results

3.4.1 Experiment 1: Interaction of culling and management effort

The predicted effects of culling on both P_1 and Q_1 increased as both the maximum cull rate (CR) and maximum number of patches (N) increased, which together accounted for most of the variation (Table 3.3; Tables A2.2b and A2.3b). When CR was low, it had only minor effects on P_1 and Q_1, except when N was high (Figure 3.2). When CR was increased to a medium level (0.5, 0.6), then values of P_1 and Q_1 suggested that culling could contain the spread of the invader, but when CR was ≥ 0.7, eradication of the species was possible if N was also high (at least 16 patches culled per year; Figure 3.2). All replicates led to eradication when CR was at least 0.8 and N was ≥ 12 patches per year, and also when CR was 0.9 and N = 8 patches per year.

Table 3.3. Principal sources of variance explained (%) in the summary statistics rate of population increase (P_1) and rate of change of patch occupancy (Q_1) for Experiment 1. Factors: maximum number of patches culled (N); maximum cull rate (CR); catchment branching (B); catchment ID number (ID)

	Catchment related factor		**Management related factor**		
	B	**ID**	**N**	**CR**	**CR*N**
P_1	4.5	4.2	22.4	44.3	13.5
Q_1	1.4	0.7	23.2	51.7	17.5



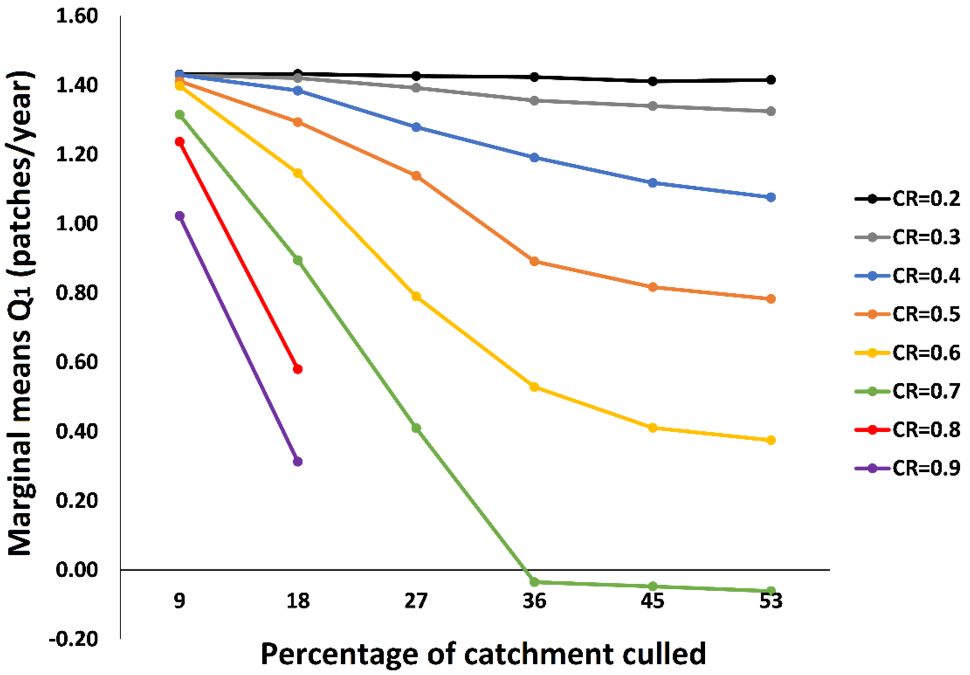


Figure 3.2. Interaction effects of the maximum cull rate (CR) and maximum number of patches culled (*N*) on the rate of population growth (P_1) and change in patch occupancy (Q_1) in Experiment 1

3.4.2 Experiment 2: Trade-off between the number of patches culled and the cull rate within each patch across a range of species

In general, the major source of variation in P_2 and Q_2 was from differences between the characteristics of the nine species (SpType, SpDispType and SpID; Table 3.4; Tables A2.2b and A2.3b). Marginal means analysis between species type (SpType and SpID) and the SCS revealed that P_2 and Q_2 could be substantially reduced when N was set at a relatively high number of patches, despite culling being at less than maximum efficiency (Figure 3.3; Figure A2.4). Five out of the nine species presented at least two scenarios in which the virtual species was eradicated in some of the replicates (Table 3.5). The scenario where 0.8 cull rate (CR) was applied in nine patches (N) had the highest number of replicates across species in which eradication occurred (152 of 729 replicates). No species was eradicated at CR < 0.7. Of the more *r*-selected species group, 82 % of slow and 28 % of intermediate dispersers were successfully eradicated during simulations at CR ≥ 0.7 (Table 3.5). In particular, the scenario where 0.8 cull rate was applied to nine patches predicted that for the *r*-selected slow dispersers, there were no replicates where the species was not eradicated. In *r*-selected fast dispersers, P_2 and Q_2 were reduced, but their populations were only predicted to be eradicated in a single replicate (Figure 3.3; Figure A2.4). Conversely, 18 % of intermediate and 61 % of slow dispersers within *K*-selected species were successfully eradicated in simulations at CR ≥ 0.7, while fast disperser abundances were reduced, but were never fully eradicated at any of the nine CR scenarios (Table 3.5; Figure 3.3; Figure A2.4).

There were also marked differences in the response of P_2 and Q_2 in relation to the different dispersal abilities of the nine species (SpDispType; Figure 3.4). Species with slow dispersal abilities required less effort to control, enabling lower numbers of patches to be culled to achieve similar outcomes as intermediate or fast dispersers at higher numbers of patches. Moreover, the intermediate and fast dispersers revealed some compensatory responses to the culling, suggesting their invasion could actually benefit from some culling scenarios through increased P_2 and Q_2.

Table 3.4. Principal sources of variance explained (%) in summary statistics rate of population increase (P_2) and rate of change of patch occupancy (Q_2) for Experiment 2. Factors: type of demographic species (SpType); type of dispersal species (SpDispType); species ID number (SpID) and specific culling strategy (SCS)

	SpType	**SpDispType**	**SpID**	**SCS**	**SpType*SCS**	**SpDispType*SCS**
P_2	33.21	34.13	6.37	11.09	3.61	1.71
Q_2	4.62	56.87	1.12	20.42	0.95	3.69

Table 3.5. Counts of replicates per scenario in which virtual species were eradicated. The maximum number of replicates possible per scenario and species is 45. Slow dispersers: Species 7, 8 and 9; Intermediate dispersers (‘Inter.’): Species 4 and 6; Fast disperser: Species 3. All other species had no scenarios where they were eradicated

	Strongly *K*-selected		**Intermediate demography**	**Strongly *r*-selected**		
Scenario	Species 4	Species 7	Species 8	Species 3	Species 6	Species 9
Dispersal ability	Inter.	Slow	Slow	Fast	Inter.	Slow
0.7 cull rate (CR), 14 patches (N)	4	2	0	1	18	23
0.8 cull rate (CR), 9 patches (N)	19	43	25	0	20	45
0.9 cull rate (CR), 5 patches (N)	1	37	7	0	0	43

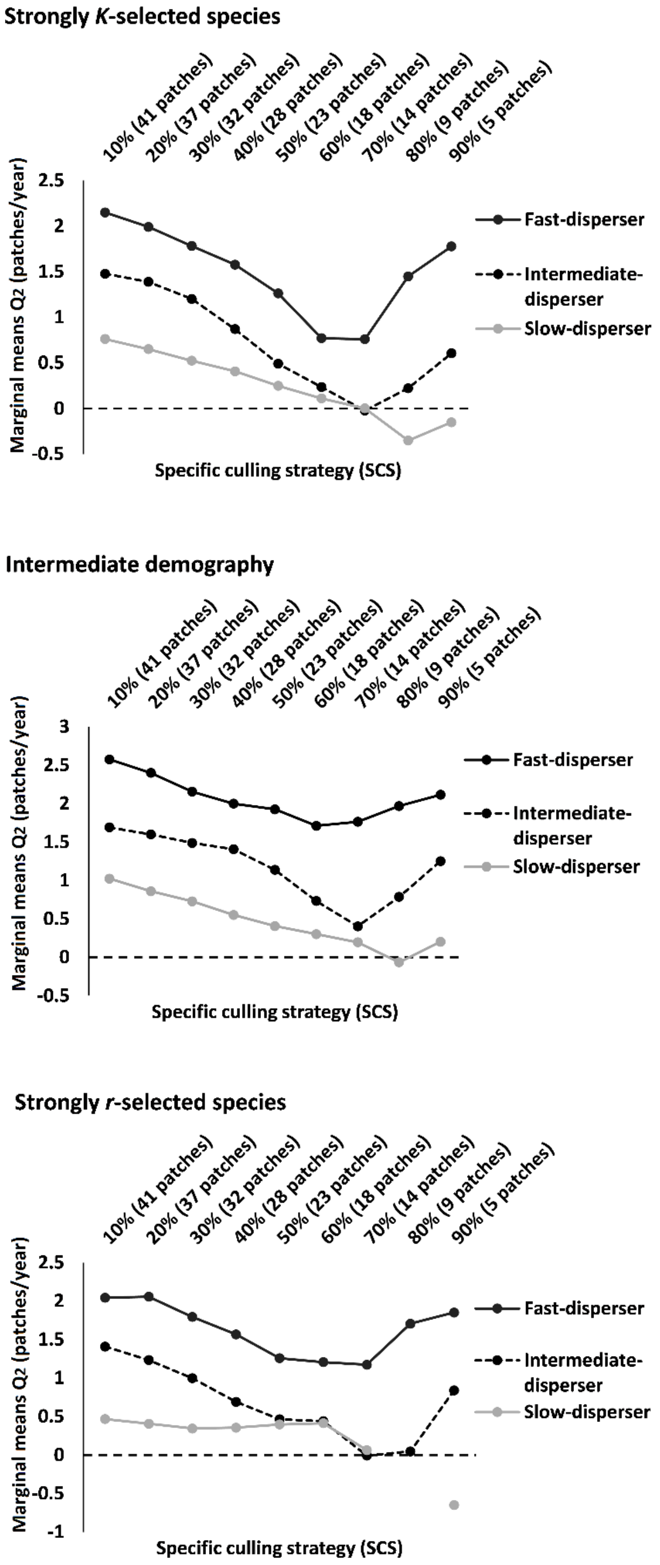


Figure 3.3. Interaction effects of the species dispersal type (SpDispType) and specified culling strategy on the rate of change in patch occupancy (Q_2) during Experiment 2. No data point shown at 80 % (nine patches) in the *r*-selected species as all replicates were extirpated

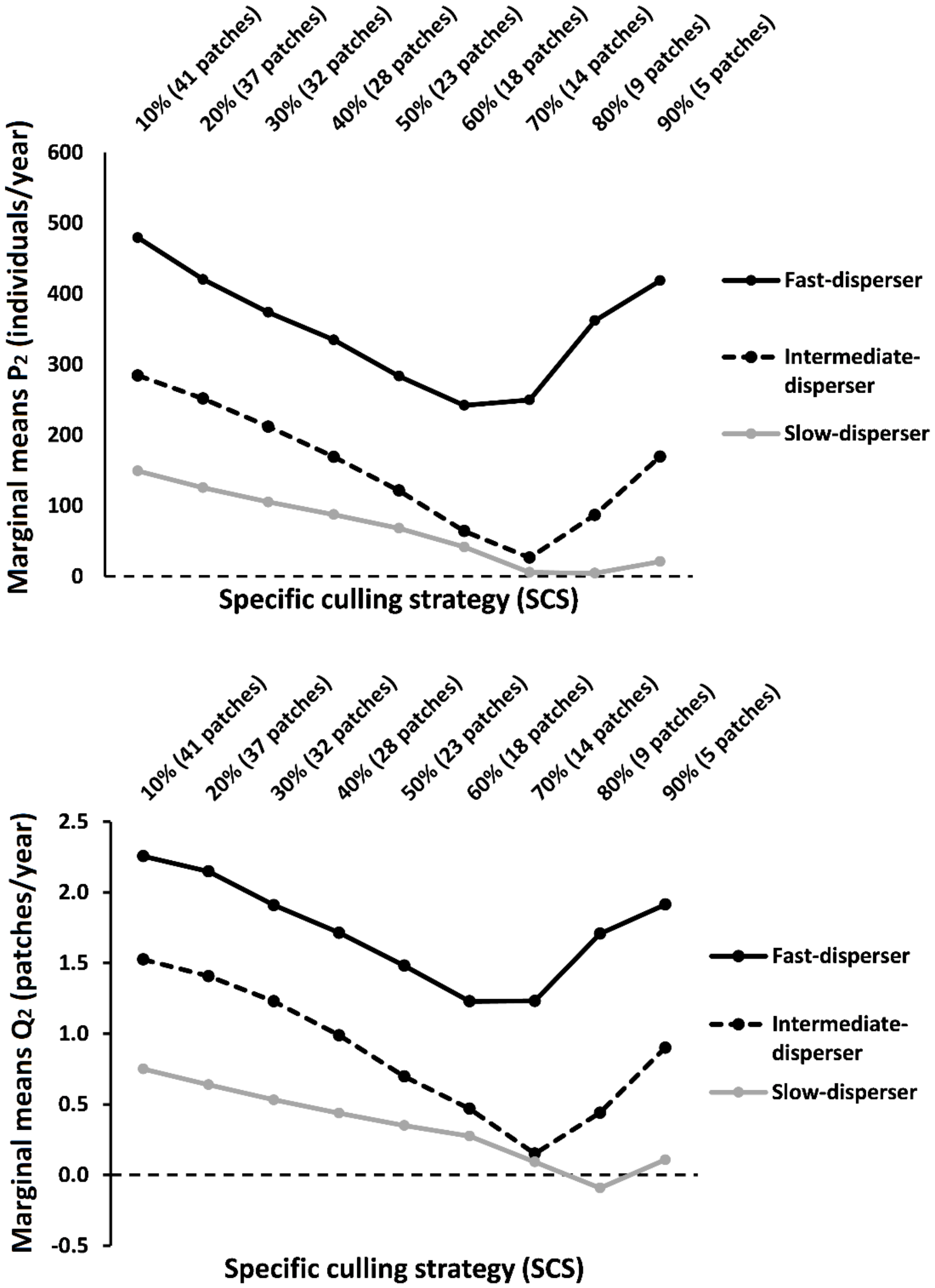
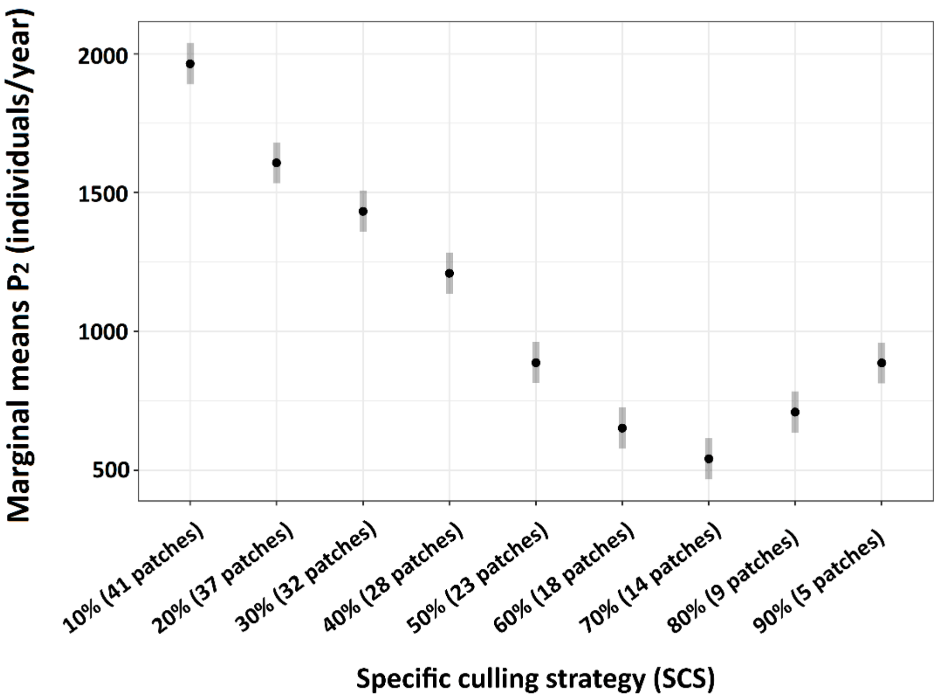


Figure 3.4. Interaction effects of the species dispersal type (SpDispType) and specified culling strategy on the rate of population increase (P_2) and change in patch occupancy (Q_2) for populations which were not eradicated during Experiment 2

3.4.3 Experiment 3: Case study on specific management to control bitterling in the River Great Ouse

Our IBM predicted a significant response in this bitterling population to the different culling scenarios in both P_2 ($F_{8,2,241} = 165.23$, $p < 0.001$) and Q_2 ($F_{8,2,241} = 1,953.5$, $p < 0.001$; Figure 3.5) analogous to that predicted in Experiment 2 for intermediate demography/dispersers (cf. Figure 3.4). Where Dominguez Almela et al. (2020) predicted bitterling would occupy 90 % of patches in the river in 2045 (Figure 3.6a), the application of a yearly SCS of CR = 0.7 and N = 14 (5 % of patches) was predicted here to result in the population occupying only 21 % of the area, which was similar to their spatial extent recorded in 1984 (Figure 3.6b).



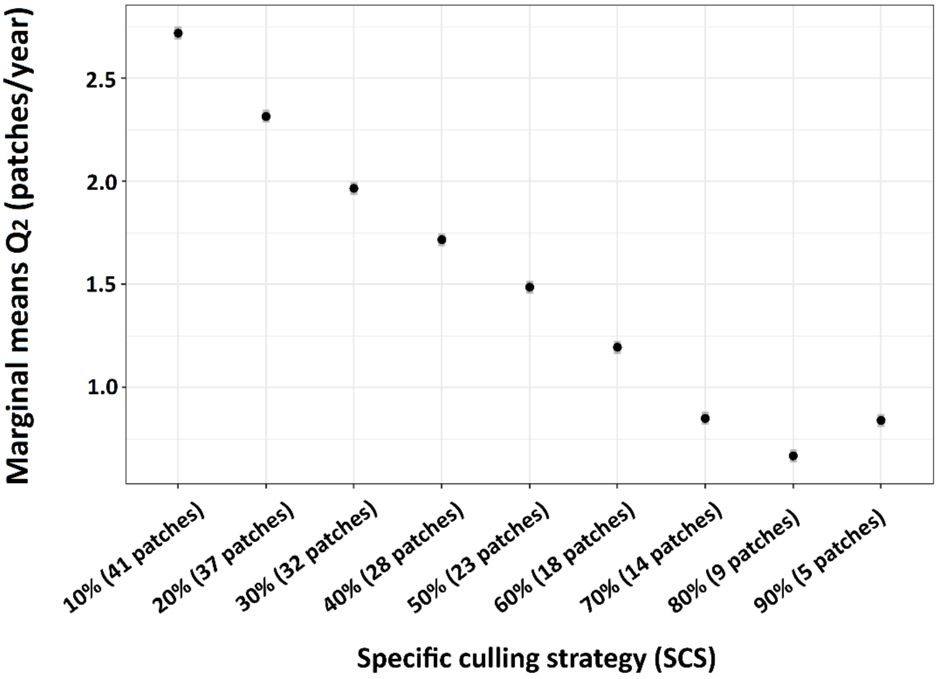


Figure 3.5. Effects of specified culling strategy on the rate of population increase (P_2) and change in patches occupancy (Q_2) of the bitterling species. Grey bars are 95 % confidence intervals for the marginal means

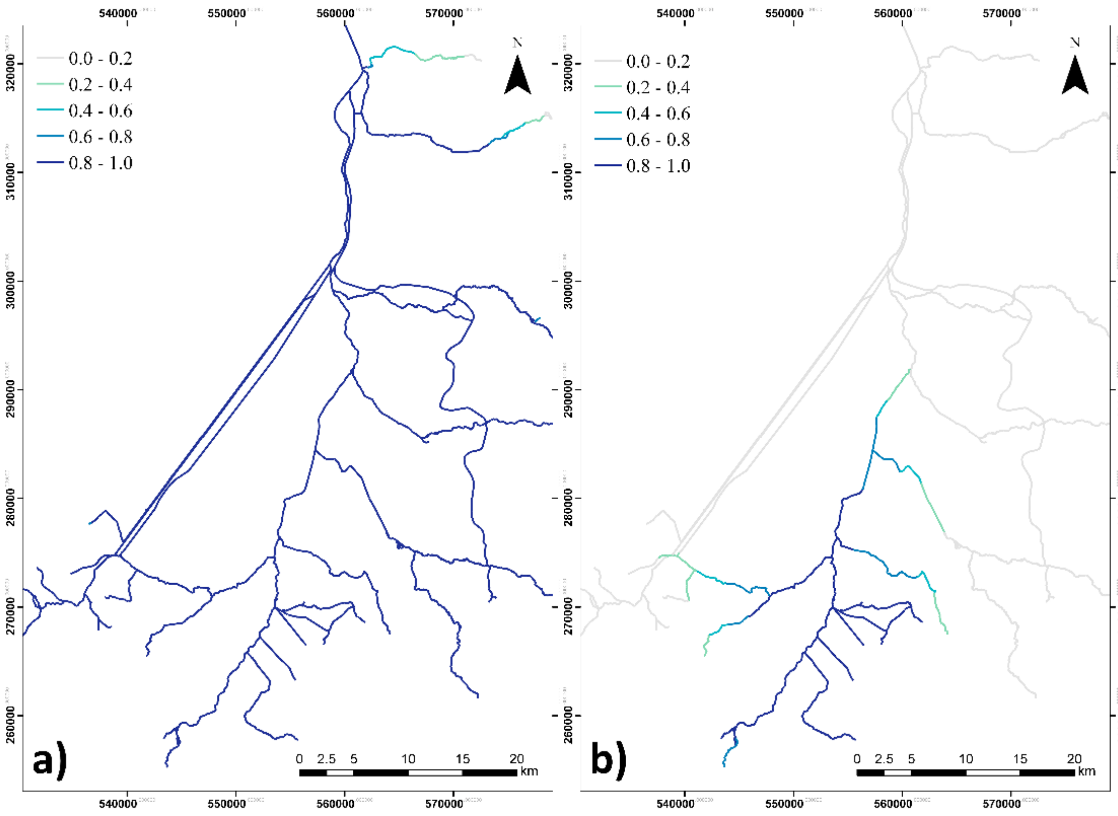


Figure 3.6. Comparison map with the predicted occupancy (by 2045) of the catchment (a) without management control (Dominguez Almela et al. 2020) and (b) after applying a yearly SCS of CR = 0.7 and *N* = 14. Colour scale: probability of occupancy ranging from low (light grey) to high (dark blue). © Crown copyright and database rights 2018 Ordnance Survey (100025252)

3.5 Discussion

Our model predictions provide a series of novel insights that should assist decision-making for managers dealing with invasive fish specifically and invasive species more generally. Our IBM identified the optimal management effort (as specific culling strategies involving the cull rate and its spatial application) for invaders across a range of demographic traits and dispersal abilities. The model predictions demonstrated that while eradication of invasive fish is possible by culling, it requires relatively high cull rates to be used, with the highest probability of eradication achieved in fish of low dispersal abilities. For fast-dispersing fish with both *r*- and *K*-selected characteristics, eradication was predicted to be difficult to achieve irrespective of the cull rate used, although the predictions did indicate that the spatial spread and abundance of the invader can be constrained. Correspondingly, for fast-dispersing invasive fishes, the predictions suggest it is imperative for management control efforts to be implemented rapidly and utilize high cull rates where feasible. Such management insights have, so far, been unobtainable from meta-analyses of empirical data (e.g. Rytwinski et al. 2019). Moreover, when the IBM was applied to invasive bitterling in the River Great Ouse, England, the spatial extent of their invasion by 2045 (90 % of the catchment) was predicted to be constrained to their 1984 distribution (21 % of the catchment) using an annual cull rate of 0.7 in 14 patches (around 5 % of the catchment). This indicates that a long-term management control strategy could substantially constrain the invasion of an alien fish in a relatively open system, even if the species could not be eradicated.

Our IBM predicted that different culling strategies result in a range of effects on the population growth and spread of invasive species. If the annual specific culling strategy was held at a fixed level across all years, then increasing the number of patches culled per year must be matched by a reduction in the cull rate per patch. The predictions indicated that a reduced cull rate, even when applied over larger spatial areas, was generally ineffective in constraining the fish dispersal and population growth rates. Correspondingly, the application of low cull rates across large spatial areas is not an effective management option. In contrast, relatively high cull rates often predicted population eradication, even when the number of patches culled were not necessarily high (e.g. a cull rate of

0.9 in only eight patches). These predictions are thus important in the context of management planning of how specific culling strategies could be applied spatially and in relation to the ability of capture methods to remove high proportions of the target species within managed patches. They also demonstrated the compensatory responses that will occur within the fish population when the cull rate is too low, whereby the reduction in population size results in subsequently higher reproductive rates and abundances, and then faster dispersal (Berry et al. 2012).

Although the IBM was effective at predicting how the cull rate affects the abundance and dispersal of the invader, determining the extent of a fish population that can be removed effectively from a population using capture methods, such as electric fishing, can be difficult. While electric fishing is considered an effective fish capture technique, it has inherent issues relating to species detectability and detection bias (Beaumont 2016). Its probability of capture is species dependent with, for example, it varying between 0.35 and 0.64 across 15 stream fish species (Reid et al. 2009). It can also be relatively ineffective at capturing early life stages of fish, where alternative methods might be more effective, such as micromesh seine nets and/or traps (Britton et al. 2011c, Nunn et al. 2001). Nevertheless, electric fishing is regularly and successfully used to remove alien fish from invaded waters when chemical treatments cannot be applied, with the meta-analysis of Rytwinski et al. (2019) reporting a 58 % success rate for population eradication and 56 % for population control over a range of alien fish species.

The predicted outcomes of the specific culling strategies on the invading populations were also strongly influenced by the invader's demographic traits. The initial virtual species, based on bitterling, had a suite of demographic traits that were similar to those of small-bodied invasive fish more generally that are considered pests in many parts of the world and so often receive considerable management attention (e.g. Britton and Brazier 2006, Britton et al. 2010b). However, invasive fish with demographic traits that are less intensively *r*-selected or even *K*-selected are also considered undesirable in many parts for the world. For example, relatively large-bodied alien fish of the Salmonidae family are often targeted for management in North America (Rytwinski et al. 2019) and common carp *Cyprinus carpio* have also received considerable management attention in many areas of the world, including Australia (Pinto et al. 2005) and South Africa (Davies et al. 2020). It was thus important to understand how these initial predictions varied according to demographic traits and dispersal abilities. The predictions revealed that population eradication was achievable in five of the nine virtual species, including species with both *r*- and *K*-selected traits, but only when the cull rate was relatively high (≥ 0.7) and when at least 14 patches were culled. However, cull rates below 0.7 never resulted in eradication. That invasive fish with *r*-selected demographic traits were predicted to be the most challenging to control and eradicate is arguably an intuitive result, as these traits, common in many invasive fish, enable the rapid development of highly abundant populations where individuals can then disperse (Gozlan et al. 2010a). The eradication of two strongly *K*-selected virtual species was predicted, but only when they were intermediate or slow dispersers and at a high cull rate. The real-world simulation of bitterling in the River Great Ouse indicated that although population eradication would not occur under any of the specific culling strategies that were simulated, strong containment was possible.

These invasion management predictions should be applied to informing real-world invasion risk assessment processes (Vilizzi et al. 2019), which are fundamentally important in prioritizing the species and habitats for management (Roy et al. 2018). Best practice guidance on risk assessments for alien species indicates that two of the four main assessment components are their probable spread and impact (Roy et al. 2018). In our summary analysis of the IBM output data, we directly predicted invader spread, and the parameter P_n can potentially predict impact due to the relationships of invader abundance with impact (Jackson et al. 2015). Consequently, provided some basic knowledge of the demographic and dispersal traits is available for a specific species, our IBM predictions should inform the risk assessment responses on their spread and impact, especially where there is strong understanding of the invader's demographic traits and dispersal abilities. This is because there were some strong differences in the responses of *r*- and *K*-selected species, and across varying dispersal abilities, to the different culling strategies. For example, 82 % of slow-dispersing *r*-selected species were eradicated at cull rates above 0.7 %

versus 61 % of *K*-selected species, while eradication of fast-dispersing species was generally predicted to be unlikely. Although detailed information on the dispersal abilities of alien fish is often lacking, dispersal patterns are also likely to be catchment specific, varying according to, for example, the flow regime, river network complexity and habitat suitability, and the extent of human modification of them (Caiola et al. 2014). Correspondingly, following the detection of a new alien fish within a river catchment, practitioners should rapidly assess its life-history traits (either directly or through literature review), its ability to disperse in the catchment (in relation to both the species' dispersal characteristics and the complexity of the river network) and its current spatial extent (Britton et al. 2011c). Concomitantly, the resource available for the control effort needs to be quantified, with identification of the desired management outcome (eradication vs. control). In combination with the predictions outlined here across the different fish life histories and dispersal abilities, and the culling gradients, this information should then enable more informed decision-making on the actual strategy to be implemented.

Our predictions thus provided considerable insights into how fish removal efforts and the traits of the target species interact to alter the outcomes of invasive fish culling strategies. Such insights are not possible from empirical studies due to their context dependencies, and often poor experimental planning (e.g. lacking baseline data and control sites; Rytwinski et al. 2019). However, we acknowledge that our modelling processes have some inherent limitations. For example, while GIS techniques can accurately represent a linear river system, the division of the river into discrete patches, as required by ‘RangeShifter’, has some subjectivity and does not faithfully represent the natural heterogeneity of actual rivers (Dominguez Almela et al. 2020). While our general results should be qualitatively robust to this discretization, future work exploring the consequences of model choices related to the resolution of the spatial grid would be valuable. Also, model initialization always introduced the fish to the catchment's upper reaches, enabling the invasion front to disperse downstream into higher order streams, where established populations of invasive fishes are often abundant (Kim et al. 2021). In reality, the release points of alien species are more stochastic, such that some dispersing aliens move from downstream to upstream areas (Vitule et al. 2012). The model also prohibited an individual from dispersing more than once in its life (Bocedi et al. 2014), an assumption potentially violated by some riverine fishes (Fausch et al. 2002, Radinger and Wolter 2014). Moreover, the model was based on a discrete introduction of fish, and while invasions can occur from a single release event, multiple releases can also occur, which can increase the probability of invasion success as it overcomes issues such as founder effects (Lockwood et al. 2005). However, a key component of eradication attempts of invasive species is preventing their re-introduction into the treated area, and so where management efforts are ongoing to control invaders, these efforts should also include increased regulation and surveillance that aim to prevent further releases (Britton et al. 2011b). Finally, throughout the model, the total specific culling strategy was fixed across all years, as this enabled the model to account consistently for the relationship between cull rate and the number of patches culled. However, it is acknowledged that in reality, resource availability might vary by year and, for high priority species, be increased in the short term. Moreover, it has already been discussed that the actual effort required to achieve the higher cull rates might exceed the levels of effort used in the model due to the increased degree of difficulty of capturing fish from small populations (Britton et al. 2011c). Consequently, while there is high confidence in our predictions of how the different cull rates applied across varying number of patches culled will affect the population of the target species, it is suggested that some caution is applied when considering that these strategies will all be of equal cost. Despite these issues, we argue strongly that the strength of our model is its ability to simulate the outcome of management interventions to control populations of invasive species that cannot be provided empirically (Dominguez Almela et al. 2020). It thus represents a major step forward in understanding how to develop strategic approaches for managing alien species in the environment.

In summary, this work provided insights into the outcomes of different control efforts on invasive fishes, and highlighted that, depending on the species characteristics, and the specific culling strategy, these outcomes can vary in target populations, but can include eradication when the target species is of low or intermediate dispersal ability and when a high cull rate is applied. These predictions strongly complement existing invasion risk assessments, and demonstrate that individual-based models are powerful tools for predicting optimal management interventions for high-risk invaders.

4 Predicting the influence of river network configuration, biological traits and habitat quality interactions on riverine fish invasions

4.1 Abstract

The relationships between species and their landscape are important for understanding migration patterns. In fluvial systems, the complexity of the river network can strongly influence the dispersal and colonisation rates of invading alien fishes, but habitat quality, species' biological traits and their location of introduction are also potentially important. However, understandings of how these factors interact in the wild to influence the spatial distribution of invasive species over time are limited from empirical studies. We developed an individual based model (IBM) to predict how these different factors influenced the invasion dynamics and population growth rates (as abundances) of nine 'virtual' alien fishes over two timeframes (10 and 30 years) in 'virtual' and 'real-world' rivers from England and Wales. The alien fishes differed in their demographic (*r*- to *K*-selected) and dispersal (fast to slow) characteristics, and the rivers in their network complexity. Irrespective of river type, species and timeframe, the main drivers of both dispersal and population growth were the location of the introduction and the mean habitat quality of the patch into which the species were released. The introduction location determined whether dispersal was mainly passive in a downstream direction (faster) or active in an upstream direction (slower), with higher habitat quality then enabling faster population growth rates. Over 30 years, invasion rates were predicted to increase as the complexity of the river network increased, as this opened multiple invasion fronts where the invader traits favoured faster dispersal. This novel IBM revealed how the complexity of the physical environment interacts with the biological traits of alien species to influence invasion outcomes, with the location of the introduction and its habitat quality being the most important factors. These results thus substantially increase understanding of the factors that influence the dispersal and colonisation rates of alien freshwater fishes.

4.2 Introduction

The relationships between animal movements and the structure of their environment are important to understand, with the variability in these movements driven both by species' ecology and the spatio-temporal scale being considered (Roberts and Angermeier 2007). Relationships between animal movements and their environment are especially important in the context of newly introduced alien species, as they will determine the species' rate of spread, and hence potential negative ecological impacts (Ross et al. 2001, Fraser et al. 2015, Davis and Darling 2017). In alien plants, simulated invasion dynamics have revealed the importance of both the connectivity of the entire landscape and the structure of the local landscape (e.g. the presence of corridors), as well as the species' dispersal ability (Andrew and Ustin 2010). Assessments of how newly introduced alien species invade novel landscapes thus requires understanding of how the landscape structure impacts upon the main processes that contribute to their spread (Grant et al. 2007, Lurgi et al. 2016), especially dispersal (important for successful colonisation) and demography (important for successful population establishment) (With 2004).

The range expansion/spread of alien species requires their ability to move from colonised into novel areas (Havel et al. 2015). For some freshwater alien taxa, adaptations for persisting in temporary environments can assist their overland dispersal by passive or active means (Havel et al. 2015), such as the cryptobiosis of rotifers (Wallace and Snell 2001). For alien fishes, however, their natural dispersal from invaded to uninvaded areas requires some level of fluvial connectivity (Gozlan et al. 2010a), and while canals can provide movement corridors between river catchments (Hickley 1986), movements and dispersal rates within catchments are dependent upon the structure and connectivity of the river network (Goldberg et al. 2010). This structure and connectivity will also affect the potential movements and distributional shifts in native species as they respond to the invasion (Crowl et al. 2008).

River networks are branched, corridor-like structures that have a number of sources (headwaters) and a mouth (where it joins either the sea or a lake); the distribution of branches (tributaries) and confluences determines the shape of the network, which can be classified using stream order methods (Strahler 1957, Shreve 1966). They can be considered as landscapes in which a set of patches form a dendritic structure that is arranged in a non-linear, spatially explicit manner (Goldberg et al. 2010). The directional flow of water within the network means that for two adjacent patches, one will be downstream from the other, and this will influence the movement of fish between them, such as whether the movement is more likely to be active (upstream direction) or passive (downstream direction) (Goldberg et al. 2010). These fish movements continue until a confluence is encountered, when a decision is required as to which branch the fish enters. Branching is often asymmetric, as one channel is often larger than the other and has a different flow regime, and this can strongly influence the decision over which branch is taken (Byers and Pringle 2006). These inter-patch movements are likely to be influenced by factors including the fish life-stage and their dispersal abilities (Goldberg et al. 2010, Phang et al. 2016). They will also depend on habitat quality of the patches, where there can be a higher energetic cost for a fish for settling into a lower versus higher habitat quality patch due to, for example, reduced prey availability, that increases their searching time (Phang et al. 2016).

Understanding the colonisation rates of alien fish in river networks is crucial for conservation management, including protecting native communities from the adverse impacts of alien invasions, especially as the ability to manage invasive fishes in the environment is inversely proportional to the extent of their spatial spread (Britton et al. 2011b, Rytwinski et al. 2019). For an invasive freshwater fish whose distribution is still spatially limited within rivers, eradication can be a feasible option for eliminating their impacts on native species, whereas for those invaders that are spreading rapidly, control and/or containment methods are usually the only feasible options (Britton et al. 2011a). The traits of invasive fish also often differ between the ‘invasion front’ and the areas where the population has already colonised (‘invasive core’): individuals at the front are more likely to express ‘dispersal-enhancing traits’ that provide them with the highest probability of dispersal success (Masson et al. 2018). There are, however, considerable knowledge gaps on how the interactions of the spatial variability in river network complexity and habitat quality with the location of the release site influence the invasion success of alien fishes, especially across species of differing dispersal abilities and life history traits. While this is likely to relate to the complexity of these interactions and a lack of empirical data (Dominguez Almela et al. 2020), recent increases in computing power and the development of individual based models (IBM) enable the use of predictive approaches to help overcome these knowledge gaps (Day et al. 2018, Rodríguez-Rey et al. 2019).

The aim of this study was thus to determine how the invasion of alien river fishes is likely to be influenced by river network complexity and habitat quality, the location of their introduction into the network, and how this varies across a range of species' dispersal abilities and life history traits. An IBM was developed and parameterised to predict how these factors interacted to influence the rates of population increase and range occupancy of nine example alien fishes over time scales of 10 and 30 years in a range of virtual and real-world river networks. We posit that: (1) river network complexity and spatial differences in habitat quality are a major determinant of the colonisation rate of alien fishes, such that more branched networks are colonised faster than less branched networks through the formation of multiple invasion fronts; (2) the introduction location in the network influences the colonisation rate, such that introductions in upstream locations result in more rapid colonisation and population growth due to fish movements in a downstream direction into areas of higher stream order (and habitat quality); and (3) alien fishes with higher dispersal abilities and life history traits that facilitate fast establishment (i.e. *r*-selected traits; Dominguez Almela et al. 2020) will colonise river networks more rapidly than fishes with the opposite suite of traits.

4.3 Methods

4.3.1 River networks

Two sets of river networks were used: (a) randomly generated, virtual river networks that enabled predictions to be made on channel configurations whose physical differences were constrained with a set of rules: total size of catchment, number of cells and number of confluences (maximum stream order of 4); and (b) actual river networks that enabled testing of the predictions from (a) using 'real-world' configurations with natural network variability between them.

4.3.1.1 Randomly generated virtual river networks

Virtual river channel networks were built using the ‘*OCNet*’ package in ‘R 4.0.1’ (R Core Team 2020, Carraro et al. 2020). The configuration of the initial state of the network had four possible values (Factor Shape, ‘S’): "I" (representing a valley); "T" (T-shaped drainage pattern); "V" (V-shaped drainage pattern); and "H" (hip roof drainage pattern). Three catchments per configuration type were created (Factor Catchment, ID; Figure 4.1), and all 12 rivers had a similar number of confluences in their network (mean = 48.6 ± 0.76 (SD)). The network distance from the outflow point was used to develop raster maps of habitat quality (as described below) of cell size 50 m using ‘ArcGIS Pro’, where catchments were divided into sections limited by the river nodes. The network distance from the mid-point of each section to the outflow point was converted to a quality score by:

$$Quality_{virtual\ rivers}\ (\%) = 100 - \frac{Distance\ \times 100}{\max\ (Distance)}$$

Using this formula, habitat quality for the alien fish increased with distance downstream, and so habitat quality increased as stream order increased (Matthews 1986, Smith and Kraft 2005). The rationale behind this assumption was that as river width increased with distance downstream, this would increase the heterogeneity of the habitat (e.g. increased size and complexity of littoral areas) that, overall, would enhance habitat quality for fish. While this can be considered a simplification of habitat quality, it meant that a single variable that relates to stream order and is relevant to alien fishes could be used (Smith and Kraft 2005).

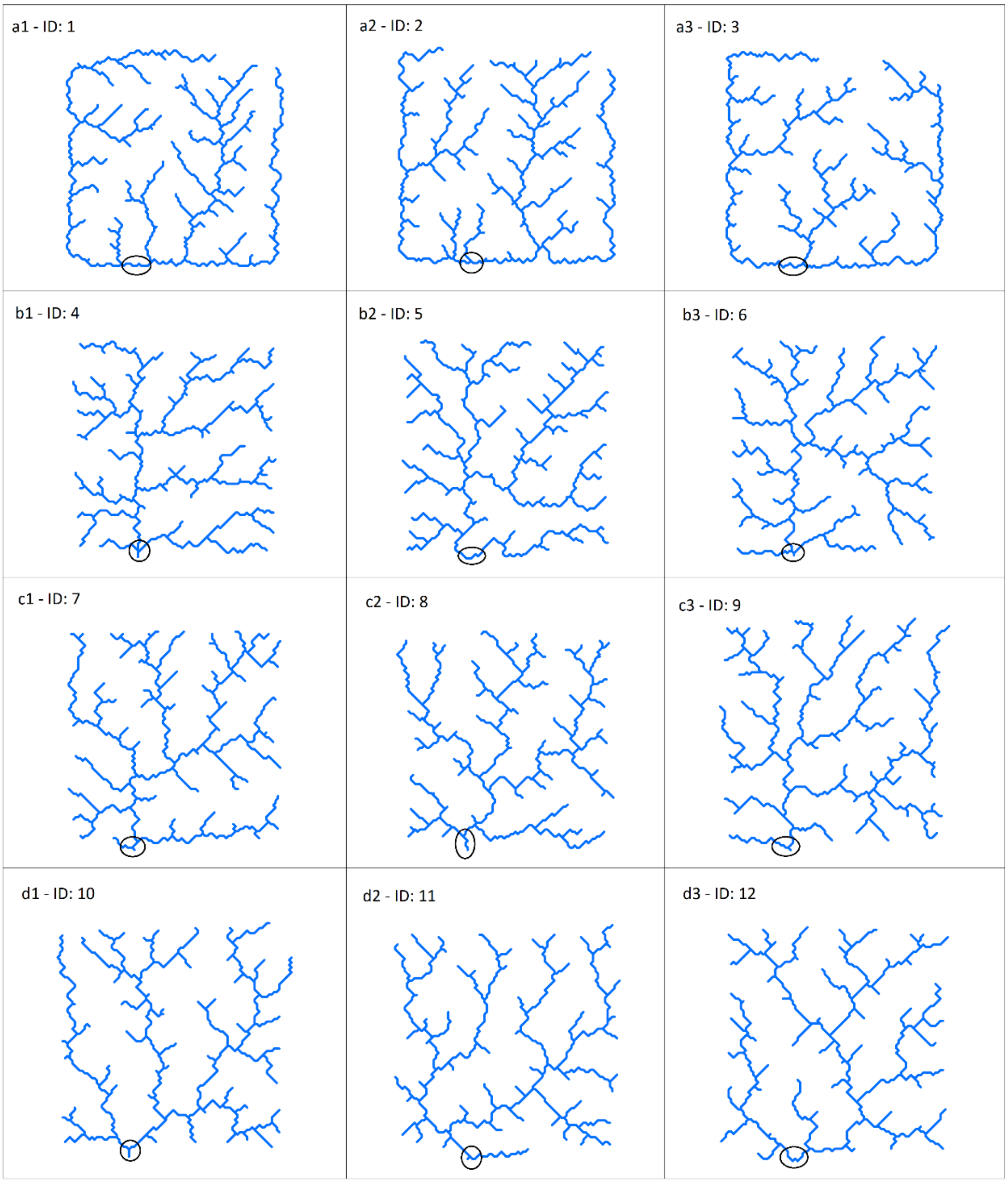


Figure 4.1. Randomly generated virtual river networks. a1-3 “H” shape; b1-3 “I” shape; c1-3 “T” shape; and d1-3 “V” shape. The outflow point is shown by a black circle

4.3.1.2 Real-world river networks

Seven river catchments in England and Wales, chosen in relation to their geographic spread and differences in their network configurations, were extracted from Ordnance Survey data: Frome, Stour, Rother, Great Ouse, Esk, Weaver and Conwy (Figure 4.2). Tiles of geometric mark-up language from OS MasterMap Water Network data (Ordnance Survey 2021) were converted into shapefiles using ‘QGIS 3.16.3’, and the individual rivers were cleaned, removing minor drainage branches (width ≤ 1 m), using ‘ArcGIS Pro’. The mean width of the channels was used to develop raster maps of habitat quality of cell size 50 m using ‘ArcGIS Pro’ by

$$Quality_{actual\ rivers}\ (\%) = width\ \times 2$$

$$\{100\ for\ Quality_{actual\ rivers} > 100\}$$

As with the virtual river networks, as the river width increased, so did the habitat quality for the alien fish. However, unlike the virtual river networks, mean channel widths of real rivers are inherently variable, and so although there were general patterns of wider sections increasingly occurring with distance downstream, areas of wider widths could also be found in more upstream areas.

Figure 4.2. Digitised river catchments in England and Wales

4.3.2 Modelling the invasion of alien fish species

The platform ‘RangeShifter v2.0’ (Bocedi et al. 2014, 2020) was used to build a spatially explicit individual-based model for a virtual invasive fish species with a stage-structured life-cycle, juveniles (< 1 year old), sub-adults (1 to 2 years) and adults (over 2 years) as per Dominguez Almela et al. (2021). The model was implemented using a cell-based approach (see Table 4.1 for full list of parameters). Reproduction was set to occur annually, after which all individuals could migrate up to once during their lifetime. The transfer phase of dispersal was modelled using the stochastic movement simulator (SMS; Palmer et al. 2011), for which the relative cost of movement was set inversely to a cell’s habitat quality (i.e. it is more costly for an individual to move upstream and into areas of poorer habitat quality). In many fish species, there is a tendency for mature males to arrive on spawning grounds before females and leave last in order to maximise their reproductive fitness, so males could settle in any non-natal cell. Mature females could only settle in cells where males were already present.

For the virtual river networks, nine models were then constructed using a set of invasive-like species (Factor ‘SpID’), extracted from Dominguez Almela et al. (2021) and adapted to a cell-based model (Table 4.2). These species demonstrated biological characteristics ranging from *K*-selected, intermediate demography to *r*-selected traits (Factor ‘SpType’), and within each group they could have either fast, intermediate, or slow dispersal abilities (Factor ‘SpDispType’). For the real-world river networks, the same set of species were used in a cell-based model to test how the predictions from the virtual catchments represented those derived from real-world contexts.

For model initialisation, three rules were set that marked the release point for the virtual alien fish (Factor Release point, ‘R’): upstream (stream order ≤ 2), mid-catchment (stream order: 2 to 3) and downstream (stream order: 4) (Figure 4.1). The initial population sizes used for each initialisation rule were similar (random generated river networks: mean 3857 ± 61 (SD); real-world rivers: mean = 5575 individuals ± 80 (SD)). The initial population sizes between the simulated and real-world river systems differed due to the real-world rivers being larger and having higher quality habitats compared to the virtual rivers. Raster cost maps were developed using ‘ArcGIS Pro’ that followed the assumptions from the habitat quality maps that habitat quality decreased, with an increased cost of dispersal, in cells that were closer to the headwater and/or where the channel was narrower. The mean cell quality scores from the release points (R) were used to build the factor variable ‘Mean habitat quality’ (H). The number of confluences over specific distances (Factor ‘Dn’), described for a given release cell (which was located in the centre-most cell of the patch of initial distribution), was the sum of the number of confluence cells within a certain distance, for four distances: 500 m (D5), 1000 m (D10), 2500 m (D25) and 5000 m (D50). An additional three distances were added to analyse the real-world rivers due to their larger size: 10000 m (D100), 25000 m (D250) and 50000 (D500) (Table 4.3a, b).

4.3.3 Model predictions and statistics

For the virtual catchments for each virtual species, 36 models were run (12 landscapes ID x 3 release points R), resulting in 324 models overall with five replicates each. For the real-world rivers, 21 models were run for each virtual species (7 ID x 3 R) with five replicates each. Subsequent testing focused on high-level summary statistics for each replicate that compared values between the catchments and according to their major differences. Four population-level variables were extracted from the model outputs: (i) rate of population increase across 10 years (P_{10}) and (ii) across 30 years (P_{30}), where 30 years was the maximum simulation period; (iii) rate of change in patch occupancy across 10 years (Q_{10}); and (iv) across 30 years (Q_{30}). Thus, P_{10} and Q_{10} reflected the short-term colonisation rates, while P_{30} and Q_{30} were used for the medium-term. All values of P and Q were calculated following the methods from Dominguez Almela et al. (2021); for P_{10}:

$$P_{10} = \frac{(pop[year = 10] - pop[year = 1])}{10}$$

where pop[year=10] is the number of individuals at year 10, and pop[year=1] is the number of individuals at year 1. Then, calculations for years 1 to 10 (*P10*), 6 to 15 (*P15*); 11 to 20 (*P20*), 16 to 25 (*P25*) and 21 to 30 (*P30*) were as per the formula above (other than substituting for the correct number of years), and the maximum mean annual increase in P was determined from:

$$P_{30} \ = \ max(P10, P15, P20, P25, P30)$$

The same approach was used to calculate the change in cell occupancy over a short-period and the maximum decadal rate of (Q_{10} and Q_{30} respectively):

$$Q_{10} = \frac{(NOccupPatches[year = 10] - NOccupPatches[year = 1])}{10}$$

where Q_{10} is the rate of change in cell occupancy for the years 1 to 10 inclusive, NOccupPatches[year=10] is the number of occupied cells at year 10, and NOccupPatches[year=1] is the number of occupied cells at year 1, etc. P_{10}, P_{30}, Q_{10} and Q_{30} were then used as the response variables within linear mixed effects models (LMMs) to account for their differences across the virtual (n = 1620) and real-world rivers (n = 945). The LMMs were fitted in the R package '*lme4*' (Bates et al. 2015) and used to select the best-fitting model according to Akaike's information criterion (AIC). The response variables P_{10}, P_{30}, Q_{10} and Q_{30} were transformed as $y' = \log(y + c)$, where c was a constant sufficiently large to offset any negative values, and the factors species ID (SpID) and catchment ID were treated as random effects in all models. In the model fitting process for the virtual catchments, selection commenced by fitting single terms to a model for all nine species: shape (S), release point (R), habitat quality (H), number of confluences over a distance (D5 to D50), species demography types (SpType) and species dispersal types (SpDispType). After retaining the best single term on the basis of the lowest AIC, additional catchment factors and their interactions were added iteratively, and the best-fitting model retained at each iteration. Finally, species effects (SpType and SpDispType) were added into the models. For the real-world rivers, a similar model selection process involved assessment of the following factors: release point (R), habitat quality (H) and number of confluences over a distance (D5 to D500). The factor catchment ID was included as a random effect, and log transformation was applied as above.

As the release points (R) and mean habitat quality (H) were always highly correlated (i.e. R for upstream reaches always had low H scores and vice-versa; Table 4.3c), all final models were manually modified to examine the variance attributable to explanatory variables present by changing their order. The number of confluences over a distance (D5 to D500) were also correlated, and only one of them was retained in the final LMMs based on the lowest AIC. The estimates of the best-fitting models were used to make predictions of P_{10}, P_{30}, Q_{10} and Q_{30} as functions of H and R (Table 4.3c).

Table 4.1. Demographic and dispersal parameters used in the IBM implemented in 'RangeShifter'

Model parameter	**Stage-structure**	**Density-dependence**	**Value**
Population dynamics			
Number of reproductive seasons/year	Adults	No	1
Proportion of males	Whole population	No	0.5
Probability of reproducing	Adults	No	1
Emigration			
Slope	Whole population	No	10
Inflection point	Juveniles	No	0
	Sub-adults	Yes	0.48
	Adults	Yes	1.23
Transfer			
Directional persistence	Whole population	No	1.5
Perceptual range (m)	Whole population	No	50
Memory size (cells)	Whole population	No	2
Settlement			

Max. no. of steps	Whole population	No	100
Slope	Whole population	Yes	-10
Inflection point	Whole population	Yes	1

Table 4.2. The demographic and dispersal parameter values used in the IBM implemented in 'RangeShifter'

Parameter	Strongly *K*-selected	Intermediate demography	Strongly *r*-selected
Fast disperser	**Species 1**	**Species 2**	**Species 3**
Fecundity	30	63.77	180
1/b (inds/ha)	823.73	1750.96	4942.34
Survival probability in juveniles	1	0.93	0.8
Survival probability in sub-adults	1	0.89	0.2
Survival probability in adults	0.5	0.4	0.1
Max. emigration probability in juveniles	0.4	0.4	0.4
Max. emigration probability in sub-adults	0.7	0.7	0.7
Max. emigration probability in adults	0.9	0.9	0.9
Max. settlement probability	0.013	0.013	0.013
Per-step mortality	0.0045	0.0045	0.0045
Intermediate dispersal	**Species 4**	**Species 5**	**Species 6**
Fecundity	30	63.77	180

1/b (inds/ha)	823.73	1750.96	4942.34
Survival probability in juveniles	1	0.93	0.8
Survival probability in sub-adults	1	0.89	0.2
Survival probability in adults	0.5	0.4	0.1
Max. emigration probability in juveniles	0.1	0.1	0.1
Max. emigration probability in sub-adults	0.18	0.18	0.18
Max. emigration probability in adults	0.18	0.18	0.18
Max. settlement probability	0.025	0.025	0.025
Per-step mortality	0.0045	0.0045	0.0045
Slow disperser	**Species 7**	**Species 8**	**Species 9**
Fecundity	30	63.77	180
1/b (inds/ha)	823.73	1750.96	4942.34
Survival probability in juveniles	1	0.93	0.8
Survival probability in sub-adults	1	0.89	0.2
Survival probability in adults	0.5	0.4	0.1

Max. emigration probability in juveniles	0.01	0.01	0.01
Max. emigration probability in sub-adults	0.05	0.05	0.05
Max. emigration probability in adults	0.14	0.14	0.14
Max. settlement probability	0.06	0.06	0.06
Per-step mortality	0.0045	0.0045	0.0045

Table 4.3. (a) Inter-correlations between statistics; (b) means by release point (R); and (c) range of habitat quality (H) for each level of release point (R)

Random generated catchments (1)

(a1)

	H	D5	D10	D25	D50
H	1				
D5	-0.12	1			
D10	0.05	0.79	1		
D25	0.32	0.36	0.58	1	
D50	0.53	0.22	0.40	0.84	1

UK rivers (2)

(a2)

	H	D5	D10	D25	D50	D100	D250	D500
H	1							
D5	-0.05	1						
D10	0.05	0.71	1					
D25	-0.18	0.47	0.51	1				
D50	-0.26	0.40	0.41	0.88	1			
D100	-0.32	-0.04	0.11	0.58	0.79	1		
D250	-0.24	-0.15	0.16	0.30	0.53	0.82	1	
D500	0.04	-0.07	0.11	0.28	0.44	0.59	0.75	1

(b1)

		H	D5	D10	D25	D50
R	Down	97.9	1.17	3	10.6	27.1
	Middle	57.9	1.67	4.33	16.2	30.7
	Up	14.8	1.5	2.83	6.75	15.5

(b2)

		H	D5	D10	D25	D50	D100	D250	D500
R	Down	50.2	0.71	1.29	2.86	4.71	9.71	28.2	48.6
	Middle	20.2	0.86	1.43	3.14	5.71	13.0	40.9	52.4
	Up	8.20	0.71	1.14	3.86	6.29	11.3	28.7	45.2

(c1)

	R		
	Down	Middle	Up
H	96.7 – 98.7	37.4 – 75.8	11.8 – 17.3

(c2)

	R		
	Down	Middle	Up
H	22.8 - 100	12.4 - 31.9	7 - 9.4

4.4 Results

4.4.1 Virtual river networks

In the virtual rivers, increased values of P_{10} and P_{30} were mainly driven by both the release point of the species (R) and mean habitat quality (H), which were highly correlated (i.e. depending which term is included first, this term explains most of the variance). In the best fitting models, R and H together accounted for 96 % of the model variance in 10 years and 91 % in 30 years (Table 4.4). Shape (S) always accounted for low variance in these models and the number of confluences (Dn) was not included in the best-fitting models for P_{10} or P_{30} (Table 4.4). For Q_{10}, R and H were also the most important variables (90 % of variation; Table 4.4), but for Q_{30}, the number of confluences within 5000 m (D50) explained 91 % of the variance (Table 4.4), the rate of range expansion increasing as the number of confluences encountered by the invader increased. P_{10} and Q_{10} were predicted to vary with H and R (Figure 4.3), where population growth rates would increase as the mean quality of the invaded area increased; in contrast, range expansion rates decreased as quality decreased. P_{10} and Q_{10} were predicted to be higher when the species had faster dispersal ability (Figure 4.3).

When considering the virtual fish species separately, the variance in P_{10} and Q_{10} was, for most species, mainly explained by R and H (P_{10}: 85 to 99 % variance explained; Q_{10}: 85 to 99 %; Table A3.1). For P_{10}, the only exceptions were the intermediate and *r*-selected individuals with fast dispersal, for which R and H accounted for only 5 to 10 % of the variance (Table A3.1). For Q_{10}, the exceptions were fast dispersers of all three demographic types, where R and H only explained 2 to 4 % of variance (Table A3.2). The influence of R and H on P_{10} and Q_{10} was lowest for fast dispersers and highest for slow dispersers; the rate of colonisation and population growth for species with faster dispersal was affected more by the number of confluences (Dn), whereas species with slower dispersal rates were affected more by habitat quality (Tables A3.1-2).

For P_{30} and Q_{30}, the number of confluences (Dn) explained most of the variance in the best-fitting models across most species (P_{30}: 55 to 75 % variance explained; Q_{30}: 50 to 93 %; Tables A3.1-2). For P_{30}, the exceptions were one intermediate and two slow dispersers (0.04 to 0.4 % variance explained)

(Table A3.1); for these species, R explained most variance, which, together with H, explained 86 to 99 % (Table A3.1). For Q_{30}, the exceptions were two slow dispersers, where again R was the best explanatory variable (82 to 94 % of variance) (Table A3.2).

4.4.2 Real-world river catchments

Model predictions of the rate of population growth (P_{10} and P_{30}) of the nine virtual alien species revealed that the best-fitted models included H and R, which together explained 97 % of the variance in 10 years and 93 % in 30 years, leaving only a small percentage explained by Dn (P_{10}: 2 %; P_{30}: 5 %; Table 4.5). As H increased, the population growth rate increased only for upstream releases; when the initial invaded area was either in the mid-catchment or downstream, population growth was inversely related to H (Figure 4.4).

For predictions of Q_{10} and Q_{30}, most model variance was again explained by H and R (Q_{10}: 96 % and Q_{30}: 78 %; Table 4.5). Approximately 10 % of the variance in Q_{30} was explained by Dn within 1000 m distance and 9 % was explained by the dispersal behaviour of the invader (Table 4.5). For upstream releases, higher rates of colonisation were predicted when the initial invaded area was of higher habitat quality (Figure 4.4). Initial invaded areas in mid-catchment or downstream areas had an inverse relationship with H. For species of higher dispersal ability, higher rates of colonisation were predicted compared to intermediate or slow dispersers (Figure 4.4).

At the species level, the number of confluences (Dn) was always included in the best-fitting models predicting P_{10} and P_{30}, but with the effective distance (D5 to D500) varying between species, although R and/or H were the most important explanatory variables (P_{10}: 92 to 99 % variance explained; P_{30}: 81 to 99 %; Table A3.3). For Q_{10} and Q_{30}, R and H were the most important variables in models (Q_{10}: 62 to 99 % variance explained; Q_{30}: 51 to 94 %; Table A3.4), although Dn was also highlighted in 5 out of the 9 models for Q_{30} (13 to 25 %; Table A3.4).

Table 4.4. Principal sources of variance explained (%) in the best-fitting models for rate of population increase (P_{10} and P_{30}) and rate of change of cell occupancy (Q_{10} and Q_{30}) in randomly generated catchments

P_{10}				**Q_{10}**			
10 years	*Log(P + 100)*			*10 years*	*Log(Q + 10)*		
Factor	**Df**	**Sum Sq**	**% variance**	**Factor**	**Df**	**Sum Sq**	**% variance**
Shape (S)	3	1.5	0.3	Shape (S)	3	0.3	0.3
Release point (R)	2	447.4	93.4	Release point (R)	2	74.4	88.9
Hab. quality (H)	1	15.7	3.3	Hab. quality (H)	1	1.4	1.7
				D5	1	0.1	0.1
SpType	2	0.3	0.1				
SpDispType	2	3.5	0.7	SpDispType	2	0.6	0.8
S*R	6	10.7	2.2	S*R	6	5.9	7.1
				S*H	3	0.8	1.0

P_{30}				**Q_{30}**			
30 years	*Log(P + 10)*			*30 years*	*Log(Q + 10)*		
Factor	**Df**	**Sum Sq**	**% variance**	**Factor**	**Df**	**Sum Sq**	**% variance**
Shape (S)	3	1.2	0.7	Shape (S)	3	0.2	1.0
Release point (R)	2	132.9	88.6	Release point (R)	2	0.0	0.0
Hab. quality (H)	1	3.4	2.3	Hab. quality (H)	1	0.0	0.0
				D50	1	17.8	90.8
SpType	2	2.7	1.8				
SpDispType	2	0.2	0.1	SpDispType	2	0.2	1.2
S*R	6	9.8	6.5	S*R	6	1.4	7.0

Table 4.5. Principal sources of variance explained (%) in the best-fitting models for rate of population increase (P_{10} and P_{30}) and rate of change of cell occupancy (Q_{10} and Q_{30}) in real-world rivers

<table>
<tr><th colspan="4">P_{10}</th><th colspan="4">Q_{10}</th></tr>
<tr><td>10 years</td><td colspan="3">Log(P + 170)</td><td>10 years</td><td colspan="3">Log(Q + 20)</td></tr>
<tr><td>Factor</td><td>Df</td><td>Sum Sq</td><td>% variance</td><td>Factor</td><td>Df</td><td>Sum Sq</td><td>% variance</td></tr>
<tr><td>Hab. quality (H)</td><td>1</td><td>333.1</td><td>62.0</td><td>Hab. quality (H)</td><td>1</td><td>32.8</td><td>41.0</td></tr>
<tr><td>Release point (R)</td><td>2</td><td>189.0</td><td>35.2</td><td>Release point (R)</td><td>2</td><td>44.0</td><td>55.1</td></tr>
<tr><td>D5</td><td>1</td><td>10.9</td><td>2.0</td><td>D25</td><td>1</td><td>1.2</td><td>1.6</td></tr>
<tr><td>SpDispType</td><td>2</td><td>3.8</td><td>0.7</td><td>SpDispType</td><td>2</td><td>1.3</td><td>1.6</td></tr>
<tr><td>H*R</td><td>2</td><td>0.9</td><td>0.2</td><td>H*R</td><td>2</td><td>0.6</td><td>0.7</td></tr>
<tr><th colspan="4">P_{30}</th><th colspan="4">Q_{30}</th></tr>
<tr><td>30 years</td><td colspan="3">Log(P + 140)</td><td>30 years</td><td colspan="3">Log(Q + 20)</td></tr>
<tr><td>Factor</td><td>Df</td><td>Sum Sq</td><td>% variance</td><td>Factor</td><td>Df</td><td>Sum Sq</td><td>% variance</td></tr>
</table>

Hab. quality (H)	1	184.7	63.1	Hab. quality (H)	1	4.6	28.7
Release point (R)	2	88.1	30.1	Release point (R)	2	7.9	49.7
D5	1	14.9	5.1	D10	1	1.5	9.7
SpDispType	2	3.0	1.0	SpDispType	2	1.4	8.9
H*R	2	1.7	0.6	H*R	2	0.5	3.0

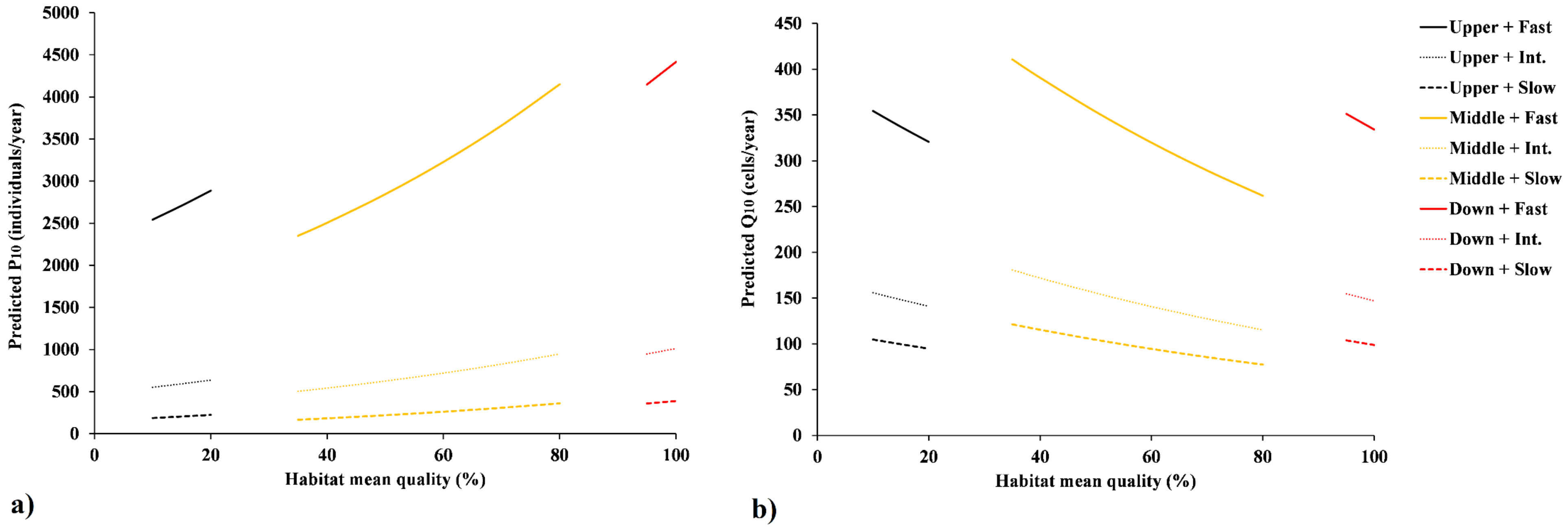


Figure 4.3. (a) Predicted rate of population growth (P_{10}) for each release point (R) vs. release point mean habitat quality (H) in virtual catchments. (b) Predicted rate of change in cell occupancy (Q_{10}) for each release point (R) vs. release point mean habitat quality (H) in virtual catchments. V-shaped drainage pattern and Dn = 5 applied

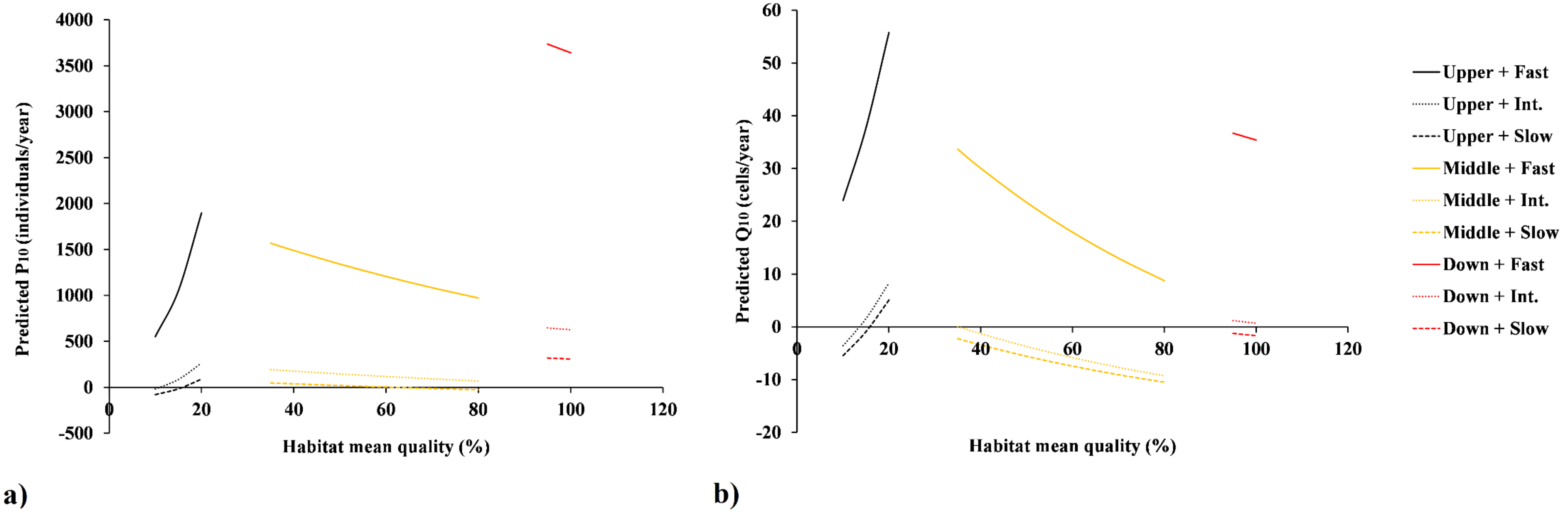


Figure 4.4. (a) Predicted rate of population growth (P_{10}) and (b) predicted rate of change in cell occupancy (Q_{10}) for each species dispersal type (fast, intermediate, slow) vs. release point mean habitat quality (H) in real-world catchments

4.5 Discussion

The management of alien species in the environment generally aims to minimise their impacts on the native communities and requires assessment of the current spatial distribution of the invader and predictions of how this will change over time (Britton et al. 2011b). For alien riverine fishes, these assessments require information on how their dispersal rates and population demographics influence their colonisation rates following their introduction (Dominguez Almela et al. 2020). Here, we applied an IBM to predict how different river network configurations and habitat quality influenced the invasion of nine virtual alien fish that varied in their dispersal abilities and life history traits, and by the location of their introduction into the network. In both the virtual and real-world river networks, the general prediction was that both population growth and cell occupancy rates were mainly driven by the location of the introduction of the species and its mean habitat quality, as predicted, but with the configuration of the network often having a relatively minor influence, contrary to prediction. The influence of the location of introduction into the network was important as it determined the overall direction of spread, i.e. whether the wider range expansion of the species required upstream or downstream movements, where downstream movements had a higher benefit as they involved movements into cells of higher habitat quality. In addition, downstream movements in fish can be passive as well as active, whereas upstream movements can only be active (Benjamin et al. 2007). It was only over the longer 30-year time period that the rate of catchment colonisation increased as the spreading population encountered more confluences (i.e. tributaries). This aspect was consistent with our prediction and conforms with empirical studies that suggest that invasion dynamics can be strongly dependent on changes in stream order, with larger, mainstem rivers having faster colonisation rates than headwaters (Radinger and Wolter 2014).

Network complexity was predicted to be important in the invasion success of virtual species with high dispersal ability, as increased numbers of river confluences elevated their colonisation rates. The movements of the fish into numerous branches opens up a larger number of range fronts, and so the expression of high dispersal ability at numerous range fronts increases their colonisation rate (Masson et al. 2018). In contrast, slow dispersers were more affected by the habitat quality of the cells into which they were introduced, as this affected their population growth during the early years of colonisation. This habitat selection and condition-dependent movement can be seen in many fish species, for which the relationship between individual decisions of movement and larger-scale population dynamics over time and space are generally important for understanding the importance of movement for species' persistence (McMahon and Matter 2006). The relationship between individual decisions and population dynamics is arguably even more important for alien species during their colonisation period, given the relationship between their establishment within cells (metric Q) and the species' rate of population growth (metric P). For example, while dispersal enables movement into new cells, it has energetic, mortality risk and time costs that can decrease the probability of establishment in those new cells (Bonte et al. 2012). Longer distance dispersers also often arrive in poorer condition than those moving shorter distances (Lange and Marshall 2016), and the quality of the individuals arriving in the new habitat is an important determinant of establishment success (Myles-Gonzalez et al. 2015). In the context of alien fishes, while r-selected species with high dispersal abilities are predicted to have faster colonisation rates, species with more K-selected life history traits and lower dispersal ability can still be successful invaders if their trade-offs are favourable between dispersal, establishment and individual quality (García-Berthou 2007).

Across all nine species, rivers and time frames, the location of the introduction into the river network was highly important in determining the rate of network colonisation, affecting both the direction of the movement needed for colonisation and the costs involved in relation to habitat quality. In real-world rivers, actual differences in channel morphology, gradient, thermal regime and physical habitat structure would strongly influence the ability of some alien fish species to survive and then establish. For example, in the River Great Ouse, a highly regulated, low energy lowland river, bitterling *Rhodeus sericeus* (small-bodied, short lifespan) and pikeperch *Sander lucioperca* (larger bodied, long life-span) are already invasive (Nolan and Britton 2018b, Dominguez Almela et al. 2020). As both of these fishes are typical of lowland rivers, they are less likely to withstand the conditions in the River Conwy, a river of higher energy running off an upland area of North Wales and where salmonid fishes are prevalent.

However, invasive salmonids, such as pink salmon *Oncorhynchus gorbuscha,* which has recently appeared in Scottish and Irish rivers (Armstrong et al. 2018, Millane et al. 2019), could potentially prosper in the Conwy, but would be unlikely to be able to enter the Great Ouse due to flood regulation structures acting as barriers to upstream movement. These real-world considerations are important, as they highlight the alien species most likely to invade these actual catchments, where the Great Ouse appears more vulnerable to the invasion by alien fishes with a wider range of traits than the Conwy. Only after these species-specific traits are considered would the location of their release be important, but with this also likely to be influenced by the actual species concerned and their ability to adapt to the new conditions. For example, rainbow trout *Oncorhynchus mykiss* is regularly released for angling into many head-waters in Britain, albeit with low invasion success (Fausch 2007), but their ability to survive in reaches downstream is likely to be much reduced due to their requirements for relatively cool, highly oxygenated waters.

Invasive freshwater fishes can present a variety of dispersal traits, with the interaction of these traits with the river network important in determining invasion outcomes (e.g. Fukuda et al. 2013, Almeida et al. 2014). The characteristics of the area of first introduction can be an important predictor of the success of colonisation as, while rivers vary considerably in their network configurations, their upper reaches tend to be relatively narrow and less suitable for fish (Kim et al. 2021). If the invader was introduced into these areas then it is likely it would need to expend considerable amounts of energy to disperse into more suitable habitats. Our simulations predicted that upstream releases resulted in higher rates of spread, mainly due to the fish being able to quickly reach the maximum carrying capacity of the low-quality cells, so they keep moving into new cells of similar or lower costs (i.e. downstream direction). Fast dispersers were predicted to colonize the real-world rivers more rapidly than the intermediate and slow invaders. Areas that were highly branched and of good habitat quality especially positively affected fast dispersers, as these enabled the fish to invest their energy on establishing abundant populations while occupying new cells in the river.

The IBM applied here provided a predictive approach for investigating the relationship between newly introduced alien species and their novel riverine environment. While investigating these relationships empirically is difficult, predictive models can also have limitations due to their simplification of real-world situations (With 2002). We made several model assumptions for reasons of parsimony. For example, the habitat quality of the randomly generated rivers was created with the assumption of upstream areas being of lower habitat quality according to their narrower width (i.e. through littoral areas potentially having less vegetation for refugia, and with the main channel having a higher flow regime and lower water level capacity). Indeed, many British rivers conform to this pattern, especially for alien cyprinid fishes where areas further downstream of higher stream order are more likely to provide more suitable habitats (Kim et al. 2021). While this simplified the modelling process, we acknowledge that some alien species introduced in downstream areas would be capable of moving upstream and could even pass structures that fragment the river (Starrs et al. 2017). Our model did not consider anthropogenic barriers, so the dispersal of the species was only limited by the costs of their dispersal. Given the extensive fragmentation of rivers in Britain (Jones et al. 2019), and indeed in Europe (Belletti et al. 2020) and the world more generally (Grill et al. 2019), future work should consider incorporating barriers into network configurations, especially as these barriers can affect the behaviour of freshwater organisms (Starrs et al. 2017, Rodeles et al. 2021). However, this would require an additional algorithm relating to barrier permeability, such as the ability of fish to move upstream according to river level (Davies et al. 2021), and whether the barrier incorporated a fish by-pass structure (Pereira et al. 2017). Interactions of the invading fish with the native community were also not considered within the model, and it is acknowledged that these interactions can be an important factor in the outcome of biological invasions where, for example, the extent of native biotic resistance and resilience to the invader can determine the extent of its establishment and spread (Alofs and Jackson 2014, Svenning et al. 2014, Thompson and Fronhofer 2019). Nevertheless, we argue that despite not being able to include the impacts of barriers on fish movements and the extent of resistance and resilience by native communities, the simulations provided a series of novel insights on the abiotic factors that influence the invasiveness of alien riverine fish, and can be used within invasion risk assessment processes to help identify the most appropriate interventions (Bampfylde et al. 2010, Britton et al. 2011a, Dominguez Almela et al. 2020).

In summary, our application of this IBM has filled a considerable knowledge gap in understanding how river network complexity, habitat quality and location of introduction influence the invasion success of alien fishes of differing life history traits and dispersal abilities. The predictions indicated that, in general, the location of the release is fundamentally important through its influence on the direction of dispersal required for the species to locate favourable habitat conditions. River network configuration was important in the longer term, such that more complex networks enabled the opening of more invasion fronts that drove an elevated colonisation rate. Species with higher dispersal abilities were able to colonise networks faster, especially when they had *r*-selected traits that facilitated establishment within cells. Correspondingly, these predictions reveal that the combination of biotic and abiotic variables can affect both dispersal and establishment processes, but that can be better understood when these processes are decoupled within predictive models.

5 Predicting the competitive interactions and trophic niche consequences of a globally invasive fish with threatened native species

5.1 Abstract

Novel trophic interactions between invasive and native species potentially increase levels of interspecific competition in the receiving environment. However, theory on the trophic impacts of invasive fauna on native competitors is ambiguous, as while increased interspecific competition can result in the species having constricted and diverged trophic niches, the species might instead increase their niche sizes, especially in omnivorous species. The competitive interactions between an omnivorous invasive fish, common carp *Cyprinus carpio*, and a tropically analogous native and threatened fish, crucian carp *Carassius carassius*, were tested using comparative functional responses (CFRs). A natural pond experiment then presented the species in allopatry and sympatry, determining the changes in their trophic (isotopic) niche sizes and positions over 4 years. These predictive approaches were complemented by assessing their trophic relationships in wild populations. Comparative functional responses revealed that compared to crucian carp, carp had a significantly higher maximum consumption rate. Coupled with a previous cohabitation growth study, these results predicted that competition between the species is asymmetric, with carp the superior competitor. The pond experiment used stable isotope metrics to quantify shifts in the trophic (isotopic) niche sizes of the fishes. In allopatry, the isotopic niches of the two species were similar sized and diverged. Conversely, in sympatry, carp isotopic niches were always considerably larger than those of crucian carp and were strongly partitioned. Sympatric crucian carp had larger isotopic niches than allopatric conspecifics, a likely response to asymmetric competition from carp. However, carp isotopic niches were also larger in sympatry than allopatry. In the wild populations, the carp isotopic niches were always larger than crucian carp niches, and were highly divergent. The superior competitive abilities of carp predicted in aquaria experiments were considered to be a process involved in sympatric crucian carp having larger isotopic niches than in allopatry. However, as sympatric carp also had larger niches than in allopatry, this suggests other ecological processes were also likely to be involved, such as those relating to fish prey resources. These results highlight the inherent

complexity in determining how omnivorous invasive species integrate into food webs and alter their structure.

5.2 Introduction

Ongoing globalisation is driving increases in biological invasions (McNeely 2001). Besides driving biological homogenisation, invasive species can have substantial consequences upon the receiving communities, including the transmission of novel pathogens, habitat degradation and hybridisation with native species (García-Vásquez et al. 2017, Hitt et al. 2003, Matsuzaki et al. 2009). As ecological impacts can also occur via direct predation or indirectly through competition for resources (Foley et al. 2017), then determining the mechanisms involved in determining the severity of these impacts is integral for invasion risk management to avoid negative and cascading effects on food webs (Britton et al. 2010d).

Although predicting the ecological impacts of alien species is an important aspect of invasion risk assessment, it remains highly challenging (Dick et al. 2017b). Considerable progress has been made in predicting the trophic impacts of aquatic invasive species in recent years using comparative functional responses (CFRs), where relatively simple aquarium experiments using alien species and their native analogues have successfully predicted high impacting invaders (e.g. Laverty et al. 2017, Paterson et al. 2015). However, a potential issue of CFRs is their experimental designs, where exposing consumer species to single prey species within tank aquaria can represent an over-simplification of more complex natural systems in which a wider range of prey resources are available (Britton 2018, Dick et al. 2014). Scaling-up experimental approaches for predicting the trophic impacts of alien freshwater fishes to mesocosms and pond enclosures have provided considerable insights into their trophic interactions with native species (Britton 2018), with suggestions that rather than share and potentially compete for similar prey resources, functionally analogous native and alien fishes often demonstrate strong patterns of trophic niche partitioning (Britton et al. 2018, Raby et al. 2020).

Determining mechanisms by which novel species integrate into native food webs and coexist with native species can provide the basis for understanding the success of highly invasive alien species (Catford et al. 2009). For example, the use of unexploited resources by the alien species minimises their competitive interactions with native species (the empty niche hypothesis [ENH]; Mason et al. 2008b, Juncos et al. 2015). Conversely, in scenarios where the prey resources are all being exploited then the increased competitive interactions can result in population niche constrictions as each species increasingly develops dietary specialisms (Jackson et al. 2016b, Mason et al. 2008a), which can also result in strong niche partitioning. Although it is commonly referred to as the niche variation hypothesis (Britton et al. 2019), here we refer to it as the trophic specialisation hypothesis (TSH) to emphasise the mechanism. Alternatively, as interspecific competition increases, the niche sizes of each species might increase as individuals diversify their diet as the prey resources deplete (Svanbäck and Bolnick 2007). While this has been referred to as the trophic niche hypothesis, here we refer it as the trophic generalisation hypotheses (TGH). In more extreme cases, asymmetric interspecific competition can result in the weaker species being competitively excluded from their original trophic niche, resulting in their reduced energetic intake that can lead to slower growth rates and lower population abundances (Chase et al. 2002).

The trophic niches of omnivorous species have the potential to be highly plastic in response to different biotic and abiotic contexts. Accurately predicting their trophic interactions with native species is then challenging, as intraspecific and interspecific variability can result in the same species generating different impacts in disparate systems (Klose and Cooper 2013). A strong example of a globally invasive omnivorous species is the common carp *Cyprinus carpio* ('carp' hereafter), a freshwater fish that whose domination of many aquatic ecosystems causes a severe threat to native fish, aquatic plants and invertebrates (Weber and Brown 2009). Consequently, the aim of this study was to initially use carp as the model alien species to predict, using two experimental approaches, their trophic interactions with a threatened native fish, the crucian carp *Carassius carassius*, a species with similar functional traits and feeding behaviours (Busst and Britton 2017). As both species are aggregative and compete exploitatively (Bajer et al. 2011, Baumgartner et al. 2008, Penne and Pierce 2008), they were used in both a CFR experiment based on using paired fish and in a relatively long-term (4 years) pond experiment in southern England, where stable isotope analysis (SIA) was used to assess the extent of their trophic interactions. Then, the results of both experiments were compared to their actual trophic relationships in wild, invaded ponds in southern England, also using SIA.

Hypotheses on the trophic interactions of carp and crucian carp can be designed from recently completed feeding studies involving the two species. First, a co-habitation aquaria experiment, which used the two species in allopatry and sympatry and exposed them to fixed feeding rations, suggested their asymmetry in their competitive interactions, as crucian carp length increments were significantly smaller in sympatry than allopatry (Busst and Britton 2015). Therefore, Hypothesis 1 was that the CFR experiment would show that carp have a higher magnitude functional response and associated parameters than crucian carp, indicating higher resource consumption efficiency. Second, a co-habitation pond enclosure experiment indicated that when the two species are in sympatry, their trophic niches do not overlap, and for crucian carp, their niche shifts to a higher trophic position than when in allopatry (Busst and Britton 2017). Consequently, in the natural pond experiment and wild ponds, Hypothesis 2 is that the trophic niches of sympatric carp and crucian carp will be highly divergent, with the trophic niche of sympatric crucian carp being smaller and at a higher trophic position than in allopatry as a result of diet specialisation (i.e. TSH).

5.3 Materials and methods

5.3.1 Study species

The crucian carp is considered native in ponds and lakes in Britain, Europe and central Asia (Wheeler 1997, 2000), although more recent evidence suggests it might have actually been introduced into Britain around 600 years ago (Jeffries et al. 2017). It is considered as threatened in England due to the loss of its preferred pond habitats and the presence of alien species, especially carp and brown goldfish *Carassius auratus* (Copp et al. 2010, Sayer et al. 2011). The carp, listed on the list of the World's Worst Global Invaders (Lowe et al. 2000), is highly invasive in many countries (Escobar et al. 2018) and has been present in England since at least the 15th century, but perhaps since Roman times (Hoole et al. 2001).

5.3.2 Comparative functional responses

The crucian carp used in the CFRs were captured using baited traps from natural populations in two adjacent ponds in Southern England. Both populations had been seeded from the source and so did not differ genetically, with two ponds used to ensure the appropriate number of fish were collected. The carp were sourced from a local hatchery where they had been pond-reared on a mix of natural and supplemental food, before being held in small outdoor ponds (1,000 L) for 2 months without supplemental feeding to promote natural foraging behaviours. Both species were then moved into an aquarium facility and held in species-specific holding tanks (90 L; 10 fish per tank) at 17 ℃ for 21 days, with daily feeding (ad libitum) with frozen chironomid larvae. The CFR experiment was completed at 17 ℃ to represent typical summer water temperatures in England (Britton 2007). Given the two species are aggregative in nature (Bajer et al. 2011, Baumgartner et al. 2008, Penne and Pierce 2008), then rather than complete the experiment on individuals, the fish were used in conspecific pairings. Prior to the CFR trials, the fish were measured with callipers (standard length [SL] to 0.1 mm), with mean lengths (±SD) of crucian carp being 66.3 ± 6.7 mm and common carp being 66.6 ± 7.7 mm, and were thus considered as size-matched.

The CFR trials were all completed in rectangular tanks (20 L volume) without substrate or refugia, and to eliminate external stimuli, were covered with a lid and the sides were also covered. Hunger levels were standardised by the experimental fish not being fed for 24 hr prior to experiments. The paired conspecifics were selected randomly from their holding tanks, released into the experimental tanks and then acclimated for 2 hr. The food resource was pelletised fishmeal (‘pellets’) of 2 mm diameter, as these provide a resource of standard dimensions that have been consumed readily by similar fish species in functional response experiments (e.g. Murray et al. 2013). The pellets were released into the tanks at one of seven specific amounts (2, 4, 8, 16, 32, 48 and 96 pellets), with each amount replicated at least three times. Each individual trial lasted 4 hr and, at their conclusion, the fish were removed from the tank and the number of unconsumed pellets counted. The derived number of consumed pellets thus represents the number consumed per conspecific pair, rather than per individual fish.

Following the conclusion of all trials, the CFRs were modelled in the R package '*frair*' (Pritchard 2014) using maximum likelihood estimation (MLE, Bolker 2010) and Rogers' (1972) Random Predator Equation (Equation 1), as the prey were not being replaced as they were consumed. Where the proportion of prey consumed decreased as prey density increased then the logistic regression produces a significantly negative result representing a 'Type II response'; in contrast, if it produces a significantly positive result then it represents a 'Type III' response (Juliano 2001). Given both species indicated a significant Type II response, then Rogers' random predator equation was determined from:

$$Ne = N_0(1 - exp\,(a(N_e h - T)))$$

where Ne is the number of pellets eaten, N_0 is the initial density of pellets, a is the attack parameter, h is the handling parameter and T is the total time available (fixed at 1). The FR data were non-parametrically bootstrapped (bias corrected and accelerated; n = 2,000) to generate 95 % confidence intervals around the mean FR curve of each species, with comparison of the 95 % confidence intervals enabling these data to be considered in a phenomenological manner with regard to population-level inferences (Pritchard et al. 2017) and with overlapping confidence intervals considered as indicating non-significant differences in the FR curves of the two species. In addition, parameter estimates [*a, h*] between the two species were compared using the z-method (Juliano 2001) via *frair:fair_compare*.

5.3.3 Natural pond experiment

Predicting the trophic interactions of crucian carp and carp was completed in a natural pond experiment in southern England between 2016 and 2019. In January 2016, juveniles of both species were sourced from local hatcheries where they had been reared in ponds, and were released into three adjacent (but unconnected), fishless (following their draining, drying and re-filling), former aquaculture ponds of approximately 400 m^2, maximum depths of 1.2 m, and with relatively clear water (secchi disk depths > 0.75 m) and highly abundant macrophyte growth (mainly *Elodea spp.*), with the water clarity remaining largely unchanged throughout the experimental period. The ponds were used as three distinct treatments, but with these not replicated due to logistical reasons preventing use of a greater number of ponds. Two of the ponds were used as allopatric controls, with 100 juvenile carp released into one pond and 100 crucian carp into the other (all < 100 mm). The third pond was used as a sympatric treatment, where the same number of fish was used (100) but split 50:50 between both species. As both species lack external features to enable differentiation of the sexes, then the sex ratios were unknown. While all three ponds had an increasing number of invasive signal crayfish *Pacifastacus leniusculus* present during the study ('crayfish' hereafter), only in the sympatric treatment in 2018 and 2019 were sample sizes sufficiently high to enable samples to be analysed ($n \geq 6$).

The ponds were then left until September 2017 to enable their tissues to become isotopically equilibrated to their new prey resources. The fish were then sampled in September 2017, 2018 and 2019 using baited fish traps set overnight. After lifting, the captured fish were removed, measured (fork length, FL, nearest mm), anaesthetised and a fin biopsy taken, and were then released back into their pond. Concomitantly, samples of macro-invertebrates (as fish putative prey resources) were taken using a sweep net and sorted for stable isotope analysis (SIA). The samples of fish fin, crayfish and macroinvertebrates were then taken to the laboratory, dried to constant mass at 60 ℃ and then analysed at the Cornell University Stable Isotope Laboratory (New York) for $\delta^{13}C$ and $\delta^{15}N$ in a Thermo Delta V isotope ratio mass spectrometer (Thermo Scientific) interfaced to a NC2500 elemental analyser (CE Elantach Inc.). Analytical precision of the $\delta^{13}C$ and $\delta^{15}N$ sample runs was estimated against an internal standard sample of animal (deer) material every 10 samples, with the overall standard deviation estimated at 0.08 and 0.04 ‰, respectively. Ratios of C:N were generally between 3.5 and 4.0, and so were not mathematically corrected for lipid (Winter et al. 2021c).

Prior to further analyses, the SI data of the fish putative prey were compared within each pond by year and between the ponds. As these revealed some considerable differences (Table A4.1), then the fish SI data could not be compared directly between the ponds and years without correction (De Santis et al. 2021). Consequently, the $\delta^{15}N$ muscle data were converted to trophic position (TP) according to (Olsson et al. 2009):

$$TP = 2 + \delta^{15}N_{fish} - \delta^{15}N_{prey} / 3.4$$

where TP and $\delta^{15}N_{fish}$ are the trophic positions and the nitrogen ratios of each individual fish, $\delta^{15}N_{prey}$ is the mean nitrogen ratio of the putative macroinvertebrate prey resources (Table A4.1), 2 is the trophic position of these prey resources (as primary consumers) and 3.4 is the generally accepted fractionation factor between adjacent trophic levels (Post 2002). The fish $\delta^{13}C$ data were converted to corrected carbon ($\delta^{13}C_{corr}$) according to the following equation (Olsson et al. 2009):

$$\delta^{13}C_{corr} = (\delta^{13}C_{fish} - \delta^{13}C_{meanMI}) / CR_{MI}$$

wherein $\delta^{13}C_{fish}$ is the $\delta^{13}C$ value of each fish, $\delta^{13}C_{meanMI}$ is the mean $\delta^{13}C$ of the macroinvertebrate prey (Table A4.1) and CR_{MI} is the carbon range ($\delta^{13}C_{max} - \delta^{13}C_{min}$) of the same macroinvertebrates (Olsson et al. 2009).

Following the correction of the SI data to $\delta^{13}C_{corr}$ and TP, the initial data analysis tested differences in these data between the two fish species in the sympatric treatment using ANCOVA, where the covariate was fish length and data for all years were combined. Then, to account for the presence of crayfish in the sympatric treatment, the significance of differences between their corrected SI data with the fish corrected SI data was tested in one-way ANOVA (with Tukey multiple comparisons of means with 95 % family-wise confidence levels). The corrected SI data were then used to calculate the trophic niche size of each fish species per pond and sampling year, using the isotopic niche as a proxy of the trophic niche (Jackson et al. 2011). While closely related to the trophic niche, the isotopic niche is also influenced by factors including growth rate and metabolism (Jackson et al. 2011). The isotopic niches were calculated as standard ellipse areas (SEA) in SIBER (A. L. Jackson et al. 2011, M. C. Jackson et al. 2012). SEAs are a bivariate measure of the distribution of individuals in isotopic space and as the ellipses enclose the core 40 % of data, they represent the typical resource use of the analysed population (De Santis et al. 2021, Jackson et al. 2011). A Bayesian estimate of SEA (SEA_B) tested differences in niche sizes between the treatments per species, calculated using a Markov chain Monte Carlo simulation (104 iterations per group; A. L. Jackson et al. 2011, M. C. Jackson et al. 2012). Differences in the size of isotopic niches (as SEA_B) were evaluated by calculating the probability that the relative posterior distributions of the niche size of the allopatric treatment were significantly smaller or larger than those of each of their sympatric niches ($\alpha = 0.05$) in SIBER. The SI data were then used to calculate isotopic niche overlap (%) between the species using SEA_c also calculated in SIBER, where subscript '$_c$' indicates a small sample size correction was used (Jackson et al. 2012). The use of SEA_c was mainly to get a representation of the extent of niche overlap between species, as it is more strongly affected by small sample sizes (< 30) than SEA_B (Jackson et al. 2012). Overlaps between the isotopic niches were calculated based on SEA_c with 95 % confidence tested for the species between their allopatric and sympatric treatments each year.

5.3.4 Wild ponds with sympatric carp and crucian carp

There were four wild ponds sampled for their populations of sympatric carp and crucian carp between July and September 2019. The ponds were all located in southern England, were between 0.5 and 1.5 ha in area and had depths to 2 m. Their exact locations are unable to be provided to protect business confidentiality, as each was run as a private fishery for catch-and-release angling. All of the fish had been present in the ponds for at least 3 years (i.e. there had been no recent stocking of fish). The fish were sampled by a combination of baited fish traps and rod and line angling during stock assessment exercises, where the species were identified, measured (FL, nearest mm) and scale samples taken (3 to 5 scales per fish), originally for age and growth analyses for fishery management purposes. It was these scales that were used for stable isotope analysis, with scales tending to have a longer isotopic half-life than fin tissue (Busst and Britton 2018). The scales were not decalcified prior to isotopic analysis, as the removal of inorganic carbonates has no significant effect on scale $\delta^{13}C$ and $\delta^{15}N$ values (Ventura and Jeppesen 2010, Woodcock and Walther 2014). They were prepared by their cleaning with distilled water before the outer portion of the scale was removed for SIA, as this ensures that the analysed tissue is from the most recent growth of each fish (e.g. the last full year of growth; Hutchinson and Trueman 2006). Only one scale was analysed per individual fish as this provided sufficient material for SIA. The samples were then prepared and analysed for $\delta^{13}C$ and $\delta^{15}N$ as per the natural pond experiment. As these SI data were only compared between the two species within each pond and not between ponds, no corrections were made to these data. As per the natural pond experiment, differences in the SI data between the species were initially tested in ANCOVA before their isotopic niches were calculated (as SEA_B and SEA_C) in SIBER.

The ethical approval process and all regulated procedures were completed under UK Home Office licence PPL 30/3277. All data analyses were completed in ‘R 4.0.5’ (R Core Team 2021).

5.4 Results

5.4.1 Comparative functional responses

In the CFR experiments, the first-order linear coefficient from logistic regressions revealed the functional responses of both species were Type II and significant (first-order linear coefficients from logistic regressions: carp: −0.03, $p < 0.001$; crucian carp: −0.02, $p < 0.001$). Parameter estimates [*a, h*] were significant for both species. There was no difference between attack parameter estimates of carp (mean ± SE: 8.62 ± 2.72) and crucian carp (4.53 ± 1.65; $z = 1.16$, $p = 0.25$). However, carp (0.025 ± 0.001) had a significantly shorter handling parameter estimate compared to crucian carp (0.12 ± 001; $z = 7.82$, $p < 0.001$). The maximum feeding estimate of carp (40.0) was considerably higher than crucian carp (8.1), with no overlap in their 95 % confidence intervals (Figure 5.1).

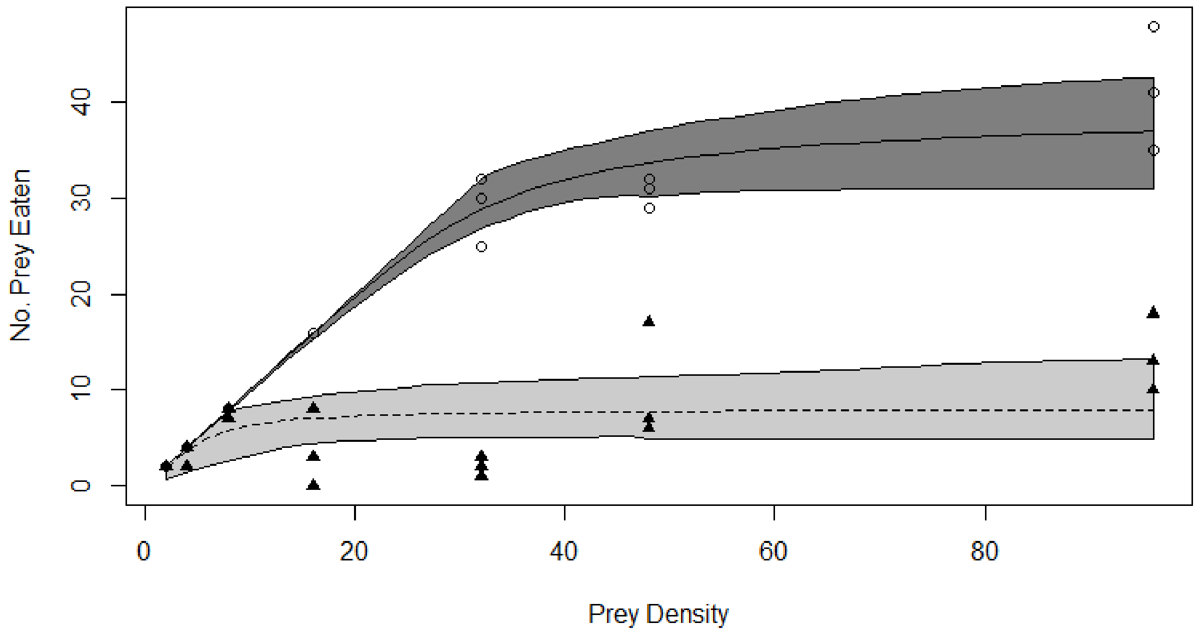


Figure 5.1. Comparative functional response plot of common carp *Cyprinus carpio* (clear circles, solid line) versus crucian carp *Carassius carassius* (black triangles, dashed line) fitted with Type II functional response curves calculated using Rogers' random predator equation. Shaded regions indicate 95 % confidence intervals around the fitted functional response from bootstrapping 999 iterations

5.4.2 Natural pond experiments

Across the three sampling years, there were considerable differences in the fish lengths of the two species due to reproduction and recruitment in the crucian carp, but with this not occurring in common carp; the differences in lengths within each species were relatively minor (Table 5.1; Table A4.1). In the sympatric treatment across all sampling years, there were significant differences in the corrected SI data between the two species ($\delta^{13}C_{corr}$: $F_{1,88} = 16.33$, $p < 0.01$; TP: $F_{1,88} = 5.18$ $p = 0.02$), where the effects of fish length as a covariate were not significant ($\delta^{13}C_{corr}$: $F_{1,88} = 0.09$, $p = 0.77$; TP: $F_{1,88} = 2.21$, $p = 0.14$; Figures 2 and 3). In the sympatric treatment, the carapace lengths of the analysed crayfish were 35 to 45 mm, with their corrected SI data differing significantly from the two fish species (ANOVA: $\delta^{13}C_{corr}$: $F_{2,91} = 43.81$, $p < 0.01$; TP: $F_{2,91} = 122.52$, $p < 0.01$; Figure A4.1). The Tukey multiple comparisons of means indicated that the differences in $\delta^{13}C_{corr}$ between crucian carp and crayfish were significant ($p < 0.01$), but were not between carp and crayfish ($p = 0.21$). For TP, the Tukey multiple comparisons indicated the differences between the species were all significant ($p < 0.01$; Figure A4.1).

The range of SI values of corrected $\delta^{13}C$ and TP was higher for both species in sympatry than in allopatry (Table A4.1). This was then reflected in their isotopic niches always being larger in sympatry than allopatry in each sampling year (Figure 5.2). Comparisons of the relative posterior distributions of the ellipse areas (as SEA_b) indicated that for carp, their isotopic niches were always significantly larger in sympatry than allopatry, whereas for crucian carp, this was only the case in 2019 (Table 5.1).

Comparison of the SI metrics for the two species in their allopatric treatments indicated similar isotopic niche sizes that slightly overlapped in their isotopic space in 2017 and 2018 (2 % and 1 %, respectively), but not in 2019 (Table 5.1; Figure 5.3a). In the sympatric treatment, the isotopic niches of carp were always larger than crucian carp in each sampling year (Figure 5.3b), although their relative posterior distributions of the ellipse areas (as SEA_b) indicated these differences were not significant (Table 5.1). Their isotopic niches (as SEA_c) also did not overlap in any sampling year (Figure 5.3b). This was also the case for the crayfish in the sympatric treatment, whose isotopic niche did not overlap with the fish species in 2018 or 2019 (Figure A4.1).

Table 5.1. Mean fork length (±95 % CL) and isotopic niche sizes (as standard ellipse areas, SEA_c and SEA_b, with 95 % CI) per species, year and treatment, in the natural pond experiment

Treatment	**Species**	**Year**	**Mean length (mm)**	**SEA_c (CI)**	**SEA_b (CI)**
Allopatric	Carp	2017	171 ± 9	0.18 (0.10, 0.28)	0.17 (0.10, 0.28)
Sympatric	Carp	2017	166 ± 6	1.18 (0.63, 1.72)	1.01 (0.55, 1.89)
Allopatric	Carp	2018	206 ± 9	0.13 (0.09, 0.17)	0.11 (0.07, 0.20)
Sympatric	Carp	2018	215 ± 7	0.46 (0.24, 0.70)	0.43 (0.26, 0.75)
Allopatric	Carp	2019	244 ± 9	0.10 (0.07, 0.12)	0.08 (0.05, 0.16)
Sympatric	Carp	2019	252 ± 8	0.57 (0.20, 0.99)	0.52 (0.33, 0.88)
Allopatric	Crucian	2017	86 ± 13	0.14 (0.07, 0.20)	0.12 (0.07, 0.23)
Sympatric	Crucian	2017	86 ± 12	0.42 (0.16, 0.71)	0.37 (0.22, 0.64)
Allopatric	Crucian	2018	103 ± 12	0.15 (0.10, 0.19)	0.13 (0.07, 0.25)
Sympatric	Crucian	2018	87 ± 9	0.28 (0.13, 0.42)	0.24 (0.14, 0.43)

Allopatric	Crucian	2019	118 ± 6		0.08 (0.04, 0.11)	0.07 (0.06, 0.08)
Sympatric	Crucian	2019	82 ± 9		0.24 (0.11, 0.37)	0.21 (0.13, 0.36)
Sympatric	Crayfish	2018	n/a		0.15 (0.06, 0.23)	0.14 (0.08, 0.24)
Sympatric	Crayfish	2019	n/a		0.20 (0.10, 0.29)	0.17 (0.11, 0.31)

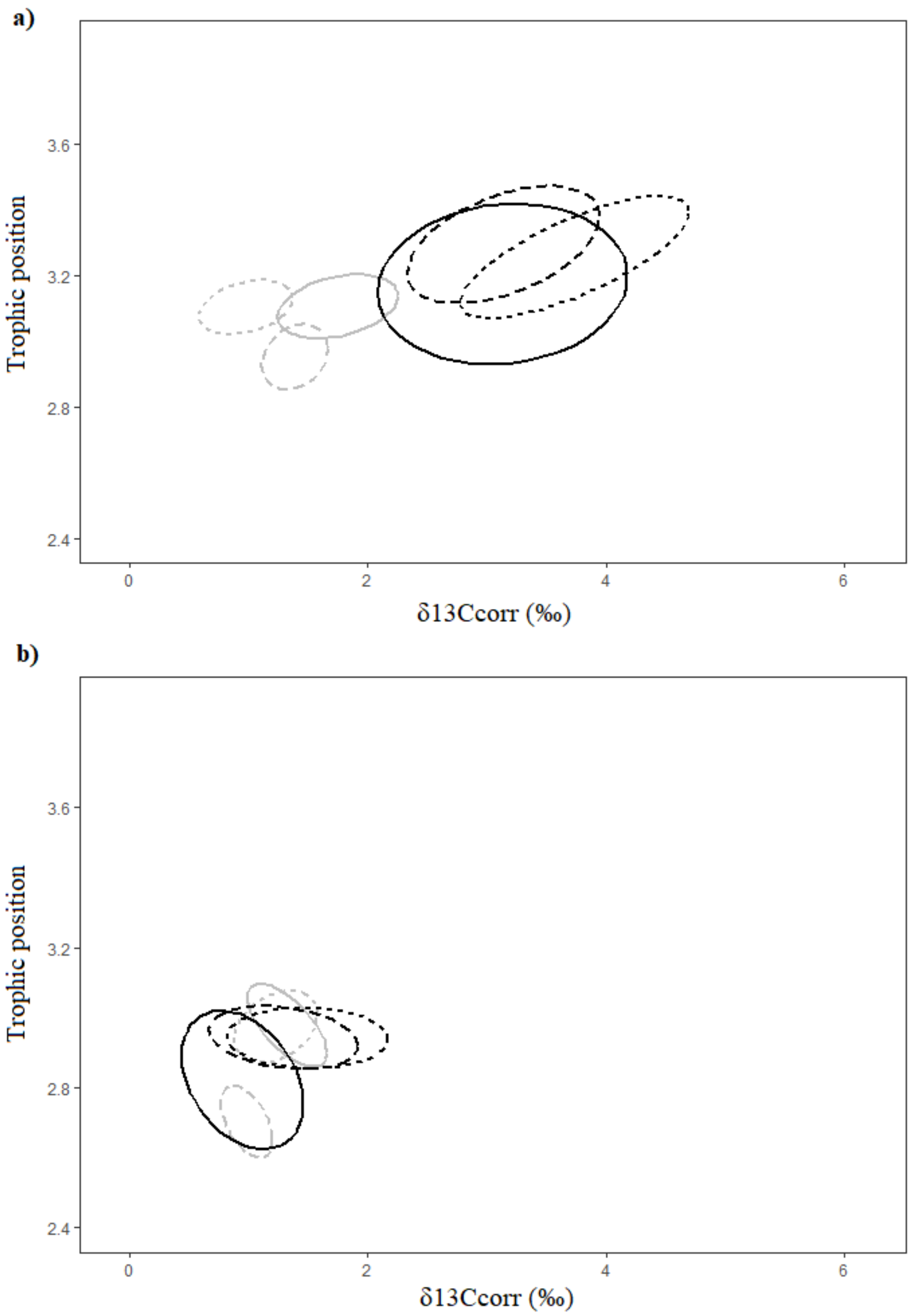


Figure 5.2. The isotopic niches (represented as standard ellipse areas, SEA_C) of (a) allopatric carp (grey ellipses) versus sympatric carp (black ellipses) and (b) allopatric crucian carp (grey ellipses) versus sympatric crucian carp (black ellipses) in 2017 (continuous line), 2018 (dotted line) and 2019 (dashed line), in the natural pond experiment

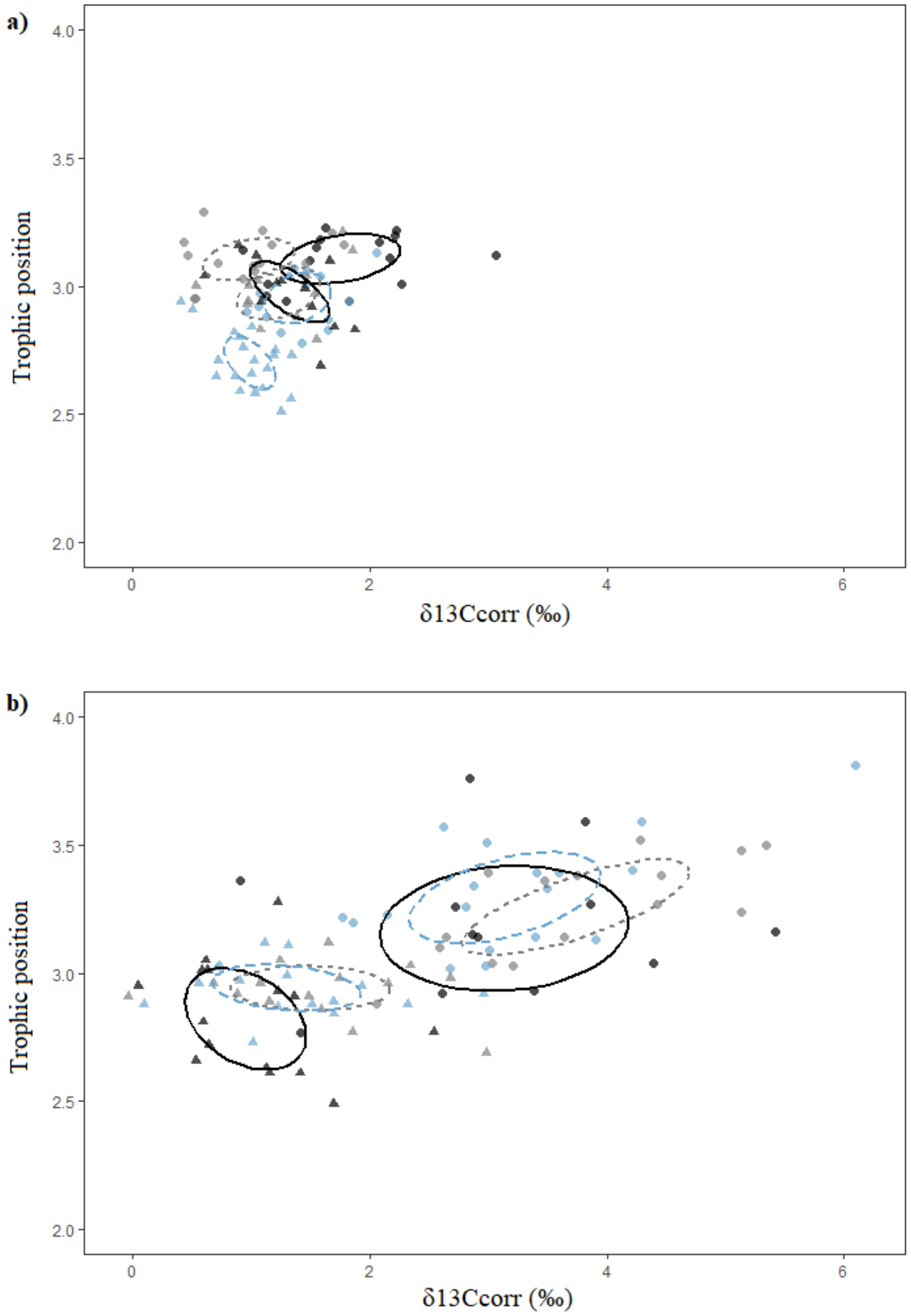


Figure 5.3. The isotopic niches (represented as standard ellipse areas, SEA_c) for (a) allopatric and (b) sympatric treatments for carp (filled circles) and crucian carp (filled triangles) in 2017 (black continuous line), 2018 (grey dotted line) and 2019 (blue dashed line), in the natural pond experiment

5.4.3 Wild ponds with sympatric carp and crucian carp

The mean lengths of the two species analysed in each pond were relatively similar, with some overlaps in their length ranges (Pond 1: carp 181 ± 58, crucian carp 134 ± 8 mm; Pond 2: carp 118 ± 46, crucian carp 69 ± 8 mm; Pond 3: carp 154 ± 15, crucian carp 179 ± 23 mm; Pond 4: carp 141 ± 10, crucian carp 147 ± 10 mm; Table A4.2). There were significant differences in both stable isotopes between the species in each pond ($p < 0.05$ in all cases; Table A4.3), where the effect of fish length as a covariate was not significant ($p > 0.05$; Table A4.3), other than for $\delta^{13}C$ in Pond 2 ($p = 0.04$; Table A4.3). The range of the SI data of carp was higher than crucian carp in all ponds except Pond 2 (Table A4.2), with this reflected in carp having larger isotopic niches than crucian carp in these ponds (Figure 5.4). However, the relative posterior distributions of the ellipse areas (as SEA_b) indicated these isotopic niches were only significantly larger in carp in Pond 3 (Table 5.2). In Ponds 2–4, there were no overlaps in the species' isotopic niches (as SEA_c), but with minor overlap apparent in Pond 1 (Figure 5.4).

Table 5.2. Isotopic niches sizes of carp and crucian carp in each wild pond (as SEA_b) and their 95 % confidence intervals (CI)

	Pond 1	**Pond 2**	**Pond 3**	**Pond 4**
Common carp	3.4 (1.9, 6.3)	1.9 (1.0, 3.3)	2.5 (1.2, 7.0)	3.6 (2.0, 6.7)
Crucian carp	2.1 (1.1, 4.3)	0.9 (0.5, 1.8)	0.6 (0.3, 1.1)	2.2 (1.1, 4.2)

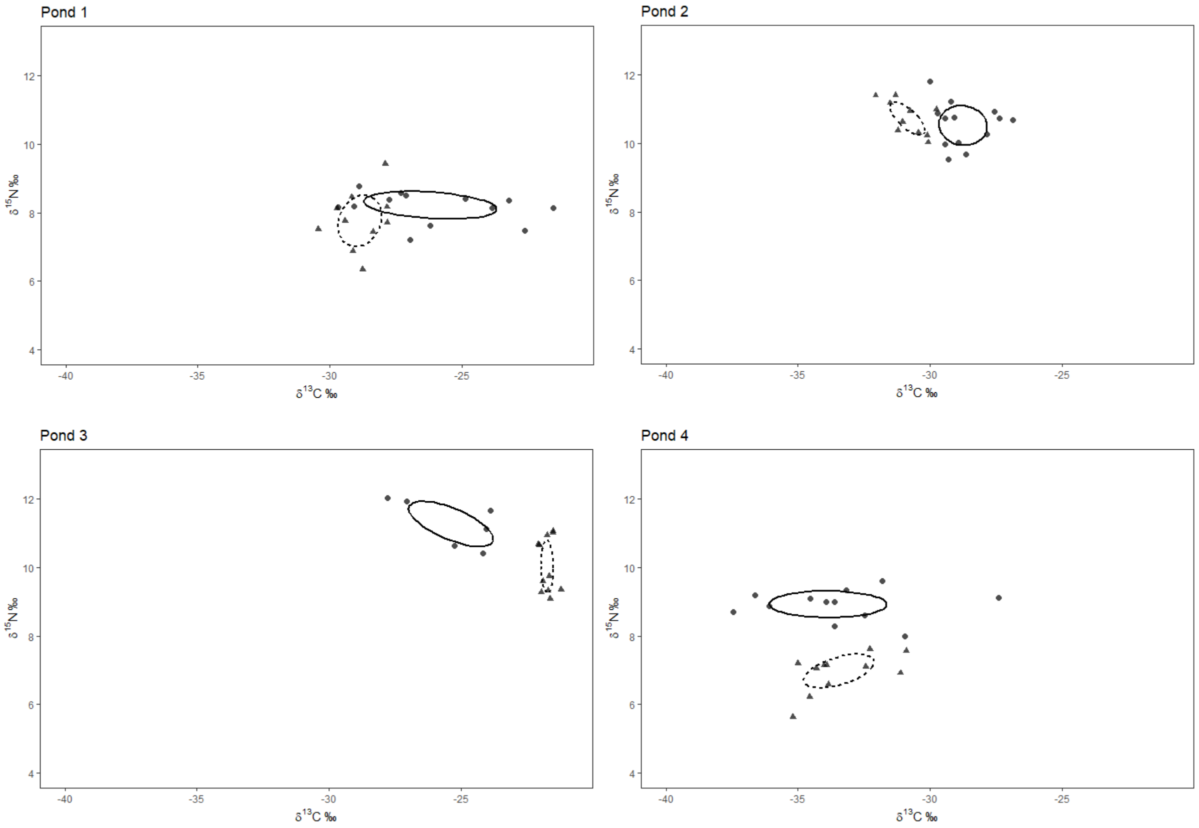


Figure 5.4. The isotopic niches (represented as standard ellipse areas, SEA_c) of carp (filled dots; continuous ellipses) and crucian carp (filled triangles; dotted ellipses) in each wild pond

5.5 Discussion

Predicting outcomes of trophic interactions between native and invasive species is a prerequisite for invasive species risk assessment and subsequent management. The CFR experiment completed here corroborated Hypothesis 1, with carp having a higher maximum feeding rate than crucian carp. When this result is considered in conjunction with the co-habitation aquarium experiment of Busst and Britton (2015), these results suggest that their competitive interactions are asymmetric, with carp accessing more prey than crucian carp. Previous pond enclosure experiments also indicated when the species are in sympatry in more natural contexts, there are considerable shifts in the position of the crucian carp trophic niche compared to allopatry, suggesting that the presence of invasive carp results in some dietary shifts in crucian carp (Busst and Britton 2017). Here, the natural pond experiment, which seeded three similar, fishless ponds with equal numbers of carp and crucian carp in allopatry and sympatry, revealed that over 4 years, there were consistent patterns of larger isotopic niches in carp than crucian carp, with these niches being strongly partitioned, as per Hypothesis 2. However, the isotopic niches for both species were considerably larger in sympatry than allopatry and there was also no consistent pattern in the change in trophic position of their niches between allopatry and sympatry. Both of these results are contrary to Hypothesis 2. In the four natural pond populations, carp also had larger isotopic niches than crucian carp, with these niches also being partitioned.

High impact invasive species are consistently predicted by CFRs (Dick et al. 2014, Dickey et al. 2020). This has been confirmed across a broad range of invasive taxa (Dick et al. 2013, Laverty et al. 2017, Madzivanzira et al. 2021), including piscivorous fish (Alexander et al. 2014). The CFR results from the present study clearly show capacity for more efficient resource consumption by invasive carp as driven by shorter handling estimates. Type II functional responses and high maximum feeding estimates are ostensibly destabilising for prey populations (Dick et al. 2014). Nevertheless, CFRs have rarely been used to imply that the invasive species are superior competitors, given that any displacement of native species by an invader might also be by driven by other mechanisms (Dick et al. 2017a, Luger et al. 2020). When in sympatry, invasive fish can outcompete native species through more efficient resource consumption when compared to each species in allopatry, even where there is no net loss on prey populations (Mofu et al. 2019). Here, we show that carp impact is driven by lower handling parameters rather than attack (i.e. search and encounter rates), indicating that in a given period of time carp are able to consume more food than crucian carp. These results are supported by the results of the growth co-habitation experiment of Busst and Britton (2015), which indicated the growth increments of carp were considerably higher than crucian carp when in sympatry as they accessed a greater proportion of the fixed food resources. In combination, these results suggest that asymmetric competition should enable carp to monopolise higher proportions of shared prey resources when in sympatry with functionally analogous species (such as crucian carp), at least in contexts where these resources are limited.

Hypothesis 2 had predicted that these isotopic niches would be constricted when the two species were in sympatry versus allopatry, indicating a more specialist diet (i.e. TSH). In these scenarios, populations become more specialised in their diet under conditions of increased interspecific competition and thus reduce their niche size (Olsson et al. 2009, Thomson 2004, Van Valen 1965). To increase the experimental complexity beyond aquaria experiments and the co-habitation pond enclosure experiments of Busst and Britton (2017), the longer-term pond experiment was used to assess the trophic interactions of invasive carp and native crucian carp, using two allopatric and one sympatric treatment (but was unable to be replicated). The allopatric treatments indicated that the isotopic niches of the two species would be similar sized and largely distinct from each other, with only minor overlap. In sympatry, the actual isotopic niches of carp were considerably largely than those of crucian carp, and these niches were strongly partitioned, with no overlap between them. Moreover, their sympatric isotopic niches were considerably larger than in allopatry, with a much wider range isotopic range evident in both species when in sympatry versus allopatry, indicating their use of a greater range of prey resources where they coexist. The isotopic niche expansion evident in our natural pond experiment thus rejects Hypothesis 2 and suggests that as resource competition (both intraspecific and interspecific) increases, each species will exploit a broader diet to maintain their energetic requirements (De Santis et al. 2021, Svanbäck and Bolnick 2007). Indeed, this has been documented in carp populations in China as a mechanism for persistence when in sympatry with invasive transgenic carp (Wang et al. 2021). The potential role of intraspecific competition on this increased trophic generalisation in the natural pond experiment was also suggested, given that the crucian carp had reproduced in the sympatric treatment and so their numerical abundance was relatively high by the end of the experiment when compared to carp.

The results from both the pond experiment and the wild pond populations indicated strong partitioning between the isotopic niches of carp and crucian carp. Partitioning was evident in the allopatric treatments of the pond experiment, thus indicating that this occurs regardless of interspecific competitive interactions, albeit the partitioning was considerably stronger in the sympatric treatment. Carp are superior competitors towards crucian carp (as per the aquaria experiments). Thus, while we posit that crucian carp increase their resource breadth in response to strong competition from carp, there is some uncertainty in how this asymmetric competition influenced the isotopic niche sizes. Despite carp being superior competitors, their niche sizes also increased in sympatry and actually had minimal overlap with the carp from the allopatric treatments, which suggests that they were displaced. During the experiment, the ponds were purposely left unmanipulated between sampling events to enable the relationships between the species to develop over time without disturbance, and thus the abundances of the prey resources were not measured. It is plausible that the increased niche size of both species in the sympatric treatment could have also been due to prey resources becoming more depleted than in the allopatric ponds, thus forcing fish to exploit a broader range of resources. Although this cannot be explicitly tested, inferences from the CFR experiments suggest that both species consume comparable amounts of prey even at low resource densities in a resource population destabilising manner. Furthermore, carp are ecosystem engineers which can alter prey communities in both abundance and richness (e.g. Kloskowski 2011, Stuart et al. 2021, Zambrano and Honojosa 1999). The larger niches in sympatry might have also been related to density dependence, given that the crucian carp reproduced in the sympatric pond (producing an established population where there were abundant individuals of 60–100 mm), whereas the carp did not as they did not reach sufficient size to be sexually mature (generally > 300 mm; Brown et al. 2005, Winker et al. 2011). There were thus higher total fish abundances in the sympatric pond versus the carp allopatric pond. However, the crucian carp also recruited strongly in their allopatric pond, where the isotopic niches were smaller versus sympatry, with little indication of displacement. This is potentially important, given dietary shifts are often apparent in fishes as their lengths increase (Davis et al. 2012, Gutmann Roberts and Britton 2018). Indeed, there was a mismatch in the lengths of the carp versus crucian carp that increased over the experimental period (differences in mean lengths in the sympatric pond in 2017 was 80 mm vs. 170 mm in 2019). This was at least partially overcome in some analyses using fish length as a covariate, where its effect on the stable isotope data was primarily non-significant, and with length differences being relatively minor between the species in the wild ponds.

In entirety, these results and inferences suggest greater complexity in the relationships between the species than was possible to be elucidated from the experimental approaches used here. Indeed, predicting trophic interactions of generalist and omnivorous native and alien species is challenging, given their dietary plasticity (Klose and Cooper 2013). Short-term simplistic - yet data intensive - controlled aquaria experiments enable precise mechanisms to be deduced, while in more complex and natural experiments, the ecological signals may take longer to become apparent or become diluted by other processes. Complementary approaches should be developed to improve predictive capacity to overcome these issues regarding ecological scale (Korsu et al. 2009, Spivak et al. 2011). This was at least partially overcome here by the complementary use of the pond experiments (enclosures in Busst and Britton (2017); entire ponds here). In this case, the results of the pond experiments were from contexts that were closer to natural scenarios but that still had some initial control over the experimental conditions, for example, ponds being fishless prior to start (Spivak et al. 2011, Tran et al. 2015). Other options for future work include the use of wild-sourced fish for all experiments. While the use of hatchery-reared carp here provided the experimental approaches with access to appropriate numbers of fish that could be size-matched to the crucian carp, hatchery-reared fish often have, compared to wild fish, lower genetic variability and poorer anti-predator responses, and can differ in aspects of their foraging behaviours (Milla et al. 2021, Tang et al. 2017, Xu et al. 2012). As such, the use of wild-sourced fish in future experiments would eliminate this potential confound, although it could also introduce new issues, such as increasing the difficulty of obtaining appropriate sample sizes of fish of the required lengths for size-matching within the trials. In addition, the presence of invasive signal crayfish in the natural pond experiment increased over time, especially in the sympatric treatment, with this unable to be avoided as the species started recolonising the ponds (as they had been extirpated when the ponds were drained and dried prior to the experiment). However, their presence was not considered as a major driver of the fish trophic ecology in the ponds due to their relatively low trophic position and isotopic niches that were strongly partitioned from the fish species, with this also consistent with previous studies on these species in pond environments (e.g. Jackson and Britton 2014).

The common carp has been described as one of the world's worst vertebrate pests (Stuart et al. 2021), implicated in the decline of threatened crucian carp in Norfolk (Sayer et al. 2020), but is highly valued for recreational angling and aquaculture (Vilizzi 2012). While aspects of the ecological impacts of invasive carp are well chronicled (e.g. Vilizzi 2012, Vilizzi et al. 2015, Weber and Brown 2009), knowledge regarding trophic impacts and outcomes for native species is limited. The approaches here demonstrate that invasive carp can act as a strong competitor with functionally analogous native species, even when they have potentially been present in sympatry for sustained periods, given carp were first introduced into Britain at least 600 years ago (Britton et al. 2010a). Where invasive carp are able to increase the size of their trophic niche to facilitate persistence in sympatry then this will ultimately alter the food web structure in resource-limited pond environments. This presents a plausible mechanism for the widespread decline of crucian carp via indirect impacts of carp invasions (Sayer et al. 2020) and one that has relevance for other native fishes threatened by the invasion of alien omnivorous fishes.

6 Dietary contributions of the alien zebra mussel *Dreissena polymorpha* in British freshwater fish suggest low biological resistance to their invasion

6.1 Abstract

Native communities can resist the establishment and invasion of alien species through consumptive and/or competitive interactions. The extent of consumptive resistance from freshwater fish to the invasion of zebra mussels *Dreissena polymorpha*, a globally invasive Ponto-Caspian species, was assessed in two areas in Britain using stable isotope analysis, where mixing models predicted the contribution of putative prey resources (including zebra mussel) to fish diet. Across the sites and species, only roach *Rutilus rutilus* were predicted to have a diet where zebra mussels contributed highly (predicted contribution: 44%), with literature suggesting that their functional morphology would have facilitated their consumption of this prey item. Predicted contributions of zebra mussels to common bream *Abramis brama* diet was comparatively low (29%), despite them being present to much larger sizes than roach, and with pike *Esox lucius*, perch *Perca fluviatilis* and pikeperch *Sander lucioperca* also predicted to have low dietary contributions of zebra mussels (0.08%, 24% and 24% respectively). These results suggest the consumptive resistance to its invasion in Britain has been low and, correspondingly, if there is a management desire to further limit the invasion of zebra mussels then relying on biological resistance to limit their invasion appears to be insufficient.

6.2 Introduction

Alien species are a pervasive agent of global change (Simberloff et al. 2013), with the consequences of invasions including both ecological and economic damage (Crystal-Ornelas and Lockwood 2020, Diagne et al. 2021). Although the number of alien species introduced into new regions remains relatively high at global levels (Dawson et al. 2017, Turbelin et al. 2017), the proportion of these introductions that develop damaging invasions tends to be relatively low (Gozlan 2008). Nevertheless, an area that has produced a relatively high number of globally invasive aquatic species is the Ponto-Caspian region (Ricciardi and

MacIsaac 2000), which comprises a large geographic extension around the Black, Azov and Caspian seas that is characterized by variable climatic and habitat conditions that provide its native species with relatively high adaptation capacity (Gallardo and Aldridge 2013). Invasive species that originate from this region include amphipods (e.g. killer shrimp *Dikerogammarus villosus*) and molluscs (e.g. zebra mussel *Dreissena polymorpha*) (Gallardo and Aldridge 2015).

In the risk management of introduced alien species, an important component is understanding the processes by which introduced species are able to colonise novel ecosystems (Dominguez Almela et al. 2020), where the establishment of the population and its integration into the native food web are fundamentally important (Britton and Gozlan 2013, Britton et al. 2018). There are a number of hypotheses on factors that influence the establishment of an introduced species and thus whether it will go on to develop an invasive population (Catford et al. 2009). These include the biological resistance hypothesis, which posits that communities of native species can mediate the establishment and performance of invasive species through competitive and/or consumptive interactions (Britton 2012, Alofs and Jackson 2014). In freshwater ecosystems, evidence suggests that the mechanisms of biological resistance are stronger from consumptive resistance than competitive resistance (Alofs and Jackson 2014), with functionally diverse communities having relatively high resistance against multiple invaders (Byun et al. 2020).

Zebra mussels are a global invader whose continued range expansion has been facilitated by their transport on boats (Robertson et al. 2020). Zebra mussels have been implicated in substantial changes in invaded freshwaters, including increased water clarity, modified nutrient cycling, altered composition of the benthic community and changes in the fish community (Hansen et al. 2020, Robertson et al. 2020). Furthermore, the ability of zebra mussels to efficiently filter water (4 L / day; Silverman et al. 1996) has been shown to impact dissolved oxygen concentrations (Strayer 2009, Wong et al. 2021) and phytoplankton/zooplankton densities (Wong et al. 2021), resulting in cascading effects (Higgins and Vander Zanden 2010, Rennie et al. 2013). However, zebra mussels can also be important dietary component of the resident fish community, with studies in North America suggesting that at least six fish species are potential predators of these mussels, with this facilitated by their mouth size, teeth and chewing abilities (French 1993). Magoulick and Lewis (2002) reported that zebra mussels were an important part of the diet of blue catfish *Ictalurus furcatus*, freshwater drum *Aplodinotus grunniens* and redear sunfish *Lepomis microlophus*. Laboratory experiments on round goby *Neogobius melanostomus* suggested they preferred consuming zebra mussels over species of clams and snails (Ghedotti et al. 1995). Studies on roach *Rutilus rutilus* indicated that larger fish would consume more mussels than smaller individuals, with fish below 160 mm in length considered as unable to consume them (Prejs et al. 1990). In a Canadian study, Wong et al. (2021) argued that although some fish may feed on zebra mussels, they would still use other prey resources as their primary dietary items and so would not act as a biological control of these invaders. The bias of studies on zebra mussels to North America indicates there are considerable knowledge gaps on their invasion elsewhere in their range, especially in relation to their integration into invaded food webs and how they contribute to consumer diets, and thus what the extent of the biological resistance is to their invasion.

Zebra mussels were introduced into Great Britain in 1824 and have since spread to a number of discrete lakes, rivers and canals, with Aldridge et al. (2004) suggesting relatively recent increases in their abundance and distribution. However, there remains limited knowledge on their invasion in Britain, including to what extent they are dietary components of fish communities, where species present include roach (as per Prejs et al. 1990). Also present is the common bream *Abramis brama*, which Nagelkerke and Sibbing (2011) considered to not be an efficient consumer of zebra mussels due to limitations set by the crushing power of their pharyngeal teeth. The objective of the current study was to assess the dietary contributions of zebra mussels to the fish community of two invaded and spatially discrete sites of Britain, where dietary contributions were predicted from the ecological application of stable isotope analysis. These dietary contributions were predicted and compared between omnivorous and piscivorous native and alien fishes, given these will differ in their putative prey resources, with the effect of body lengths of individual fish also tested on the dietary predictions. We posit that zebra mussels are an important component of the diet of at least some fish species in invaded waters in Britain and these fish species would have thus provided some consumptive resistance to their invasion.

6.3 Materials and methods

6.3.1 Site details

Site 1 was the Gloucester-Sharpness Canal in western England that is connected to the River Severn estuary at its downstream end (51.7249 N, 2.4733 W). This canal was constructed to allow for navigation of goods from the sea to Gloucester docks; 25 m wide and 5 m deep (Nolan and Britton 2018a). Sampling was focused in the areas downstream of Gloucester, where the fish assemblage is dominated by the cyprinid species roach *Rutilus rutilus* and common bream *Abramis brama* ('bream' hereafter), with perch *Perca fluviatilis* and invasive pikeperch *Sander lucioperca* also present (J. R. Britton, personal observations). Site 2 was the River Bure in eastern England. This river is 87 km in length, flowing south-east towards Breydon Water estuary at Great Yarmouth. Along with its tributaries, the Rivers Ant and Thurne, it forms the northern area of the Broads National Park, a wetland of significant ecological importance (Natural England 2020, Winter et al. 2021c). The River Ant is mentioned as being colonised by zebra mussels in Aldridge et al. (2004). The area is characterised by multiple small shallow lakes termed 'Broads' (medieval peat diggings) less than 40 ha in size. As the landscape is generally flat, the catchment is tidal for approximately 45 km inland. The focal area under study here was upstream of the upper limit of saline incursion at Horning (Winter et al. 2021c), where the river was approximately 25 m wide with depths to 1.5 m. Depths of the connected lakes were typically ~1.5 m and did not exceed 3 m. Across the two reaches, the fish assemblage has limited diversity, being dominated by roach and bream, with perch and pike *Esox lucius* also present (Table 6.1). Both sites had Zebra mussels present in all sampled areas, being abundant on areas such as submerged boat moorings.

Table 6.1. Species, number of individuals (n), tissue type, $\delta^{13}C$ and $\delta^{15}N$ stable-isotope ratios (Mean ± SD) and range by fish site

Site	Species	n	Tissue	Mean $\delta^{13}C$ (‰)	$\delta^{13}C$ range (‰)	Mean $\delta^{15}N$ (‰)	$\delta^{15}N$ range (‰)
1	Bream	15	Scale	-26.42 ± 0.77	(-27.66, -24.81)	15.56 ± 0.72	(14.03, 16.44)
	Perch	10	Scale	-26.15 ± 0.66	(-27.51, -25.13)	15.82 ± 1.00	(14.64, 17.98)
	Pikeperch	14	Scale	-25.61 ± 0.59	(-26.43, -24.40)	17.31 ± 0.94	(15.64, 18.91)
	Zebra mussel	18	Muscle	-35.45 ± 1.42	(-37.72, -33.56)	11.86 ± 0.60	(10.81, 12.88)
	Chironomidae		Whole	-30.19 ± 1.26	(-32.19, -28.27)	11.06 ± 0.79	(10.13, 12.39)
	Gammaridae		Whole	-31.28 ± 1.27	(-32.99, -29.13)	12.14 ± 0.85	(10.32, 13.12)
	Macrophyte		Whole	-30.08 ± 0.88	(-31.12, -28.83)	9.28 ± 0.27	(9.05, 9.72)
2	Bream	28	Fin clip	-28.52 ± 1.30	(-30.92, -25.57)	17.07 ± 0.73	(15.69, 18.69)
	Perch	9	Fin clip	-28.77 ± 1.39	(-31.90, -26.84)	17.59 ± 1.77	(14.92, 20.73)
	Pike	15	Fin clip	-27.71 ± 1.24	(-30.98, -25.69)	19.35 ± 0.65	(18.19, 20.31)

	Roach	11	Fin clip	-30.04 ± 1.12	(-31.98, -28.56)	16.55 ± 1.25	(14.13, 18.16)
	Zebra mussel		Muscle	-34.26 ± 0.34	(-34.69, -33.87)	11.92 ± 0.14	(11.73, 12.06)
	Gammaridae		Whole	-36.11 ± 0.82	(-36.86, -34.97)	13.67 ± 0.11	(13.52, 13.77)
	Killer shrimp		Whole	-30.63 ± 0.33	(-31.07, -30.27)	15.36 ± 0.70	(14.44, 16.13)

6.3.2 Sampling

The main sampling period for Site 1 was April to June 2017 where, due to the habitat of the canal (depth, width, boat traffic), sampling by traditional capture methods (e.g. electric fishing, seine netting) was not feasible. Rod-and-line angling was used as an alternative, where scales were collected from captured fish and used subsequently in stable isotope analysis (SIA). This scale collection was facilitated by the Environment Agency, the inland fishery regulatory body of England, who established a network of anglers within the area, where the participating anglers recorded their catches and were trained in the collection of scale samples that were used initially in age and growth analyses for fisheries management purposes (Nolan and Britton 2018b). Following their capture, the fish were identified to species, measured (fork length, nearest mm), and between 3 and 5 scales removed from the area below the dorsal fin and above the lateral line, and stored in a small paper envelope. In the same period, putative prey resources were sampled using long-handled sweep-nets, where macroinvertebrate samples were dominated by Gammaridae and Chironomidae. Also present in these samples were zebra mussels and macrophytes.

The main sampling period for site 2 was September 2018. Roach and perch were also sampled from the main river by angling, as sampling by typical fish capture methods (e.g. electric fishing, seine netting) was not feasible for the same reasons as per site 1. The captured fish were identified to species, measured for fork length (nearest mm) and a pelvic fin biopsy taken and frozen. Concomitantly, samples of amphipods were collected using a sweep net, with subsequent identification in the laboratory indicating the presence of species of Gammaridae and the invasive killer shrimp. This method was also used to collect samples of zebra mussels from colonised areas (e.g. boat moorings). There were few areas of macrophyte in the main river and so samples were not collected for subsequent analysis as per site 1. For bream, samples were also collected in the vicinity of the areas where the putative prey resources were collected using rod-and-line angling as per the roach and perch, with the same biometric data recorded and fin biopsy taken, but with the samples collected in April 2018. Only bream that subsequently foraged in the areas around the tagging site were used in analyses, as other individuals present were identified as spawning migrants from reaches further downstream and the River Thurne (Winter et al. 2021a, b, c)

6.3.3 Stable isotope analysis

For the fish at site 1, scales were the tissue used for SIA, with scale decalcification not performed prior to their analysis. This was because although comparisons of acidified versus non-acidified scales have revealed some differences in their isotopic data, the actual changes tend to be minor and not considered biologically relevant. For example, Ventura and Jeppesen (2010) demonstrated that the method resulted in mean changes in $\delta^{13}C$ (± SD) of 0.18 ± 0.12 and in $\delta^{15}N$ of -0.21 ± 0.24. The preparation of the scales thus comprised of cleaning with distilled water and then the removal of the outer portion of the scale for analysis. The latter process was completed to ensure the analysed tissue represented only the most recent growth of the fish (generally, the last full year of growth; Hutchinson and Trueman 2006, Bašić and Britton 2015). For the fish analysed, only one scale was used per individual, as this provided enough material for analysis. For fish at site 2, the fin biopsies were used for SIA. For the analyses of macro-invertebrates at both sites, three replicate samples were used per family, where a sample comprised of between one and three individuals (dependent on their body sizes). Zebra mussels were used individually, with preparation involving removal of their shell and a sample of soft tissue taken for SIA. All samples were dried to constant mass at 60 °C prior to their analysis at the Cornell Isotope Laboratory, New York, U.S.A. Stable isotope analytical details were as per Busst and Britton (2017), with lipid correction not necessary as C:N ratios indicated very low lipid content (< 4.0; Post et al. 2007).

6.3.4 Data analyses and mixing models

Differences in the stable isotope data between the omnivorous fish species per site were initially tested in ANCOVA, with fish fork length included as a covariate, with differences in length within the piscivorous fish then were tested in one-way ANOVA per site ($\alpha = 0.05$ in all cases). For visual representation of the stable isotope data per site, the isotopic niches of each fish species, expressed as standard ellipse areas (SEA_C), were calculated in the R package '*SIBER*' (Jackson et al. 2011), where the ellipses enclose 40 % of the stable isotope data and so represent the core niche of the species (Jackson et al. 2012).

The stable isotope data for both sites were then applied to Bayesian mixing models which allowed for diet predictions based on posterior probability distributions of the contribution of relative proportions of the putative prey resources per fish species. For both sites, two models were run in the package '*MixSIAR*' (Stock et al. 2018) to predict the dietary contributions of the putative prey resources: (1) omnivorous fishes; and (2) piscivorous fishes. Separate models were run as these species required the use of different putative prey resources, with Carassou et al. (2008) suggesting that mixing models for piscivorous fish should use specific fractionation factors in models rather than use those used for dietary predictions of fishes that tend to feed primarily on invertebrates (Table 6.2). For the omnivores, bream and perch were the consumer species used in the models for site 1, and bream, perch and roach for site 2. For the piscivorous fishes, pikeperch were the consumer species used for site 1 and pike for site 2. Each model was then run at two levels: (1) at the population/community level ('population' hereafter; providing mean predicted dietary contributions per species); and (2) at the individual level (predicted diet composition per individual fish). All models were run using normal run length (chain length: 100,000 iterations with burn-in of 50,000, with posterior thinning (thin: 50) and 3 chains). Model diagnostics were based on Gelman-Rubin and Geweke (Stock and Semmens 2016) to track algorithm convergence.

6.3.5 Mixing model prey resources and fractionation factors

For site 1, the putative prey resources used in the mixing models for the omnivorous fish species were macrophytes ('plants'), macroinvertebrates ('invertebrates') and zebra mussel. For the 'invertebrates' prey resource, the stable isotope data of Gammaridae and Chironomidae were tested for the significance of their differences using t-tests. Differences in $\delta^{13}C$ were not significant (t-test: $t_{12.8} = -1.58$, $p = 0.14$), but were significant for $\delta^{15}N$ ($t_{12.4} = 2.41$, $p = 0.03$) (Figure 6.1a). However, the mean difference in $\delta^{15}N$ between the groups of 0.73 ‰ was not considered biologically significant (Figure 6.1a). Correspondingly, for their use as putative prey resources in the mixing model, their data were combined into a single resource. In these models, the isotopic fractionation values between the prey resources and consumers used were initially based on values generated from laboratory feeding trials of Busst and

Britton (2017) (Table 6.2). However, it was decided these fractionation factors should use higher standard deviation values around the mean values in order to account for uncertainties relating to the different consumer species, and scales being used as the analysed tissue rather than fin tissue (Table 6.2). Moreover, different fractionation factors were used for the different prey resources, where the factors used were highest for plants and reduced for invertebrates and then zebra mussels/fish (Table 6.2). This was to account for patterns in the fractionation factors detected between prey resources of that differ in their protein content, where prey items of lower protein content tend to have higher fractionation factors (Busst and Britton 2017; Table 6.2). For site 2, the putative prey resources differed to site 1, comprising Gammaridae, killer shrimp and zebra mussel, where the stable isotope values per resources were sufficiently different to enable them to be entered separately into models (Table 6.2). While the basis of the fractionation factors used at Site 2 was as per Site 1, the values used were different to Site 1 as fin tissue was now the analysed tissue, which tends to have more depleted δ^{13}C and enriched δ^{15}N values than scales (Busst and Britton 2015). For the piscivorous fish models, the same fractionation factors were used as per the omnivore models (Table 6.2). In site 1, the putative prey resources for pikeperch were freshwater prey fishes (common bream, perch and roach of lengths ≤170 mm), 'invertebrates' and zebra mussel. In site 2, the putative prey resources for pike were also freshwater prey fishes (common bream, perch and roach with length ≤170 mm), and then Gammaridae, killer shrimp and zebra mussel.

All statistical analysis and graphical outputs were performed using 'R 4.0.5' (R Core Team 2021).

Table 6.2. Diet fractionation factors (± SD) between the consumers and the putative prey resources used in the stable isotope mixing models for Site 1 (consumer tissue analysed: scale) and Site 2 (consumer tissue analysed: fin)

Site 1

Putative prey resources	**$\delta^{15}N$ (‰)**	**$\delta^{13}C$ (‰)**
Zebra mussels, fish	2.05 ± 0.50	3.95 ± 0.50
Invertebrates (Gammaridae/Chironomidae/killer shrimps)	2.55 ± 0.50	5.70 ± 0.50
Plants	3.55 ± 0.50	5.95 ± 0.50

Site 2

Putative prey resources	**$\delta^{15}N$ (‰)**	**$\delta^{13}C$ (‰)**
Zebra mussels, fish	3.00 ± 0.50	3.00 ± 0.50
Invertebrates (Gammaridae/Chironomidae/killer shrimps)	3.50 ± 0.50	4.80 ± 0.50

6.4 Results

6.4.1 Stable isotope data

For the analysed omnivorous fish species in site 1, perch were between 121 and 217 mm (mean ± SD): 172 ± 28 mm), whereas common bream were 127 to 476 mm (mean 297 ± 126 mm). Differences in their stable isotope data were not significant between species ($\delta^{13}C$: $F_{1,22} = 1.56$, $p = 0.22$; $\delta^{15}N$: $F_{1,22} = 0.46$, $p = 0.50$; Figure 6.1a), where the effect of fish length as a covariate was also not significant ($\delta^{13}C$: $p = 0.33$; $\delta^{15}N$: $p = 0.87$). For the piscivorous pikeperch in site 1, their lengths were 345 to 780 mm (mean 573 ± 107 mm), which had a significant effect on $\delta^{13}C$ ($F_{1,12} = 16.87$, $p < 0.01$) but not $\delta^{15}N$ ($F_{1,12} = 0.08$, $p = 0.77$).

For site 2, common bream lengths were 286 to 491 mm (mean: 414 ± 50 mm), perch were 121 to 224 mm (mean: 151 ± 32) and roach were 98 to 217 mm (143 ± 35). Differences between the species in their stable isotope data were not significant between species ($\delta^{13}C$: $F_{1, 44} = 2.22$, $p = 0.12$; $\delta^{15}N$: $F_{1, 44} = 2.23$, $p = 0.12$) (Figure 6.1b), with the effect of fish length as a covariate also not significant ($\delta^{13}C$: $p = 0.62$; $\delta^{15}N$: $p = 0.44$). For the piscivorous pike, their lengths were 471 to 1014 mm (mean: 754 ± 147 mm), and length had a significant effect on $\delta^{13}C$ ($F_{1,13} = 5.39$, $p = 0.04$), but not $\delta^{15}N$ ($F_{1,13} = 2.71$, $p = 0.12$).

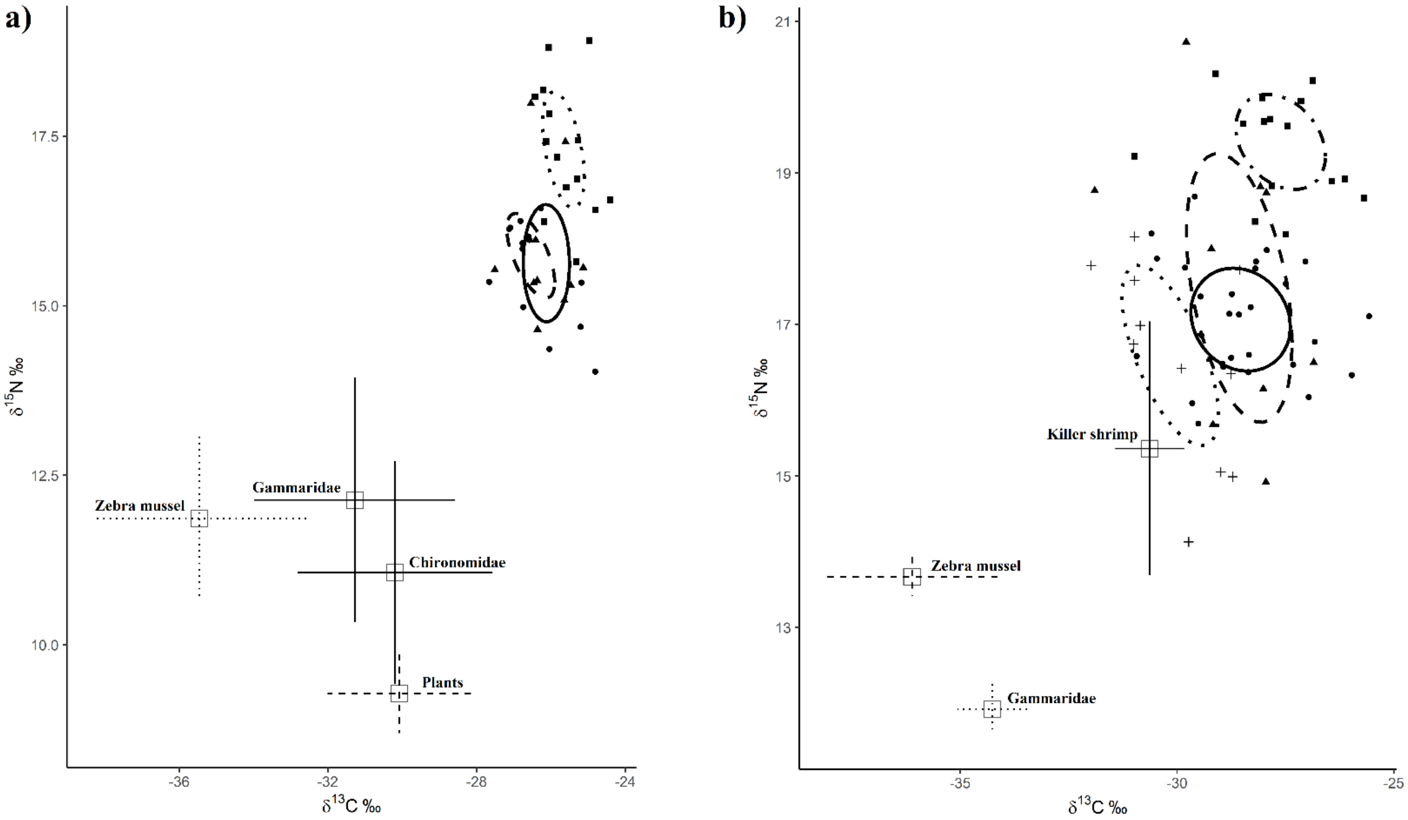


Figure 6.1. The stable isotope data and isotopic niches (as standard ellipse areas; SEAc) for the consumer species used in the stable isotope mixing models, where (a) Site 1 (circle point, dashed ellipse: bream; triangle point, continuous ellipse: perch; square point, dotted ellipse: pikeperch); and (b) Site 2 (circle point, continuous ellipse: bream; triangle point, dashed ellipse: perch; cross point, dotted ellipse: roach; square point, dashed-dotted ellipse: pike). Mean values are displayed for the putative prey resources (± SD)

6.4.2 Stable isotope mixing models - omnivorous fishes

In site 1, the mixing models for bream and perch at both population- and individual-levels predicted that the ‘invertebrates’ prey resource had the highest contribution to the diets of both fish species, whereas zebra mussels were predicted to have a low dietary contribution irrespective of fish size (< 16 %; Table 6.3, Figure 6.2). In site 2, population models predicted killer shrimp was the prey resource with the highest contribution to the diets of bream and perch, followed by Gammaridae, and with zebra mussels again predicted to have a low dietary contribution. The individual models provided similar predictions, with Gammaridae predicted as the main prey resource for these two fish species, followed by killer shrimp (Table 6.4). Predictions for roach at the population level suggested a greater contribution of zebra mussels to diet than the other fish species (44 %), but with the individual models suggesting Gammaridae was their main dietary source (Table 6.4). For roach, predictions suggested zebra mussels had relatively high dietary contributions for all fish sizes (Figure 6.3).

Table 6.3. Mean predicted dietary contributions, and their standard deviation and 5 and 95 % credible intervals, from Bayesian mixing models (population and individual level models) of the prey resources of invertebrates (Gammaridae and Chironomidae), macrophytes ('plants') and zebra mussels to the diet of common bream and perch at Site 1

Population level

Species	**Source**	**Mean**	**SD**	**5 %**	**95 %**
Bream	Invertebrates	0.69	0.30	0.06	0.96
	Plants	0.19	0.26	0.00	0.77
	Zebra mussels	0.12	0.08	0.01	0.28
Perch	Invertebrates	0.73	0.34	0.03	0.99
	Plants	0.19	0.31	0.00	0.89
	Zebra mussels	0.08	0.08	0.00	0.24

Individual level

Species	**Source**	**Mean**	**SD**	**5 %**	**95 %**
Bream	Invertebrates	0.54	0.02	0.07	0.96
	Plants	0.31	0.01	0.00	0.81
	Zebra mussels	0.15	0.03	0.01	0.41
Perch	Invertebrates	0.54	0.02	0.06	0.96
	Plants	0.32	0.04	0.00	0.83
	Zebra mussels	0.14	0.03	0.01	0.39

Table 6.4. Mean predicted dietary contributions, and their standard deviation and 5 and 95 % credible intervals, from Bayesian mixing models (population and individual level models) of the prey resources of Gammaridae, killer shrimps and zebra mussels to the diet of common bream ('bream'), perch and roach at Site 2

Population level					
Species	**Source**	**Mean**	**SD**	**5 %**	**95 %**
Bream	Gammaridae	0.28	0.17	0.05	0.59
	Killer shrimp	0.43	0.09	0.26	0.55
	Zebra mussels	0.29	0.12	0.09	0.47
Perch	Gammaridae	0.34	0.22	0.03	0.71
	Killer shrimp	0.44	0.12	0.21	0.61
	Zebra mussels	0.22	0.14	0.03	0.46
Roach	Gammaridae	0.35	0.24	0.03	0.79
	Killer shrimp	0.20	0.09	0.05	0.35
	Zebra mussels	0.44	0.18	0.09	0.70

Individual level					
Species	**Source**	**Mean**	**SD**	**5 %**	**95 %**
Bream	Gammaridae	0.45	0.09	0.07	0.88
	Killer shrimp	0.37	0.11	0.05	0.70
	Zebra mussels	0.19	0.05	0.01	0.57
Perch	Gammaridae	0.43	0.11	0.05	0.88
	Killer shrimp	0.39	0.11	0.04	0.76

	Zebra mussels	0.18	0.06	0.01	0.62
Roach	Gammaridae	0.51	0.12	0.08	0.91
	Killer shrimp	0.25	0.08	0.03	0.58
	Zebra mussels	0.24	0.07	0.01	0.71

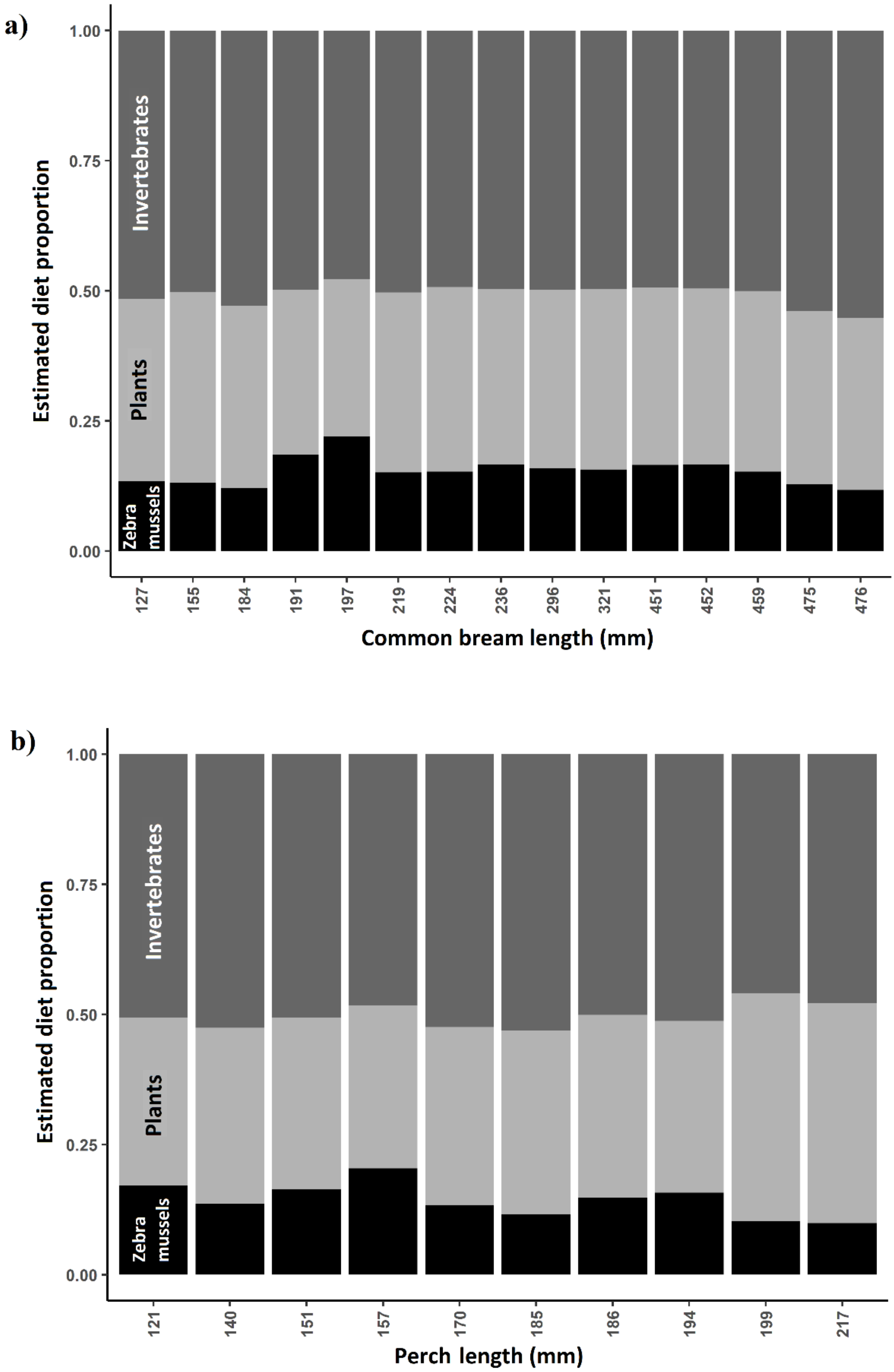


Figure 6.2. Estimated dietary prey contributions (0–1) to the diet of individual fish by body length for site 1: (a) common bream and (b) perch. Prey sources as overall means: invertebrates (dark grey), plants (light grey) and zebra mussels (black)

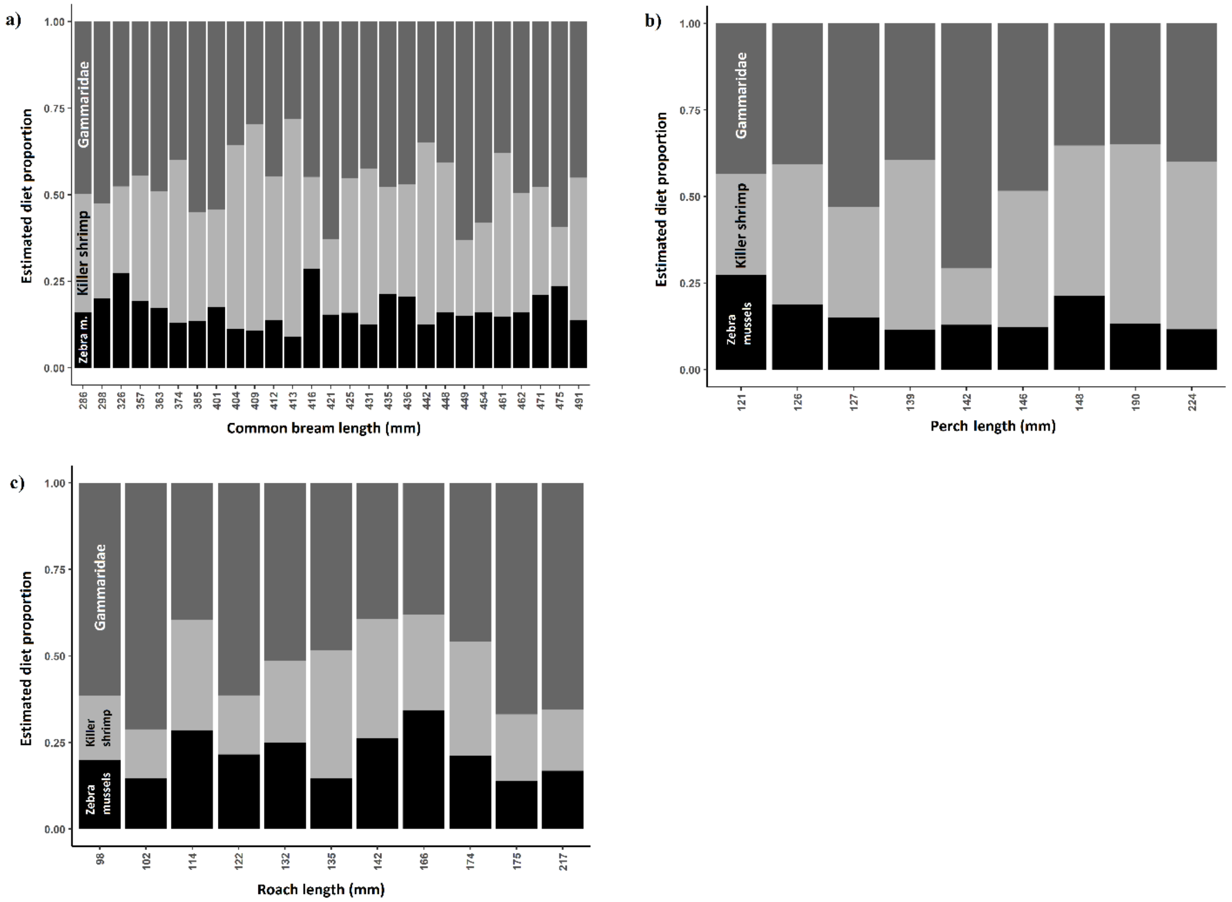


Figure 6.3. Estimated dietary prey contributions (0 - 1) to the diet of individual fish by body length for site 2: (a) bream, (b) perch and (c) roach. Prey sources as overall means: Gammaridae (dark grey), killer shrimps (light grey) and zebra mussels (black)

6.4.3 Stable isotope mixing models - piscivorous fishes

For pikeperch in site 1, the mixing models predicted that prey fish resources had the highest dietary contributions at both the population-level and individual-level (Table 6.5), with this evident for all fish lengths present (Figure 6.4a). Predictions for zebra mussel were 24 % at the population level and 17 % at the individual level (Table 6.5; Figure 6.4a). For site 2, the predictions for pike also indicated that prey fish resources also contributed highly to their diet, irrespective of fish size, followed by killer shrimp (Table 6.5; Figure 6.4b). Both zebra mussels and Gammaridae were predicted to contribute less than 18 % of dietary resources (Table 6.5; Figure 6.4b).

Table 6.5. Mean predicted dietary contributions from Bayesian mixing models of fish, invertebrates, and zebra mussels to the diet of piscivorous fishes (pikeperch and pike) at population and individual levels, showing their standard deviation and 5 and 95 % credible intervals

Population level					
Species	**Source**	**Mean**	**SD**	**5 %**	**95 %**
Pikeperch	Fish	0.68	0.07	0.565	0.784
	Invertebrates	0.07	0.07	0.004	0.214
	Zebra mussels	0.24	0.06	0.138	0.335
Pike	Fish	0.53	0.21	0.09	0.79
	Gammaridae	0.14	0.09	0.02	0.29
	Killer shrimps	0.25	0.20	0.02	0.65
	Zebra mussels	0.08	0.06	0.01	0.20

Individual level					
Species	**Source**	**Mean**	**SD**	**5 %**	**95 %**
Pikeperch	Fish	0.73	0.06	0.47	0.95
	Invertebrates	0.09	0.02	0.00	0.34
	Zebra mussels	0.17	0.04	0.02	0.39
Pike	Fish	0.36	0.03	0.04	0.78
	Gammaridae	0.18	0.07	0.02	0.42
	Killer shrimps	0.42	0.08	0.07	0.80
	Zebra mussels	0.05	0.01	0.00	0.18

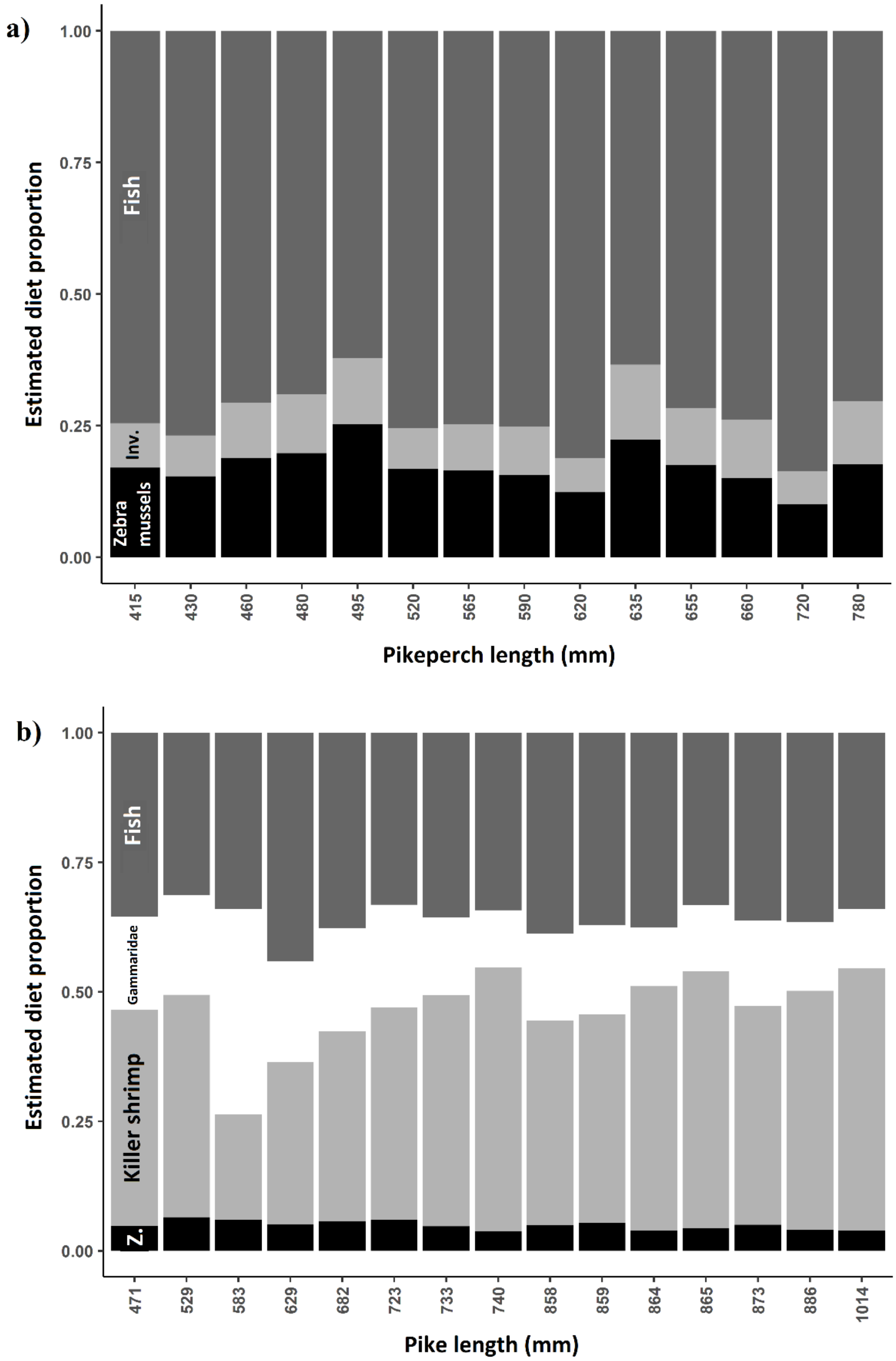


Figure 6.4. Estimated dietary prey contributions to the diet of individual piscivorous fishes by body length (0–1): (a) pikeperch with fish (dark grey), invertebrates (light grey) and zebra mussels (black), and (b) pike with fish (dark grey), Gammaridae (white), killer shrimps (light grey) and zebra mussels (black). Prey source shown as overall mean per individual

6.5 Discussion

The increased distribution of zebra mussels in British freshwaters (Aldridge et al. 2004) has presented a novel prey resource for the native fish communities. Across the five fish species analysed here, only roach, a fish ubiquitous to British lowland freshwaters (Britton 2007), had predictions that zebra mussels were contributing strongly to their diet. The population level model of 44 % is consistent with Prejs et al. (1990), who suggested a predator-prey interaction between the two species, and Millane et al. (2012) who detected roach consumed them in Lough Sheelin, Ireland, in all seasons. For the other fish species, zebra mussels were never predicted to comprise of more than 29 % of their diets at the population level.

Common bream of over 400 mm were present in samples taken from both sites, with their diets predicted to primarily consist of ‘invertebrate’ prey resources (covering Gammaridae, Chironomidae and killer shrimp, depending on the site). These results are consistent with other dietary studies on common bream that have highlighted the importance of macroinvertebrates as prey resources for the species, with Chironomidae often being a dominant prey source (e.g. Giles et al. 1990, Kakareko 2001). Although not sampled here, zooplankton can also be important in their diet, although usually only in fish of below 200 mm and in situations where there is a lack of macro-invertebrates available (Kakareko 2001). Zebra mussels were predicted to be only a minor component of their diet in both sites here, with this potentially related to their extensive branchial sieve which could make difficult to for them to ingest molluscs and limitations on their ability to crush the mussels imposed by the architecture of their pharyngeal teeth (Nagelkerke and Sibbing 2011). Similarly, the analysed perch primarily consumed the ‘invertebrates’ prey resource at the population level, with this also consistent with other studies suggesting the importance of similar prey resources in their diet (Giles et al. 1990, Dörner et al. 2003). While there were no studies suggesting perch regularly prey upon zebra mussel, Mavrin and Strel’nikova (2011) suggested that when the species are in sympatry, with zebra mussels feeding extensively on zooplankton, juvenile perch might have to switch to macro-invertebrate prey from their early stages. This was also noted by Shcherbina and Bezmaternykh (2019), who also suggested that zebra mussel colonies also provide refuge for macroinvertebrates, increasing the difficulty of prey detection for perch during foraging. Roach were suggested in the literature as an important consumer of zebra mussels (Prejs et al. 1990, Millane et al. 2012) and, while they were only analysed here in one site, the diet predictions here suggested all of the analysed fish had consumed some zebra mussels in recent months. However, this included individuals of below 160 mm length, whereas empirical studies have suggested a clear size threshold where these fish would not generally prey upon them (Prejs et al. 1990). Nagelkerke and Sibbing (2011) suggested that, functionally, roach are ‘superior’ in static crushing hard and brittle materials (like the shells of zebra mussels), compared to species such as common bream, emphasising those functional attributes such as gape size, strong pharyngeal teeth and the ability of chew prey items could be important for efficient feeding on these bivalves (French 1993).

For piscivorous fish species, only fish above 170 mm were analysed, a size when the species tends to be an obligate piscivore (e.g. Nolan and Britton 2018a). Pikeperch primarily fed upon freshwater fish (70 % at both population and individual levels), with a low contribution of the ‘invertebrates’ resource (< 10 % both levels). Pike also had freshwater fish as their most important dietary resource, but with the alien killer shrimp also important in their diet. Recent studies on pike diet based on stable isotope data have indicated that macro-invertebrates can comprise a key component of their diet, irrespective of their body length, indicating some functional plasticity (Chapman and Mackay 1990, Pedreschi et al. 2015, Nolan et al. 2019). Moreover, invasive killer shrimp have been detected as displacing native amphipod species in invaded waters, with fish species (including perch) responding by replacing native amphipods in their diet with the invasive ones (Eckmann et al. 2008). In Site 2, invasive killer shrimp were in sympatry with native amphipods and with both making substantial contributions to fish diet generally. Correspondingly, the influence of this Ponto-Caspian amphipod on the diet of freshwater fish in Britain might prove to be higher than zebra mussel.

These results suggest that roach was the only analysed fish species that used zebra mussels within their diet in more than a minor way, suggesting that the extent of consumptive resistance on zebra mussel colonisation and spread was likely to be limited in the analysed sites. While roach are ubiquitous in most regions of lowland Britain, populations tend to be dominated by fish below 200 mm (Britton 2007), which are unlikely to be capable of consuming large quantities of bivalves. Similarly, while French and Bur (1992) revealed that although freshwater drum *Aplodinotus grunniens* predated heavily on these molluscs, they suggested this predation pressure would have little effect on the invasion of zebra mussels due to their rapid reproduction and growth. This suggests that where there is a management requirement to prevent the establishment of zebra mussel populations, or reduce their abundance, then reliance on biological resistance and/ or biological control methods is not recommended. Thus, the application of chemical control methods would be required instead, but while these can substantially reduce their populations, these methods tend to also cause a high degree of collateral damage in non-target species (Aldridge et al. 2004, Lydeard et al. 2004). Awareness on the use of biosecurity (i.e. cleaning and drying techniques) to prevent introductions, rather than manage new and on-going invasions, tends to be used more, but clearly does not reduce their impacts in already invaded waters (Melly and Hanrahan 2020, Smith et al. 2020).

6.6 Conclusions

The results from two invaded sites in England, one in the east and one in the west, suggest that in lowland areas at least, the consumptive resistance to the invasion of zebra mussel in Britain appears to have been limited. While it is acknowledged that the spatial and temporal extent of our sampling was limited, the results were largely consistent with studies elsewhere in the invaded range of zebra mussels, suggesting that while more in-depth studies might be interesting, they are unlikely to provide any novel insights. However, our analyses were based only on stable isotope analysis, with other methods of dietary analyses not being used, such as stomach contents analyses, which can provide both consistent (e.g. Nolan and Britton 2018a) and contrary results (e.g. Locke et al. 2013, Hamidan et al. 2016). Nevertheless, these results do suggest that if the invasion of Britain by zebra mussels is going to be contained, a more active management approach must be taken to prevent spread of existing populations and the establishment of new one.

7 General discussion

Introductions of alien species continue to accelerate worldwide, resulting in some invasions that impact ecosystems or that are predicted to do so in upcoming years (Guareschi et al. 2021). Human activity, especially that supporting economic growth, continues to expand, which is likely to further alter the environment and facilitate more introductions and invasions (Dickey et al. 2021). Invasions in freshwater systems can have high context-dependency, where the combination of biotic traits (species-specific demographic and/or dispersal characteristics), environmental factors (landscape and/or dispersal pathways characteristics), the receiving native community (competitive interactions) and human activities (propagule pressure) can alter the outcome of introductions (Catford et al. 2009, Enders et al. 2020, Campbell and Mandrak 2021). Therefore, understanding those factors that contribute to a successful invasion (i.e. introduction, establishment and spread) could enhance predictions of the temporal spread of a newly introduced species, assess any associated impacts (e.g. on the ecosystem, human health or economy) and enable the application of optimal management programmes (Hulme 2006, Genovesi et al. 2013, Liu et al. 2017).

The aim of this thesis was to combine modelling and empirical approaches to generate new insights into the different factors that facilitate the development of invasions by alien species in freshwater systems. From the modelling perspective, I built an initial individual-based model (IBM) for the invasive fish bitterling, with the lack of biological and ecological knowledge on that species meaning it was combined with approximate Bayesian computation (ABC) to inversely extract the model parameters from population monitoring data in the River Great Ouse, England (Chapter 2). This model was then used to explore the outcomes of different management scenarios, with further expansion to investigate the outcomes for species with different demographic and dispersal traits using a range of theoretical systems (Chapter 3). The same model species were used to examine the role of landscape-related factors on theoretical and real-world systems, the latter being a series of rivers in England and Wales (Chapter 4). Regarding the empirical approaches, I investigated the competitive interactions of two trophically analogous species (invasive vs. native) using stable isotope analysis and comparing in-aquaria experiment data with wild populations in England (Chapter 5). Finally, I predicted the diet of different freshwater fishes across two sites in England using stable isotope data to identify whether there was any role of biological resistance in the invasion of England by zebra mussel (Chapter 6).

7.1 Predicting the invasion success of alien species

When a species is introduced into a new environment, in order for it to develop an invasive population, it must complete the invasion pathway. This pathway comprises of three main stages: introduction (whether accidental or deliberate), establishment (species traits must adapt to the new conditions with subsequent survival of potential threats, and the formation of a sustainable population) and spread (further dispersal subject to landscape and potential barriers) (Blackburn et al. 2011). The invasion outcomes can differ between systems for the same species (Uden et al. 2015), which can add some complexities when transferring an existing risk assessment to a new susceptible area. For example, Copp et al (2007) indicated that the topmouth gudgeon *Pseudorasbora parva,* that successfully invaded many inland waters across Europe, failed to do so in a particular pond in England, with no clear indicators on why this may have happened. The alien guppy *Poecilia reticulata* failed to invade waters in Florida due to the presence of the eastern mosquitofish *Gambusia holbrooki* (Tuckett et al. 2021). Thus, even species which are known to be highly invasive can be introduced but fail to establish and disperse in some contexts, leading to some spatial heterogeneity in introduction outcomes (Kulhanek et al. 2011). This highlights the importance of continuing to investigate and improve knowledge of the different factors that may play a role in determining the outcome for invasion of a specific introduction.

Predictive approaches can be used to increase understanding of the factors that influence invasion outcomes and enable more informed decision making on management strategies at different stages of an invasion (Kolar 2004) and warn if there are susceptible areas where further conservation approaches should be considered (Fletcher et al. 2016). Early action has been proven the most effective way of dealing with freshwater introductions (N’Guyen et al. 2016), but modelling an ongoing invasion can also help to predict future dispersal of the alien species and advise on containment measures to stop further spread along the system (Samson et al. 2017, Day et al. 2018, Perrin et al. 2021). Such models require a large number of parameters to represent the process(es) that it is predicting, which can be a difficult, non-friendly approach (Thompson et al. 2021). However, the work outlined in this thesis demonstrates that modelling invasive species dispersal and management in freshwater systems is possible and, with the right tools, relatively easy to implement (Chapter 2-4).

The IBMs presented in here have, however, had to overlook some crucial factors that influence invasion outcomes due to the need to keep models relatively simple. For example, the biological resistance of native communities to the invader, such as from predation and/or interspecific-competition, and the influence of the changing environmental conditions (e.g. climate change) are important influences on invasion oucomes (both now and in future) and so are important to understand (Gallien et al. 2010). However, the challenges of introducing many different components into a model are related to their inherent difficulty when it comes to understanding due to, for example, the complexity of their interactions (Thompson et al. 2021). A combination of different models may help to reach stronger conclusions about the process. For example, a future model ensemble, in which there is accounting for different predictions for the same (or ecologically similar) model species and systems when different parameters are used, will potentially increase understanding of how these interacting issues affect species in different contexts. In addition, an integrated global-scale database that includes: (i) survey data, population growth and dispersal information of invasive species; and (ii) environmental characteristics and associated ecosystem and socio-economic impacts of already invaded areas could inform future predictive approaches and species-specific scenarios, which could strongly benefit model development and predictions, and subsequent management (Bobeldyk et al. 2015, Poland et al. 2021).

7.1.1 Population and dispersal dynamics

Obtaining biological and ecological data on the focal alien species is the first step in attempting to develop a successful modelling approach with, for example, the species' demographic and dispersal traits playing a key role in its population increase and dispersal velocity (Moyle and Marchetti 2006, Liu et al. 2017). The scientific literature can be prolific for a species that is of common interest, especially if it has also been used in aquaculture and/or has a long invasion history. For example, the common carp is a highly invasive fish across the world that can provide high economic benefits and food security but that also degrades freshwater systems through its ecological engineering activities (Vilizzi et al. 2015). Therefore, there is a strong knowledge base on the species in different regions (e.g., Australia (Koehn 2004), Americas (Zambrano and Hinojosa 1999), Africa (Winker et al. 2011), China (Xu et al. 2012) and Europe (Vilizzi 2012)). The zebra mussel has become a major problem for some industries (e.g., water treatment works, irrigation systems and power stations) due to colonies forming around important structures, which led to substantial investments in eradication and control, and high research effort around monitoring and controlling of the species (e.g., Americas (Lewis et al. 1997), Great Britain (Aldridge et al. 2004) and Europe (van der Velde et al. 2010)), so resulting in a large literature base.

Parameterising a model can be relatively straight forward when these volumes of scientific knowledge are available, but even then, there are specific parameters that remain difficult to obtain. For example, the carrying capacity of the system can be highly uncertain unless there is access to strong population monitoring data (Cramer and Ackerman 2009, Stigebrandt 2011). In freshwater systems, this type of data is rare for most species. The general lack of data when monitoring invasive species could lead to underestimation of parameters or confusion in determining the specific invasion stage for a particular species at a time (Perrin et al. 2021). The opposite scenario can be found where monitoring data are available for a particular system/species, but there is insufficient knowledge for building the model. In this thesis, I have demonstrated it is possible to work backwards using monitoring data to estimate the model parameters by using approximate Bayesian computation (‘ABC’; Chapter 2). However, this type of modelling can be time consuming due to the high number of iterations that need to be performed to achieve robust model estimates (e.g. Turner and Van Zandt 2012). Notwithstanding, it does enable many model combinations to be obtained that can explain data patterns very well (Csilléry et al. 2010). Therefore, I suggested to use the best set of parameter combinations that match the monitoring data to improve the accuracy of predictions and their credibility intervals. Weighting parameters can also help to add credibility to the data and would help the algorithm to better estimate the candidate models (Csilléry et al. 2010).

Overall, this approach is only feasible if the monitoring data have a good coverage (i.e. high spatial and temporal coverage) that, in general, is hard to obtain for many freshwater invasive species (Leprieur et al. 2009). However, there are exceptions, such as where alien species were introduced with no intention of removals, such as salmonid fishes (Townsend 2003) where recruitment data for their populations remains very important for local fishery management (Barry et al. 2020). Providing a complete time-series dataset (as per Chapter 2) can reduce the amount of error associated with this Bayesian technique, but it must always be interpreted carefully, with statistical testing of the goodness-of-fit between the simulated and the observed data (Csilléry et al. 2010).

7.1.2 Management scenarios

One of the most important aspects of biological invasions is the management of the invader, which can determine its rate of spread - or indeed whether it manages to spread at all (Britton et al. 2011b). Species with contrasting traits arguably require different control methods (Buhle et al. 2005) and, in some cases, the removal techniques may even increase the reproductive success of the population via compensatory responses (Evangelista et al. 2015) and result in negative consequences for ecosystem functioning (Závorka et al. 2020). Here, I have investigated the effect of those demographic and dispersal traits in the outcomes of different management scenarios (Chapter 3). The set of species used did not correspond to any specific invasive species due to the potential for an extended literature review process in conjunction with the likelihood that for many species, the data required would be lacking anyway (Perrin et al. 2021). The exception here was the already-built model for bitterling from Chapter 2, which was first used as part of the set of virtual species (using a unique best fitting values parameter combination) and, afterwards, to create the real-world case study (using all 250 best parameter combinations as developed in Chapter 2). The development of each of the virtual species was performed using a virtual species based on bitterling as the starting point to create an additional eight invasive species that each had distinct demographic and dispersal traits. The extent of these trait differences between the species was considerable (> 25 %) and so the objective of using nine species with distinct suites of traits was realised. Using virtual species allowed for full control of the data used (Hirzel et al. 2001) and enabled successful evaluation of how different species traits would lead into different management outcomes (Chapter 3).

Management programmes of invasive species can be expensive and often involve multiple exercises that, in entirety, might achieve eradication but that in isolation would be futile, and would also fail if applied to a species that has already achieved a wide distribution (Simberloff et al. 2013), but could still slow its dispersal throughout the system (Vander Zanden and Olden 2008). Here, trade-offs between management resource availability and control methods were applied to reproduce budget-restricted situations (Chapter 3). However, it is acknowledged that the scenarios created were kept relatively simple, such as by deliberately keeping the annual management resource (i.e. the removal effort) constant over time, as this typically represents many management programmes undertaken by government agencies and so decisions are needed on how this resource is spent. For example, the management of the non-native signal crayfish *Pacifastacus leniusculus* in Great Britain followed legislation from the government policies and was not changed during the first 15 years of implementation (Stebbing et al. 2012). Here, by holding resources constant, I was able to highlight the optimal use of these limited management resources. There might be occasions when more resource is available in some years than others, in which case this could be adopted into a future modelling process. In addition, global datasets on up-to-date economic costs per invasive species are now available, which could help policy-makers understand the possible impacts associated with allowing further dispersal of the invader and how other regions have managed similar situations (Diagne et al. 2020). The combination of risk assessments, knowledge of global policy approaches and predictive tools that enable management resources to be accounted for, could thus help to manage invasive species more comprehensively.

7.1.3 Abiotic factors

The context-dependency of biological invasions means that the landscape that the species is invading becomes another critical component of the modelling process (Ross et al. 2001). While introduced species can adapt quickly to the new environmental conditions, this will depend on the characteristics of the environment itself (Moyle and Marchetti 2006, Astorg et al. 2021). In freshwater systems, rivers differ substantially from each other due to, for example, their underlying geology, altitude, climate, land-use and anthropogenic alteration. Correspondingly, there are differences in the species assemblage (Robbins and Pyron 2021). When the alien species is introduced, it thus experiences a range of native species and different abiotic characteristics that could result in low probability of establishment and invasion (Ross et al. 2001).

Here, I identified some characteristics that impact biological invasions in river catchments (Chapter 4). A theoretical approach was developed where I specifically explored those physical factors in randomised virtual landscapes, and afterwards tested them in real world rivers. However, it is acknowledged that the abiotic factors were created by seeking simplicity within the interpretation of the individual-based model outputs (Pais and Cabral 2017). For example, habitat quality represents a wide range of characteristics (e.g. native community diversity, catchment conditions, flow regime) that is highly complex to represent in a modelling context. Therefore, habitat quality was represented here in relation to channel width and distance from the river source. Therefore, this parameter might have been over-simplified and future work should look for ways of adding greater complexity or expanding the number of variables to investigate for completeness (Ruesink 2005). Accounting for this, the work presented here indicated that the theoretical approach used in the virtual generated landscapes mimicked the real-world rivers, with similar conclusions drawn, which highlights the usefulness of this approach to help overcome scientific uncertainty.

7.2 Predicting the ecological interactions between native and invasive species

The empirical approaches performed as part of this thesis aimed to complement the predictive modelling work by providing some insights into case-specific invasive species, while also using alternative approaches for investigating the ecological outcomes of introductions of invasive species. These helped to focus on those aspects that were might have been omitted in the modelling processes discussed above due to their complex role in the invasion process that prevented their incorporation into the model architecture. Thus, future studies should aim to better integrate both approaches given they strongly complement each other, such as through developing theoretical and empirical frameworks in which the theoretical work improves the process understanding on invasions, while empirical work tests that understanding in real-world scenarios.

7.2.1 Trophic niche

The introduction of an invader into a novel environment can produce a response from the native community, which can result in competitive interactions and/or shifts in the overall structure of the aquatic food web (Eagles-Smith et al. 2008, Britton et al. 2010d). The ecological interactions between invasive and native species have been investigated to allow for a better understanding of their relationships, with competition considered as a process that is key to predicting how a new species integrates into the native community (Tran et al. 2015, Britton 2018). These trophic interactions can result in overlapping of trophic niches if the species use similar resources (Busst and Britton 2017). Species might restrict their diet breadth and thus trophic niche in competitive circumstances (i.e. shift to a more specialist diet), but the converse can also occur, where larger niches result that are also divergent from other species (Jackson and Britton 2014).

In this thesis, I revealed an example of niche diversification, where two trophically analogous cyprinid species that co-exist in the wild revealed increased trophic niche sizes in sympatry that were diverged in both experimental and wild contexts (Chapter 5). The use of both aquaria and field trials enabled both processes and patterns to be better understood and, for the particular topic of biological invasions, improved knowledge on an already recognised highly invasive species.

7.2.2 Biotic resistance

Not every introduced species that is released into a novel environment goes on to successfully establish a population. On some occasions, the native community impedes establishment and dispersal, preventing invasions from developing (Britton 2012). However, not every native community will have the resilience and resistance to prevent the invasion, with biotic resistance insufficient to prevent establishment and/or dispersal. For example, the native community might be disturbed through anthropogenic activities, suppressing population abundances and elevating the probability of invasion success (Kremer and da Rocha 2016). This potentially low resistance to an invasion from the native community is important to acknowledge in order to assist management decision making.

In this thesis, I tested the dietary contribution of zebra mussel in different fish species that co-habit with this globally invasive mollusc (Chapter 6). The main technique applied here relied on stable isotope analysis using Bayesian mixing models to provide predictions on the long-term composition of native fish diet. The results indicated that the fish rarely consumed the mussels and thus resistance would have been low. However, it is acknowledged that Bayesian methods are predictive rather than empirical, and complementary approaches, such as stomach content analysis (SCA), could have provided greater insights. However, the application of SCA would have required substantially more fish to be sampled, which was outside of the scope of this work, and this sampling would have had to be lethal given the species used were agastric and thus stomach flushing would have been unsuitable. In addition, only two sites were analysed here, so future research on this invasive species could aim to look at greater spatial replication using sites with similar fish assemblages to the ones used here. However, these limitations do not reduce the findings here that indicated, for the first time in Britain, that the contribution of zebra mussel to native fish diets is low and likely to be insufficient to provide any substantial resistance to their spread.

7.3 Recommendations

The initial goals of this thesis were achieved, with the successful development of models for predicting the establishment and dispersal of alien fish in river networks and how this can be affected by abiotic factors and management programmes. The use of empirical approaches complemented this predictive modelling by identifying how processes that could not be incorporated into the models can also affect alien fish invasions.

The predictive approaches focused on two main processes: population (i.e. reproduction, growth or mortality rates) and dispersal dynamics (i.e. emigration, transfer and settlement). Therefore, there was deliberate omission of other important key processes that could influence the outcome of an invasion, such as how the introduced species interacts with native species in the community. As per Chapter 4, the food webs and trophic niches of the species can shift as a result of trophic interactions with the introduced species, with the extent of these dependent on, for example, the native assemblage, resource availability and invader’s traits (Britton et al. 2010d, Benjamin et al. 2011, Jackson and Britton 2014). As per Chapter 5, introducing the invasive species into areas with species that would compete with them, or predate upon them, opens the possibility of biotic resistance to limit the probability of establishment and subsequent dispersal of the species, and/or reduce their abundance. These key process goes in hand with the characteristics of the invaded landscape, which I simplified in the models to the concept of ‘habitat quality’. This simplification could thus be masking important influences of habitat on invasion outcomes that should be explored using future modelling approaches. For example, river flow is a fundamentally important physical characteristic of river that is subject to seasonal variability (Dettinger and Diaz 2000), and could influence the dispersal of all invader’s stages (i.e. juveniles, sub-adults or adults) (Truscott et al. 2006, Gido et al. 2013). The presence of barriers that are only permeable to fish during certain time-related events (e.g. floods) are also important to consider (Kerby et al. 2005). In addition, climate change will be increasingly important in the context of alien species invasions through its influences on both water temperature through warming and river flows through altered precipitation patterns (Rahel and Olden 2008, Mainka and Howard 2010, Roche et al. 2020). Thus, the development of more complex models that can incorporate more biological, physical and climatic components is an important next step that could expand our current knowledge on invasions and improve associated management actions.

7.4 Concluding remarks

In summary, this thesis has provided a series of important insights into the strengths and weakness of individual-based models when applied to freshwater invasive species. Further, it has been combined with stable isotope analysis, comparative functional responses and Bayesian mixing models to closer investigate specific case studies of highly invasive species within Great Britain. The results have highlighted the importance of improving current knowledge on biological invasions as this increases the probability that management practices can be successful in their interventions. Future avenues of research should be used to improve our predictive power and competencies, which can be based on integrating predictive and empirical approaches more holistically, enabling expansion of current knowledge on the ecological impacts and management of invasive species in freshwater ecosystems.

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9 Appendices

9.1 Appendix 1

Table A1.1. Shape and parameters (Alpha, Beta) of prior distributions fitted to data from the literature and expert opinion, and best-fitted posterior values obtained from the ABC method

Model parameter	**Stage-structure**	**Shape**	**Alpha**	**Beta**	**Best-fitted value**
Population dynamics parameters					
Rate of density dependence (**1/b**)	Whole population	Gamma	3	0.003	1750.96
Fecundity (**ø**)	Adults	Gamma	10	0.2	63.77
Survival rate (**σ**)	Juveniles	Beta	40	5	0.93
	Sub-adults	Beta	5	5	0.89
	Adults	Beta	10	10	0.40
Emigration parameters					
Asymptote (**D**)	Sub-adults	Beta	0.1	9.9	0.18
	Adults	Beta	10	40	0.18
Inflection point (**β**)	Sub-adults	Gamma	15	15	0.48
	Adults	Gamma	15	15	1.23
Transfer parameters					
Step mortality probability (**SMc**)	Whole population	Beta	1.1	20	0.01

Settlement parameters					
Settlement probability (**S**)	Whole population	Beta	50	5	0.84

Table A1.2. Pearson correlation matrix of the posterior parameters of the fitted model. Bold font denotes combinations that are significant ($P < 0.05$), ** denotes ($P < 0.01$). Symbols for the parameters are defined in table 3.1 with sub-headings 0, 1 and 2 corresponding consecutively to the fish stage-structure: juveniles, sub-adults and adults

	1/b	**ø**	**σ_0**	**σ_1**	**σ_2**	**D_1**	**D_2**	**β_1**	**β_2**	**SMc**	**S**
1/b		0.00	0.02	**-0.21****	-0.02	**-0.47****	0.10	-0.03	**0.19**	0.15	0.06
ø			0.09	0.01	-0.06	-0.03	0.10	0.06	0.04	0.03	-0.14
σ_0				0.05	-0.05	0.01	-0.05	-0.05	0.11	0.07	-0.14
σ_1					0.07	**-0.17**	-0.06	0.02	-0.02	0.06	0.07
σ_2						**-0.16**	0.02	0.03	0.02	0.01	0.13
D_1							**-0.19**	0.00	-0.09	**0.24****	-0.11
D_2								0.02	0.12	-0.15	0.09
β_1									-0.10	0.16	-0.12
β_2										0.05	**0.20**

SMc	-0.06

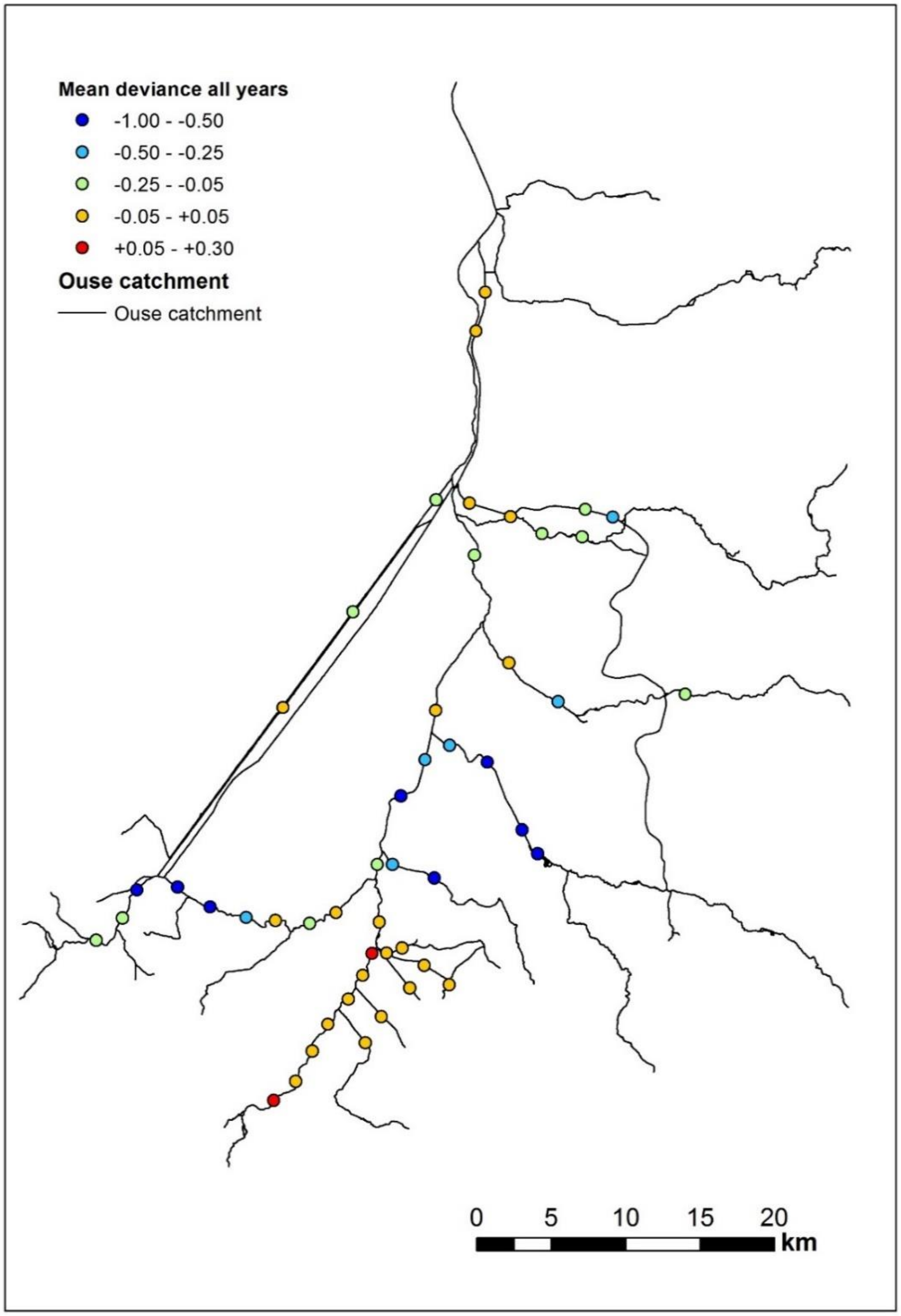


Figure A1.1. Map of temporally averaged model deviance in presence of bitterling across years. Colour scale: over-predicted (red) underpredicted (blue). Crown copyright and database rights 2018 Ordnance Survey (100025252)

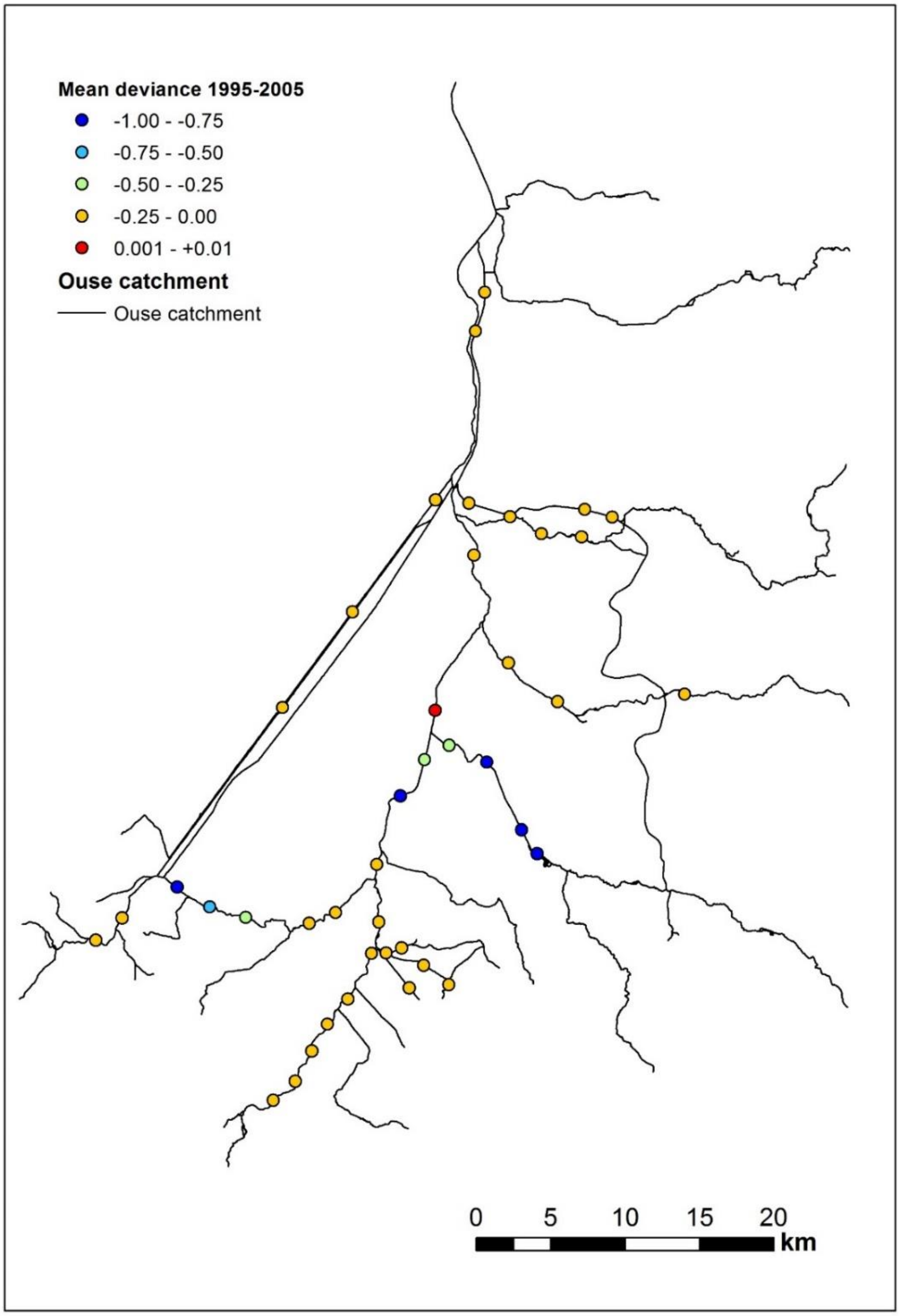


Figure A1.2. Map of temporally averaged model deviance in presence of bitterling for years 1995–2005. Colour scale: over-predicted (red) under-predicted (blue). Crown copyright and database rights 2018 Ordnance Survey (100025252)

9.2 Appendix 2

Appendix A2.1. Methods for experiments 0a, 0b: Efficacy of culling by system complexity, culling method/timing, and species' development stage

These initial experiments were conducted for the initial virtual fish (of experiment 1), and tested the effects of management factors that influenced population control efforts according to P_1 and Q_1. These varied in how the culling was applied spatially (factor M - either at 'random' or 'random biased towards the most recently colonized patches') and temporally in relation to dispersal (T – either 'before' or 'after' dispersal), and by the culling effort applied (as the maximum number of patches culled, N) and the stage(s) culled (S). Both experiments were applied to each of the nine catchments (ID), which correspond to the three catchment-branching types (B) and their replicates (Figure 3.1). Experiment 0b (270 parameter combinations) built upon the results of Experiment 0a (342 combinations) by applying a greater range of, and finer resolution to, the maximum number of patches culled (N) at the expense of fixing the culling method (M) and the timing of culling (T).

Appendix A2.2. Results experiment 0a: Efficacy of culling according to system complexity; culling method/timing and species' development stage

The characteristics of the catchment (B; ID) accounted for approximately 25 % of the variation in the rate of population increase (P_1) and 20 % of the variation in the rate of change in patch occupancy (Q_1) (Tables A2.2a, A2.3a). Culling generally suppressed the population growth rate in the moderate and highly branched catchments more than in the low branched catchments (Figure A2.1). In the no culling scenario, the patches in low-branched catchments (both in the main stem and tributaries) were colonized almost one year earlier than the medium- and high-branched catchments.

The effect of the culling method (M) on P_1 and Q_1 was relatively weak (< 5 % variance explained), but 'random biased towards the most recently colonized patches' reduced both rates more effectively than 'random' culling. There was no effect on the model outputs whether the cull was applied pre- or post-dispersal. Culling of juveniles always had a greater effect on P_1 than culling sub-adults or adults. This effect was greater when the maximum number of patches culled (N) was increased for juveniles. When the culled stage was adults or sub-adults, increasing N initially resulted in slightly increased P_1; reductions in P_1 only occurred when N increased to 15 (Figure A2.2). Values of Q_1 were lowest when juveniles were being culled at N = 15; Q_1 decreased for both juveniles and sub-adults for $N \geq 10$ patches compared with other combinations (Figure A2.2).

Appendix A2.3. Results experiment 0b: Efficacy of culling according to system complexity and species' development stage

Across this experiment, the characteristics of the catchment (B; ID) accounted for approximately 22 % of the variation in P and 15 % of the variation in Q_1 (Tables A2.2a, A2.3a). The effect of culling in a catchment of low branching was less effective than those of higher branching (as in Experiment 0a). The stage culled (S) had the greatest effect on P_1, accounting for more than a third of the variation, whereas the maximum number of patches (N) had the greatest effect on Q_1 (Tables A2.2a, A2.3a). Increasing the number of patches culled substantially reduced P_1 and Q_1 if juveniles were culled, whereas the reduction in P_1 was less marked if sub-adults were culled (Figure A2.3). Conversely, if adults were culled, then increasing N resulted in P_1 increasing, but with little change in Q_1 (Figure A2.3).

Appendix A2.4. Adaptive Management of Invasive Species: Example Guide for Experiment #1

‘RangeShifter v2.0’ was used to reproduce the simulations in batch mode, i.e. all the parameters are provided to the program in several files that must contain the following:

1. Landscape Map
    a. Habitat quality map layer (x9 catchments) - Raster format at 50m resolution with each cell holding a habitat quality score.
    b. Patch map layer (x9 catchments) - Raster format at 50m resolution with manual delimitations of non-overlapping patches of a similar size.
    c. Cost map layer (x9 catchments) – Raster format at 50m resolution with each cell holding inverse values of habitat quality score.
2. Species Distribution Map (x9 catchments) – Raster format at 50m resolution with 10 patches at the upstream end of the catchment to delimit the initial population.
3. Population and Dispersal Parameters – please see Table 3.2 (Expt. #1 used only species 5) and Table A2.1.
4. Management Scenarios – please see Table 3.1 (Expt. #1 contained 6 level of N * 8 level of CR = 48 scenarios)

Total simulations performed during Expt. #1: 48 scenarios * 9 catchments = 432 simulations. Each simulation was replicated 5 times.

‘RangeShifter’ produced one main output for each patch-based simulation: The Range file, which contained replicate number, year and total number of individuals present. Using ‘R Studio’, we extracted the high-level summary outputs named as P_1 and Q_1 following the method shown in the manuscript.

Appendix A2.5. Adaptive Management of Invasive Species: Example Guide for Experiment #2

‘RangeShifter v2.0’ was used to reproduce the simulations in batch mode, i.e. all the parameters are provided to the program in several files that must contain the following:

1. Landscape Map
    a. Habitat quality map layer (x9 catchments) - Raster format at 50m resolution with each cell holding a habitat quality score.
    b. Patch map layer (x9 catchments) - Raster format at 50m resolution with manual delimitations of non-overlapping patches of a similar size.
    c. Cost map layer (x9 catchments) – Raster format at 50m resolution with each cell holding inverse values of habitat quality score.
2. Species Distribution Map (x9 catchments) – Raster format at 50m resolution with 10 patches at the upstream end of the catchment to delimit the initial population.
3. Population and Dispersal Parameters (x9 species) – please see Table 3.2 and Table A2.1.
4. Management Scenarios – please see Table 3.1 (Expt. #2 contained 9 Specific Culling Scenarios)

Total simulations performed during Expt. #2: 9 scenarios * 9 catchments * 9 species = 729 simulations. Each simulation was replicated 5 times.

‘RangeShifter’ produced one main output for each patch-based simulation: The Range file, which contained replicate number, year and total number of individuals present. Using ‘R Studio’, we extracted the high-level summary outputs named as P_2 and Q_2 following the method shown in the manuscript.

Appendix A2.6. Adaptive Management of Invasive Species: Example Guide for Experiment #3

‘RangeShifter v2.0’ was used to reproduce the simulations in batch mode, i.e. all the parameters are provided to the program in several files that must contain the following:

1. Landscape Map: Gt. Ouse River
    a. Habitat quality map layer - Raster format at 50m resolution with each cell holding a habitat quality score based on the real river width.
    b. Patch map layer - Raster format at 50m resolution with manual delimitations of non-overlapping patches of a similar size.
    c. Cost map layer – Raster format at 50m resolution with each cell holding inverse values of habitat quality score.
2. Species Distribution Map – Raster format at 50m resolution with the initial distribution of bitterling in 1983.
3. Population and Dispersal Parameters – bitterling 250 posterior parameter distributions extracted from Dominguez Almela et al. 2020.
4. Management Scenarios – please see Table 3.1 (Expt. #3 contained 9 Specific Culling Scenarios)

Total simulations performed during Expt. #3: 9 scenarios * 1 catchment * 250 posterior parameter distributions = 2250 simulations. Each simulation was replicated 5 times.

‘RangeShifter’ produced one main output for each patch-based simulation: the Range file, which contained replicate number, year and total number of individuals present. The confident intervals allow for variation between posterior parameter sets and within them (i.e. the five replicates in each case). Therefore, using ‘R Studio’ we firstly averaged each set of five reps to give a single prediction for each posterior * scenario, and then determined the 95 % C.I. across the 2250 samples. Afterwards, we extracted the high-level summary outputs named as P_2 and Q_2 following the method shown in the manuscript.

Table A2.1. Common demographic and dispersal parameters used for the virtual species from Table 3.1

	Model parameters	Stage-structure	Density-dependence	Value
Population dynamics parameters	**Number of reproductive seasons/year**	Adults	No	1
	Proportion of males	Whole population	No	0.5
	Probability of reproducing	Adults	No	1
Emigration parameters	**Slope**	Whole population	No	10
	Inflection point	Juveniles	No	0
		Sub-adults	Yes	0.48
		Adults	Yes	1.23
Transfer parameters	**Directional persistence**	Whole population	No	1.5
	Perceptual range (m)	Whole population	No	50
	Memory size (cells)	Whole population	No	2
Settlement	**Max. no. of steps**	Whole population	No	100

Slope	Whole population	Yes	-10
Inflection point	Whole population	Yes	1

Table A2.2a. Principal sources of variance explained (%) in the summary statistics rate of population increase (P_1) for experiments 0a and 0b. Factors: cull method (M); stage(s) culled (S); maximum number of patched culled (N); catchment branching (B); catchment ID number (ID)

Experiment 0a				***Experiment 0b***			
Factor	**Df**	**Sum Sq**	**% variance**	**Factor**	**Df**	**Sum Sq**	**% variance**
M	1	103703	2.6	S	2	1017105	37.0
S	2	1178515	29.3	N	9	266741	9.7
T	1	1287	0.0	ID	2	334600	12.2
N	3	218957	5.4	B	6	288710	10.5
ID	2	569151	14.2	S:N	18	335897	12.2
B	6	419702	10.4	S:ID	4	18384	0.7
M:S	2	37477	0.9	N:ID	18	39585	1.4
M:T	1	4158	0.1	S:B	12	26881	1.0

S:T	2	68541	1.7
M:N	3	51149	1.3
S:N	6	483011	12.0
T:N	3	33586	0.8
M:ID	2	738	0.0
S:ID	4	13370	0.3
T:ID	2	560	0.0
N:ID	6	36125	0.9
M:B	6	518	0.0
S:B	12	30574	0.8
T:B	6	2079	0.1
N:B	18	76229	1.9
N:B	54	42494	1.5
S:N:ID	36	18379	0.7
S:N:B	108	47503	1.7
Residuals	1080	315440	11.5

M:S:T	2	2998	0.1
M:S:N	6	25188	0.6
M:T:N	3	3384	0.1
S:T:N	6	34196	0.9
M:S:ID	4	1067	0.0
M:T:ID	2	1161	0.0
S:T:ID	4	768	0.0
M:N:ID	6	4667	0.1
S:N:ID	12	31633	0.8
T:N:ID	6	4702	0.1
M:S:B	12	5559	0.1
M:T:B	6	604	0.0

S:T:B	12	2966	0.1
M:N:B	18	9569	0.2
S:N:B	36	34011	0.8
T:N:B	18	3432	0.1
M:S:T:N	6	6640	0.2
M:S:T:ID	4	1376	0.0
M:S:N:ID	12	4680	0.1
M:T:N:ID	6	3465	0.1
S:T:N:ID	12	4154	0.1
M:S:T:B	12	3376	0.1
M:S:N:B	36	9828	0.2
M:T:N:B	18	7857	0.2

S:T:N:B	36	7954	0.2	
M:S:T:N:ID	12	2955	0.1	
M:S:T:N:B	36	8074	0.2	
Residuals	1728	465502	11.6	

Table A2.2b**.** Principal sources of variance explained (%) in the summary statistics rate of population increase for experiments 1 (P_1) and 2 (P_2). Factors: cull method (M); stage(s) culled (S); maximum number of patched culled (N); catchment branching (B); catchment ID number (ID)

Experiment 1				***Experiment 2***			
Factor	**Df**	**Sum Sq**	**% variance**	**Factor**	**Df**	**Sum Sq**	**% variance**
CR	7	2999011	44.3	B	2	929635	0.7
N	5	1.51E+06	22.4	ID	6	779828	0.6
ID	2	307117	4.5	SpType	2	41455938	33.2
B	6	2.83E+05	4.2	SpDispType	2	42606709	34.1
CR:N	31	9.15E+05	13.5	SpID	4	7952971	6.4
CR:ID	14	51812	0.8	SCS	8	13845299	11.1
N:ID	10	43891	0.6	B:SCS	16	64941	0.1
CR:B	42	51071	0.8	ID:SCS	48	139900	0.1

N:B	30	29491	0.4	SpType:SCS	16	4503230	3.6
CR:N:ID	61	39196	0.6	SpDispType:SCS	16	2138033	1.7
CR:N:B	173	95776	1.4	SpID:SCS	31	1256231	1.0
Residuals	1474	441640	6.5	ID:SpID	64	3544755	2.8
				ID:SpID:SCS	478	1687281	1.4
				Residuals	2663	3942689	3.2

Table A2.3a. Principal sources of variance explained (%) in the summary statistics rate of change of patch occupancy (Q_1) for experiments 0a and 0b. Factors: cull method (M); stage(s) culled (S); maximum number of patched culled (N); catchment branching (B); catchment ID number (ID)

Experiment 0a				***Experiment 0b***			
Factor	**Df**	**Sum Sq**	**% variance**	**Factor**	**Df**	**Sum Sq**	**% variance**
M	1	2.9	4.1	S	2	16.9	24.8
S	2	5.1	7.4	N	9	19.8	29.0
T	1	0.4	0.5	ID	2	5.5	8.1
N	3	16.2	23.5	B	6	4.5	6.5
ID	2	7.8	11.3	S:N	18	9.5	13.9
B	6	5.7	8.3	S:ID	4	0.4	0.5
M:S	2	1.4	2.0	N:ID	18	0.2	0.3
M:T	1	0.1	0.2	S:B	12	1.6	2.4

S:T	2	1.6	2.3
M:N	3	2.3	3.4
S:N	6	6.5	9.5
T:N	3	0.9	1.4
M:ID	2	0.0	0.1
S:ID	4	0.4	0.5
T:ID	2	0.0	0.0
N:ID	6	0.4	0.5
M:B	6	0.3	0.5
S:B	12	0.9	1.2
T:B	6	0.1	0.1
N:B	18	2.1	3.0
N:B	54	1.3	1.9
S:N:ID	36	0.3	0.4
S:N:B	108	1.5	2.1
Residuals	1080	6.8	10.0

M:S:T	2	0.2	0.3
M:S:N	6	1.1	1.5
M:T:N	3	0.1	0.1
S:T:N	6	1.3	1.9
M:S:ID	4	0.0	0.1
M:T:ID	2	0.0	0.0
S:T:ID	4	0.0	0.0
M:N:ID	6	0.1	0.1
S:N:ID	12	0.3	0.4
T:N:ID	6	0.1	0.1
M:S:B	12	0.1	0.2
M:T:B	6	0.0	0.1

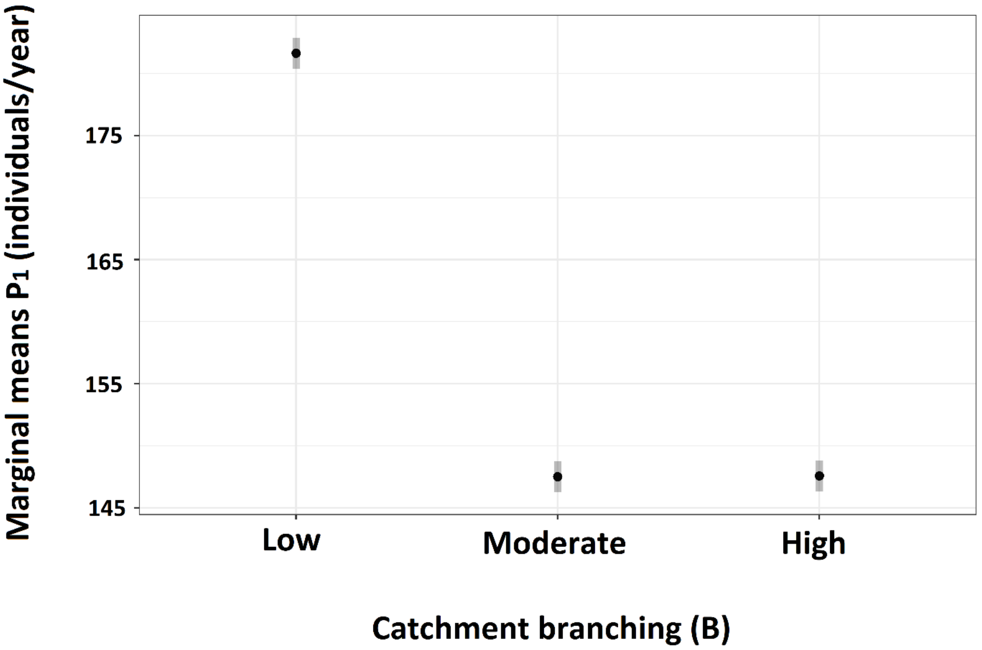
S:T:B	12	0.1	0.1
M:N:B	18	0.2	0.3
S:N:B	36	1.1	1.7
T:N:B	18	0.2	0.2
M:S:T:N	6	0.2	0.3
M:S:T:ID	4	0.0	0.0
M:S:N:ID	12	0.0	0.0
M:T:N:ID	6	0.0	0.0
S:T:N:ID	12	0.1	0.1
M:S:T:B	12	0.1	0.1
M:S:N:B	36	0.2	0.3
M:T:N:B	18	0.2	0.3

S:T:N:B	36	0.2	0.3	
M:S:T:N:ID	12	0.1	0.1	
M:S:T:N:B	36	0.3	0.4	
Residuals	1728	7.8	11.3	

Table A2.3b. Principal sources of variance explained (%) in the summary statistics rate of change of patch occupancy for experiments 1 (Q_1) and 2 (Q_2). Factors: cull method (M); stage(s) culled (S); maximum number of patched culled (N); catchment branching (B); catchment ID number (ID)

Experiment 1				***Experiment 2***			
Factor	**Df**	**Sum Sq**	**% variance**	**Factor**	**Df**	**Sum Sq**	**% variance**
CR	7	263	51.7	B	2	11.4	0.6
N	5	118	23.1	ID	6	13.4	0.8
ID	2	7	1.4	SpType	2	81.6	4.6
B	6	3	0.7	SpDispType	2	1005.4	56.9
CR:N	31	89	17.5	SpID	4	19.9	1.1
CR:ID	14	1	0.2	SCS	8	361.1	20.4
N:ID	10	0	0.1	B:SCS	16	1.3	0.1
CR:B	42	3	0.6	ID:SCS	48	4.4	0.3

N:B	30	1	0.3	SpType:SCS	16	16.9	1.0
CR:N:ID	61	2	0.4	SpDispType:SCS	16	65.2	3.7
CR:N:B	173	4	0.7	SpID:SCS	31	20.9	1.2
Residuals	1474	18	3.5	ID:SpID	64	29.5	1.7
				ID:SpID:SCS	478	32.6	1.8
				Residuals	2663	104.3	5.9



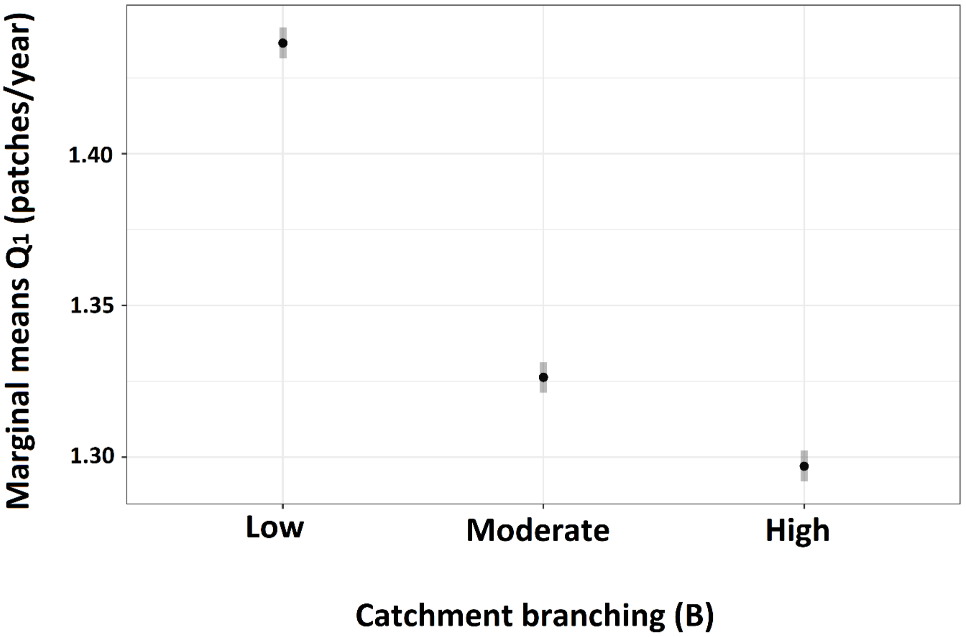


Figure A2.1. Effects of catchment branching (low, moderate, high) on the rate of population increase (P_1) and change of patches occupancy (Q_1) during Experiment 0a. Grey bars are 95 % confidence intervals for the marginal means

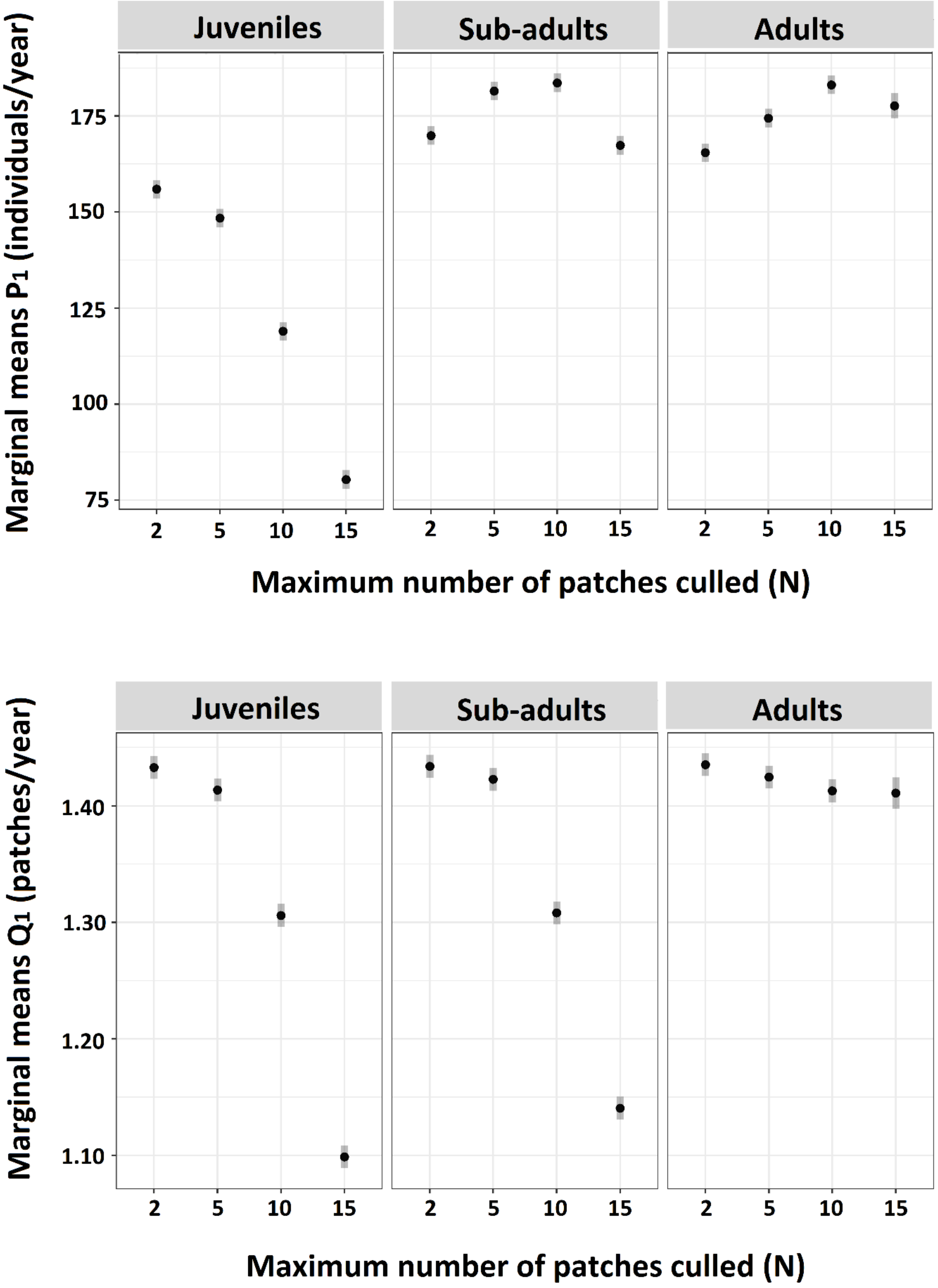


Figure A2.2. Interaction effects of stage culled (juveniles, sub-adults, adults) and the maximum number of patches culled (N) on the rate of population increase (P_1) and change of patches occupancy (Q_1) during Experiment 0a. The grey bars are 95 % confidence intervals for the marginal means

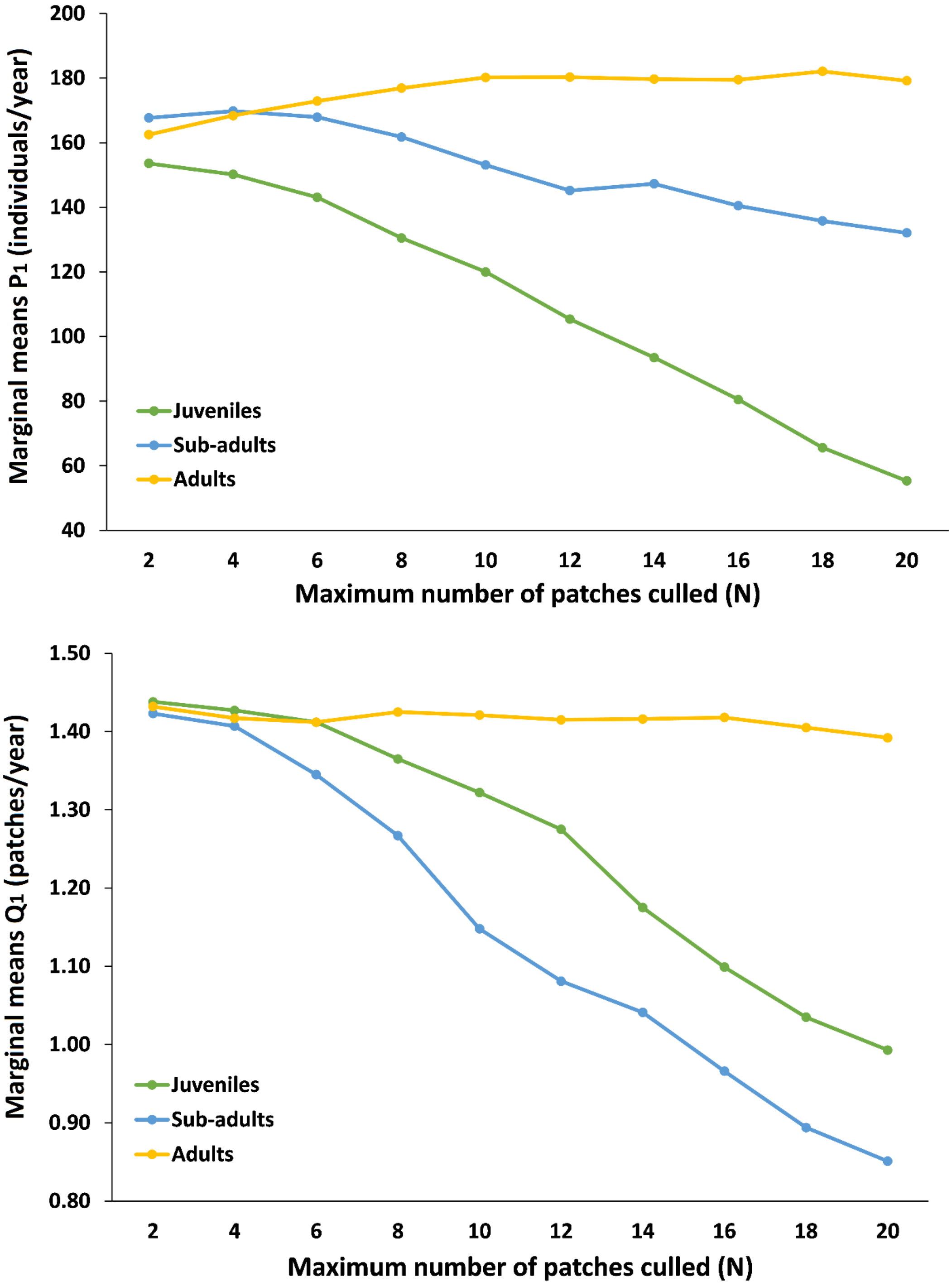


Figure A2.3. Interaction effects of stage culled (S) and the maximum number of patches culled (N) on the rate of population increase (P_1) and change in patch occupancy (Q_1) in Experiment 0b

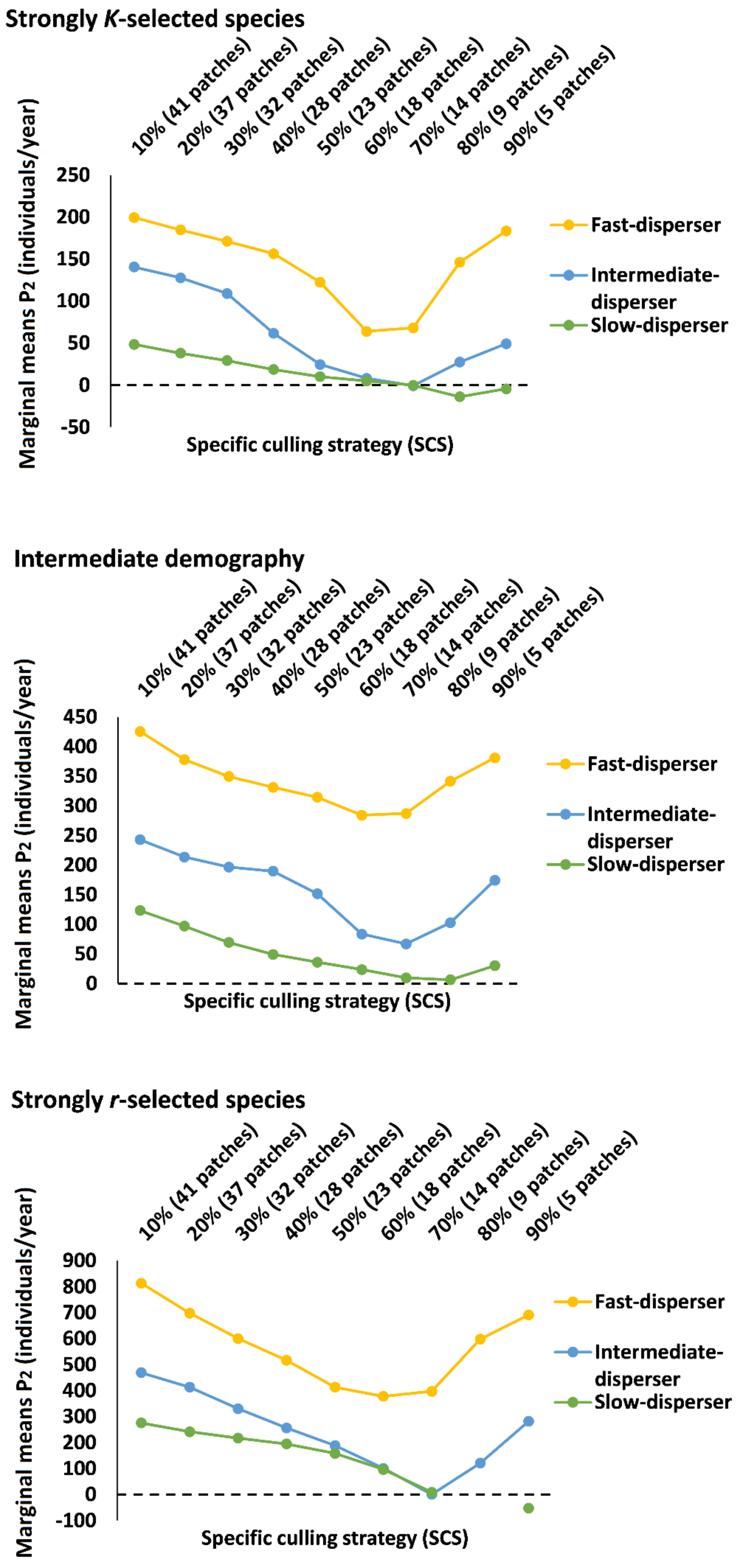


Figure A2.4. Interaction effects of the species dispersal type (SpDispType) and specified culling strategy (SCS) on the rate of population increase (P_2) during Experiment 2. No data-point shown at 80 % (9 patches) in r-selected species as all replicates were extirpated

9.3 Appendix 3

Table A3.1. Principal sources of variance explained (%) for best-fitted model per species type (*K*- selected, intermediate demography and *r*-selected) and dispersal type (fast, intermediate and slow) for P_{10} and P_{30} in randomly generated virtual rivers. Numbers in brackets indicate the value of n for the term Dn in the model

P_{10}				
		k-selected species	*Intermediate demography*	*r-selected species*
	Factor	**% variance**	**% variance**	**% variance**
Fast	Shape (S)	0.2	0.5	1.1
	Release point (R)	83.1	8.6	4.5
	Hab. quality (H)	2.2	1.8	0.9
	Dn	8.4 [50]	84.7 [100]	85.7 [50]
	S*R	5.8	4.0	7.1
	S*H	0.4	0.4	0.8

Intermediate	Shape (S)	0.4	0.2	0.4
	Release point (R)	2.1	0.7	2.2
	Hab. quality (H)	90.6	96.3	89.7
	Dn	2.2 [25]	0.3 [5]	0.0 [10]
	S*R	3.2	0.5	4.0
	S*H	1.5	2.1	3.8
Slow	Shape (S)	0.2		
	Release point (R)	1.9	95.7	97.8
	Hab. quality (H)	94.1	4.3	2.2
	Dn	0.1 [5]	0.0 [100]	0.1 [5]
	S*R	1.4		
	S*H	2.3		

P_{30}				
		k-selected species	*Intermediate demography*	*r-selected species*
	Factor	**% variance**	**% variance**	**% variance**
Fast	Shape (S)	2.6	1.9	1.3
	Release point (R)	3.5	10.1	7.9
	Hab. quality (H)	1.0	0.2	1.4
	Dn	66.3 [50]	73.9 [50]	55.7 [25]
	S*R	25.6	11.3	31.9
	S*H	1.1	2.6	1.7
Intermediate	Shape (S)	11.5	0.5	10.4
	Release point (R)	2.2	84.2	5.2
	Hab. quality (H)	0.2	1.9	1.9

	Dn	61.2 [100]	0.0 [5]	57.1 [100]
	S*R	22.5	12.1	25.0
	S*H	2.3	1.3	0.3
Slow	Shape (S)	2.2	0.6	
	Release point (R)	5.3	88.9	95.9
	Hab. quality (H)	0.3	1.0	3.9
	Dn	75.8 [50]	0.4 [5]	0.2 [100]
	S*R	14.7	8.9	
	S*H	1.8	0.2	

Table A3.2. Principal sources of variance explained (%) for best-fitted model per species type (*K*- selected, intermediate demography and *r*-selected) and dispersal type (fast, intermediate and slow) for Q$_{10}$ and Q$_{30}$ in randomly generated virtual rivers. Numbers in brackets indicate the value of n for the term Dn in the model

Q$_{10}$				
		k-selected species	*Intermediate demography*	*r-selected species*
	Factor	**% variance**	**% variance**	**% variance**
Fast	Shape (S)	0.2	0.5	0.3
	Release point (R)	0.7	4.0	2.3
	Hab. quality (H)	1.8	0.2	0.5
	Dn	88.1 [50]	89.2 [50]	88.2 [50]
	S*R	0.7	5.0	7.2
	S*H	8.6	1.1	1.6
Intermediate	Shape (S)	0.4		0.3

	Release point (R)	84.4	8.9	85.6
	Hab. quality (H)	0.9	90.6	1.0
	Dn	1.6 [100]	0.5 [10]	0.0 [10]
	S*R	11.8		12.5
	S*H	1.0		0.6
Slow	Shape (S)	0.2		
	Release point (R)	87.1	95.5	98.1
	Hab. quality (H)	4.1	4.1	1.1
	Dn	2.0 [25]	0.4 [100]	0.7 [10]
	S*R	5.2		
	S*H	1.4		
Q_{30}				

		k-selected species	Intermediate demography	r-selected species
	Factor	**% variance**	**% variance**	**% variance**
Fast	Shape (S)	0.6	0.8	0.8
	Release point (R)	14.6	2.1	11.8
	Hab. quality (H)	0.0	0.0	0.0
	Dn	65.7 [50]	83.8 [50]	72.1 [50]
	S*R	13.8	9.8	13.0
	S*H	5.3	3.5	2.3
Intermediate	Shape (S)	5.3		3.2
	Release point (R)	21.8	6.8	9.8
	Hab. quality (H)	2.0	0.0	0.2
	Dn	50.5 [50]	93.2 [50]	71.7 [25]

	S*R	16.8		15.1
	S*H	3.6		
Slow	Shape (S)	1.5	0.4	
	Release point (R)	2.0	82.7	94.6
	Hab. quality (H)	0.1	0.0	5.0
	Dn	81.3 [50]	6.5 [25]	0.4 [50]
	S*R	12.3	10.4	
	S*H	2.9		

Table A3.3. Principal sources of variance explained (%) for best-fitted model per species type (*K*- selected, intermediate demography and *r*-selected) and dispersal type (fast, intermediate and slow) for P_{10} and P_{30} in the real-world rivers. Numbers in brackets indicate the value of n for the term Dn in the model

P_{10}				
		k-selected species	*Intermediate demography*	*r-selected species*
	Factor	**% variance**	**% variance**	**% variance**
Fast	Release point (R)	2.5	2.9	1.7
	Hab. quality (H)	91.3	89.3	91.0
	Dn	5.6 [5]	5.6 [5]	6.4 [5]
	R*H	0.5	2.2	0.9
Intermediate	Release point (R)	98.0	97.1	97.3
	Hab. quality (H)	0.4	0.5	0.7
	Dn	1.6 [5]	1.4 [5]	1.1 [5]

	R*H		1.1	0.8
Slow	Release point (R)	98.3	98.2	99.3
	Hab. quality (H)	0.5	0.3	0.0
	Dn	1.2 [100]	1.5 [5]	0.7 [5]
	R*H			

P_{30}

		k-selected species	*Intermediate demography*	*r-selected species*
	Factor	**% variance**	**% variance**	**% variance**
Fast	Release point (R)	5.2	78.1	4.7
	Hab. quality (H)	76.1	10.6	76.1
	D5	13.2 [5]	6.2 [5]	14.4 [5]
	R*H	5.6	5.1	4.8

Intermediate	Release point (R)	4.8	92.0	88.9
	Hab. quality (H)	86.6	2.0	0.7
	Dn	7.3 [5]	2.9 [5]	4.9 [5]
	R*H	1.4	3.1	5.5
Slow	Release point (R)	3.4	92.7	97.3
	Hab. quality (H)	88.8	0.7	1.6
	Dn	6.7 [5]	5.4 [5]	1.1 [5]
	R*H	1.1	1.2	

Table A3.4. Principal sources of variance explained (%) for best-fitted model per species type (*K*- selected, intermediate demography and *r*-selected) and dispersal type (fast, intermediate and slow) for Q_{10} and Q_{30} in real-world rivers. Numbers in brackets indicate the value of n for the term Dn in the model

Q_{10}				
		k-selected species	*Intermediate demography*	*r-selected species*
	Factor	**% variance**	**% variance**	**% variance**
Fast	Release point (R)	89.9	61.5	84.2
	Hab. quality (H)	5.4	0.4	5.1
	Dn	4.7 [50]	8.5 [25]	8.2 [50]
	R*H		29.6	2.4
Intermediate	Release point (R)	97.0	71.2	97.2
	Hab. quality (H)	1.8	6.0	1.4
	Dn	1.2 [50]	22.8 [100]	0.5 [250]

	R*H			0.9
Slow	Release point (R)	97.2	97.7	98.2
	Hab. quality (H)	1.1	1.6	0.3
	Dn	1.7 [250]	0.7 [250]	1.5 [250]
	R*H			

Q_{30}

		k-selected species	*Intermediate demography*	*r-selected species*
	Factor	**% variance**	**% variance**	**% variance**
Fast	Release point (R)	52.8	82.3	50.6
	Hab. quality (H)	0.1	0.2	0.6
	Dn	24.7 [5]	0.7 [500]	21.3 [5]
	R*H	22.4	16.7	27.4

Intermediate	Release point (R)	79.8	65.5	93.6
	Hab. quality (H)	4.9	12.2	0.0
	Dn	13.0 [100]	19.0 [10]	6.4 [10]
	R*H	2.3	3.4	
Slow	Release point (R)	91.6	96.9	86.4
	Hab. quality (H)	2.0	0.1	0.2
	Dn	6.4 [5]	3.0 [5]	13.3 [10]
	R*H			

9.4 Appendix 4

Table A4.1. Mean and range (min/max) of lengths (L) and corrected stable isotope data ($\delta^{13}C$ and TP) per year during allopatric and sympatric treatments.

Treatment	Species	Year	L	min/max	$\delta^{13}C_{\text{corrected}}$	min/max	TP	min/max
Allopatric	Carp	2017	170.7	(145, 226)	1.8 (±0.6)	(0.9, 3.1)	3.1 (±0.1)	(2.9,3.2)
Allopatric	Carp	2018	206	(179, 254)	1.0 (±0.4)	(0.4, 1.8)	3.1 (±0.1)	(2.9, 3.3)
Allopatric	Carp	2019	244.1	(224, 298)	1.4 (±0.3)	(0.9, 2.0)	2.9 (±0.1)	(2.8, 3.1)
Allopatric	Crucian	2017	86.3	(68, 157)	1.3 (±0.4)	(0.6, 1.9)	3.0 (±0.1)	(2.7, 3.2)
Allopatric	Crucian	2018	102.6	(69, 164)	1.3 (±0.4)	(0.5, 1.8)	3.0 (±0.1)	(2.8, 2.2)
Allopatric	Crucian	2019	118.3	(98, 144)	1.0 (±0.3)	(0.4, 1.3)	2.7 (±0.1)	(2.5, 2.9)
Sympatric	Carp	2017	165.7	(149, 188)	3.1 (±1.2)	(0.9, 5.4)	3.2 (±0.3)	(2.8, 3.8)
Sympatric	Carp	2018	215.2	(194, 239)	3.7 (±1.0)	(2.1, 5.3)	3.3 (±0.2)	(2.9, 3.5)
Sympatric	Carp	2019	251.7	(221, 287)	3.2 (±1.0)	(1.8, 6.1)	3.3 (±0.2)	(3.0, 3.8)

Sympatric	Crucian	2017	86.1	(63, 165)	1.0 (±0.6)	(0.0, 2.5)	2.8 (±0.2)	(2.5, 3.3)
Sympatric	Crucian	2018	87.1	(52, 120)	1.6 (±0.8)	(0.0, 3.0)	2.9 (±0.1)	(2.7, 3.1)
Sympatric	Crucian	2019	81.9	(66, 100)	1.3 (±0.7)	(0.1, 3.0)	2.9 (±0.1)	(2.7, 3.1)

Table A4.2. Mean and range (min/max) of lengths (L) and raw stable isotope data ($\delta^{13}C$ and $\delta^{15}N$) during the co-habiting ponds experiments.

	Species	**L**	**min, max**	**$\delta^{13}C$ (±sd)**	**min, max**	**$\delta^{15}N$ (±sd)**	**min/max**
Pond 1	*Carp*	180.5	(120, 450)	-26.1 (±2.6)	(-29.7, -21.6)	8.2 (±0.5)	(7.2, 8.8)
	Crucian	133.5	(120, 155)	-28.9 (±0.9)	(-30.4, -27.8)	7.8 (±0.8)	(6.3, 9.4)
Pond 2	*Carp*	117.7	(50, 300)	-28.7 (±1.0)	(-30.0, -26.9)	10.6 (±0.6)	(9.5, 11.8)
	Crucian	69.1	(55, 100)	-30.8 (±0.7)	(-32.1, -29.8)	10.8 (±0.5)	(10.0, 11.4)
Pond 3	*Carp*	153.8	(131, 182)	-25.4 (±1.7)	(-27.8, -23.9)	11.3 (±0.7)	(10.4, 12.0)
	Crucian	179.3	(121, 242)	-21.7 (±0.3)	(-22.1, -21.2)	10.1 (±0.8)	(9.1, 11.1)
Pond 4	*Carp*	140.8	(120, 180)	-33.5 (±2.7)	(-37.4, -27.4)	8.9 (±0.5)	(8.0, 9.6)
	Crucian	147.2	(130, 170)	-33.4 (±1.5)	(-35.2, -30-9)	6.9 (±0.6)	(5.6, 7.6)

Table A4.3. Results of analysis of covariance for the effects of species (common carp and crucian carp) on raw stable isotope data ($\delta^{13}C$ and $\delta^{15}N$) adjusted for fish length for wild ponds with sympatric carp and crucian carp.

		$\delta^{13}C$			**$\delta^{15}N$**		
Ponds	**Variable**	***Df***	***F***	***P***	***Df***	***F***	***P***
1	Species	1, 20	25.9	<0.001	1,20	26.7	<0.001
	Length	1, 20	2.4	0.1	1, 20	3.7	0.07
2	Species	1,20	52.9	<0.001	1,20	32.2	<0.001
	Length	1, 20	4.9	<0.05	1, 20	3.5	0.07
3	Species	1,14	67.4	<0.001	1,14	55.4	<0.001
	Length	1, 14	0.01	0.9	1, 14	0.3	0.6
4	Species	1,20	6.7	<0.05	1,20	7.9	<0.05
	Length	1, 20	0.2	0.6	1, 20	0.8	0.4

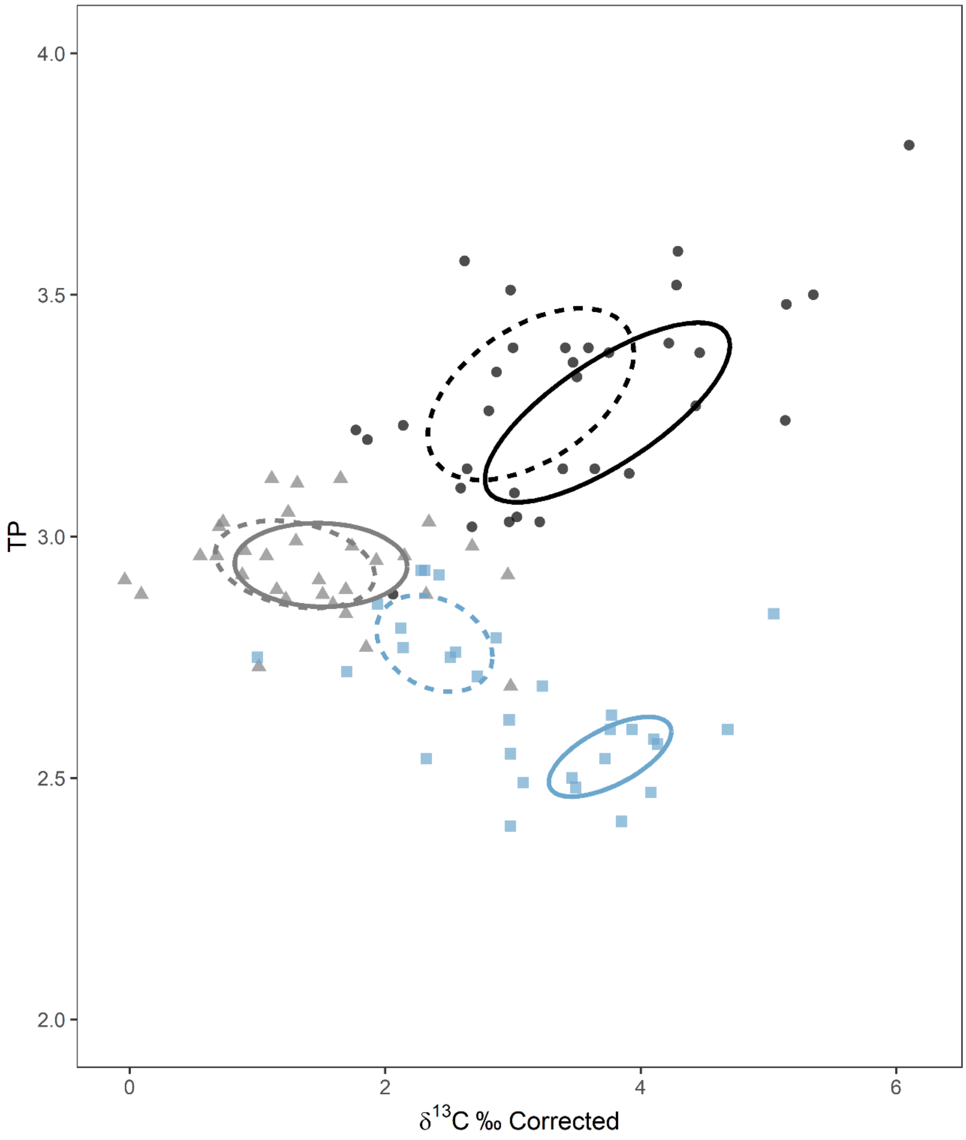


Figure A4.1. The isotopic niches (represented as standard ellipse areas, SEA$_C$) in the sympatric treatment for carp (black filled circles), crucian carp (grey filled triangles) and signal crayfish (blue filled squares) in 2018 (continuous line) and 2019 (dotted line), in the natural pond experiment.