Predicting the ecological consequences of river management for a riverine cyprinid fish

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"*No man ever steps in the same river twice, for it's not the same river and he's not the same man.*" - **Heraclitus of Ephesus**

Abstract

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Current river management seeks to resolve a compromise between stakeholder interests, ecosystem services provision and conservation aims, especially in relation to assessment of ecosystem health. While management decisions should be evidenced-based, current population and habitat models fail to incorporate fish behaviour and the interactions between fish and their environment, thus limiting their ability to predict management-relevant, population responses to environmental change. In order to address these weaknesses, an individual-based model is developed and parameterised to predict the distribution and growth of roach (*Rutilus rutilus*), a common, generalist, freshwater fish; known to be typically dominant in heavily modified rivers. Such a model seeks to build on current management models and practices, with emphasis on improving recruitment of juvenile roach. Virtual forager parameters are derived from foraging experiments, published investigations, models of roach behaviour and bioenergetics. Data collected from field studies in a typical, highly modified, lowland river are used to describe the environment and initial fish population with subsequent data on fish population trends used to validate the IBM, under a pattern-oriented modelling approach; specifically growth rate and habitat distribution patterns. River management practices including the removal of in-stream aquatic macrophytes and regulation of flow regime for flood risk management are predicted as potentially damaging to roach recruitment, subsequent year-class strength and therefore, populations in subsequent years. Recommendations for more sympathetic management schemes are provided. The modelling framework described here can be used to produce robust predictions of roach population patterns in riverine habitats and allows the user to test the impact of environmental change on cyprinid fish, enabling the modelling system to be used to develop proactive, evidence-based management in light of current rates of environmental change.

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Author's declaration

I confirm that the work presented in this thesis is my own work, with the following exceptions:

Chapter 2 is published in collaboration with Richard Stillman, Rodolphe Gozlan and Robert Britton as:

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In addition, the individual-based model used in Chapters 5 and 6 used the MORPH framework created by Stillman (2008). The data on roach and environmental characteristics from the upper River Stour and the River Wensum were collected by the Environment Agency and similar data from the River Great Stour were reported by Copp (1992) and Garner (1995).

1. Introduction

1.1 Managing freshwater resources

Many of the challenges in freshwater resource management arise from the inherent difficulty of reconciling the societal benefits that arise from exploiting a range of provisioning ecosystem services with the impacts this exploitation has for the multiple physical, hydrological and ecological processes of the resource. Whilst there is often a desire to work with these processes in a management context, a lack of appropriate tools and evidence that assist the decision-making process is apparent. Thus, evidence-based management interventions require researchers to develop greater understanding of the dynamic, multi-scale interactions that occur in natural systems, as well as building predictive models at a suitable level of usability and predictive clarity to ensure the long-term sustainability of ecosystem service exploitation.

Freshwater ecosystems are a crucial resource used by society for potable water, sewage treatment and disposal, sport fishing, aquaculture, and protection from natural hazards such as flooding (Costanza et al. 1997; Kuylenstierna et al. 1997; Acreman & Ferguson 2010; Gozlan & Britton 2013). As freshwater resources are so ecologically, economically and socially important, stakeholder interests are broad and varied, creating a complex and demanding management landscape (Vorosmarty et al. 2010; Dudgeon et al. 2006; Gozlan & Britton 2013). Moreover, as open and dynamic systems, freshwater resources are under threat from issues including pollution, abstraction, over-exploitation and biological invasions that present problems for current and future users, managers and stakeholders (Dudgeon et al. 2006, Vörösmarty et al. 2010). The factors commonly influencing freshwater ecosystems from a fish ecology and fisheries perspective are that of habitat loss and disturbance that arise through human activity. In riverine systems, this tends to be in the form of flow regulation, reduced flows through abstraction, temperature modifications, habitat disturbance and loss that arise through in-channel activities such as gravel removal and in-stream macrophyte management (Downs & Thorn 2000).

Current approaches in fisheries management can be characterised as a general trend away from single-species to a whole ecosystem paradigm (FAO 2012). Models used in fisheries research have been based on either population metrics, such as stock sizes and

limits, or more recently, based on the environmental influences and potential populations sizes, such as the habitat model HABSCORE that uses habitat variables to predict fish population size for fishes of the Salmonidae family (Milner et al. 1998). These approaches, however, are limited by the study of potential effects in isolation, i.e. population models can underplay or ignore the role that some environmental factors have on key processes, whilst habitat models do the same for species and population characteristics (Grimm & Railsback 2005). Finally, both these approaches centre on changes at the population scale, and therefore, important behaviours and interactions of individuals that comprise the population are often overlooked (Grimm & Railsback 2005).

In order to model the wide-ranging and complex interactions that occur within ecosystems, researchers are developing new tools, allied with increased computing power and recent developments in the design frameworks used to create these tools. One such modelling approach is individual-based modelling, where the interaction between individuals and their environment, and the consequences, are modelled predictively in computer simulations (Grimm & Railsback 2005; Stillman 2008). This allows for a more realistic representation of natural systems by simulating systems dynamically and across multiple scales, whilst also considering potential interactions and their outcomes. By validating against real systems and refining these methods in an iterative process, it is possible to achieve an approach to management that is more ecosystem-centric and enables responses to environmental change to be predicted (Grimm & Railsback 2012).

1.2 Individual based modelling and its role in ecological management
Managers of freshwater ecosystems face challenges dealing with multiple environmental stressors and environmental change across varying spatial scales whilst meeting the needs of diverse groups of stakeholders, and ensuring that decisions are well tailored to often complex, dynamic systems but rely on a firm evidence-base (Rogers 2006). Although management decision-making should be evidence-based, it is not always feasible to collect and interpret the appropriate data and information due to resource constraints. An experimental approach may be used, but this suffers from issues of relevancy and general applicability for outcomes due to differences between systems or in the same system undergoing environmental change (Maddock 1999).

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Experimental investigations of ecological systems are also limited by time, replicability and the availability of suitable sites (Carpenter et al. 1995). Lastly, an experimental approach is not always possible when, for example, investigating scenarios with potentially severe negative consequences, such as parasitism, biological invasions or extreme management scenarios. Fortunately, alternative approaches for describing, investigating and testing ecosystem management solutions exist.

Predictive ecological modelling is an approach that has the potential to provide managers with a tool to guide their decision-making (Sutherland & Freckleton 2012). Such ecological models vary greatly in size and complexity, providing information from a purely theoretical to an entirely applied basis. Basic analytical models of populations, based on differential equations, such as the Lotka-Voleterra equation (Lotka 1925; Volterra 1926; Billard 1977) or Holling's Disk Equation (Holling 1959) have provided vital sources of theoretical understanding of predator-prey interactions. When unaltered, however, they fail to consider the environment or more complex interactions with other abiotic and biotic factors, and as such are of limited use in applied scenarios (Grimm & Railsback 2005, 2012). Alternative modelling systems of use for ecosystem managers are habitat assessment models, such as HABSCORE and PHABSIM that utilise measured habitat variables for predicting population size and outcomes (Milner et al. 1998; Maddock 1999). While these have been of great utility to fishery and freshwater managers (Spence & Hickley 2000), they are reliant on assessments of population levels and habitat quality, meaning that they require field data that limits the scope of predictions should site conditions change, such as with reduced flow or macrophyte removal (Guisan & Zimmermann 2000). Habitat assessment models are further limited by their focus on environmental factors that are unable to account for any adaptive responses by individuals within the population to changes in habitat characteristics (Guisan & Zimmermann 2000). Synergy between ecological disciplines, linking species traits, habitat and ecosystem functioning in a unifying ecological theory has been promoted as addressing some of these shortcomings (Loreau 2010).

A major source of resilience to habitat change and disturbance is in behavioural adaptability at the individual level (Caro 2007). As populations are made up of individuals, how these individuals respond to environmental change may determine the impact such changes or disturbances have on the entire population (Sih et al. 2004).

While the importance of animal behaviour in conservation work is widely recognised, its full potential has not yet been realised (Buchholz 2007; Caro 2007). In the past, conservation management has either ignored or only partially utilised the role behaviour has to play in conservation due to issues of complexity and relevant scales. While incorporating behavioural traits into conservation research represents a significant challenge, the potential benefits arguably justify the task (Buchholz 2007).

Caro (2007) suggested that a potential explanation for poor integration between animal behaviour and conservation biology is the lack of an established method for combining the two approaches. Individual based models (IBMs) represent such a method, whereby individual organisms are treated as discrete entities and during the simulation they interact with both the environment and other individuals (Judson 1994; Grimm & Railsback 2005). Individuals display adaptive behaviours from behavioural decisions based on both the environment and the individual's own state or condition (Stillman et al. 2001; Stillman & Goss-Custard 2010). These adaptive behaviours seek to return the highest possible perceived fitness for that individual, i.e. 'fitness-maximising behaviour' (Grimm & Railsback 2005; Stillman & Goss-Custard 2010). Such behaviour will differ between individuals; for example, a satiated fish might make a different decision compared to a poorly nourished fish under the same environmental conditions. As fitness maximising behaviour is a product of natural selection, it is assumed that animals in an IBM should respond to changes in environmental conditions in the same way as animals in the real world (Stillman et al. 2000; Stillman 2008). This means IBMs have less reliance upon historical data and, as fitness maximising behaviour should remain unchanged under different biological conditions, predictions can be made for a wide range of scenarios (Stillman 2008). These predictions stem directly from the decisions made by the modelled individuals, their interactions with the environment and each other, as well as behaviours that emerge from these interactions (Grimm & Railsback 2005). By simulating numerous individuals over a period of time, patterns emerge at larger scales, such as the population level.

While the computing power and design frameworks used to create individual-based models have only recently made possible the simulation of sufficient numbers of individual interactions to simulate populations, such frameworks have already described the components required for an individual-based model. Uchmanski & Grimm (1996)

define four components of an IBM: 1) there is change and/or growth in individuals over their lifecycle; 2) there is resource use by individuals; 3) the modelled individuals represent real and whole individuals; and 4) there is a degree of variability between individuals. If any of these components are not met then the model should be referred to as an individual-orientated model (Grimm & Railsback 2005). This approach to IBMs has been successful in producing robust predictions for population dynamics under scenarios of environmental change and disturbance in a range of species and applications, including the management of costal birds populations (Stillman & Goss-Custard 2010; Toral et al. 2012), aggregation of sea snails (Stafford et al. 2007), the impact of land use practices on wood mice (Liu et al. 2013) and the growth of tree species (Philips et al. 2003). IBMs have also been successfully used to describe aspects of fish population ecology, notable examples include: individual-based Stream Trout Research and Environmental Assessment Model (inSTREAM) for brown trout in North America (Railsback et al. 2009) and the roach IBMs created by Holker et al. (2002) and Holker & Breckling (2001, 2002, 2005). The latter example detailing the use of controlled bio-energetic experiments to inform an IBM of roach in a lake system, with emphasis on long-term predictions of growth and habitat choice. Finally, the MORPH framework described by Stillman (2008) has been successfully repurposed from describing growth and population dynamics of wading birds to describe similar outcomes in salmonid fish in chalk streams (Phang et al. in prep). This highlights the potential for the construction of IBMs based on the parameterisation of existing frameworks (West et al. 2011).

The complexity of IBMs can vary from simple models to very large, specific models, with complexity dependent upon the number and type of behaviours and interactions which are being modelled. The challenge is to create a model of sufficient complexity to accurately represent a complex community or ecosystem such that meaningful predictions can be made, whilst considering limitations of time, computing power and removing all unnecessary processes (Grimm & Railsback 2005). The validity of the model predictions and, therefore, the utility of the model itself, should follow a 'pattern-orientated modelling' approach. As such, model predictions and assumptions made during model construction are validated by comparison of the patterns predicted by virtual individuals against patterns observed in real populations (Grimm & Railsback 2005).

1.3 The value of freshwater resources, fish communities and fisheries

Natural resources are economically important and also provide vital ecosystem provision and services (Foley et al. 2005; Gozlan & Britton 2013). Besides being a large contributing factor in national living standards, these ecosystems provide both biotic and abiotic resources which can be exploited to further economic, cultural, aesthetic, and knowledge based markets (Dudgeon et al. 2006).

Freshwater ecosystems also represent important habitats for an often high biodiversity of plant, invertebrate and fish species. Despite representing only 0.8% of the global surface area, freshwater ecosystems contain 6% of all described species, making them biodiversity hotspots that are also often found in proximity to human activity (Dudgeon et al. 2006; Chambers et al. 2008). Freshwater systems are, however, under threat as global environmental changes cause significant impacts to ecological systems, including the widely exploited freshwater ecosystems (Walther et al. 2002). Given the demands placed on freshwater systems by increasingly large and demanding human populations, degradation in the health of freshwater systems globally is inevitable (Vorosmarty et al. 2010). Such degradation may result from a low number of broad threats, such as water pollution, habitat disturbance, altered flow regimes, over-exploitation, climate change and the introduction of invasive species (Dudgeon et al. 2006; Gozlan et al. 2006, Hogg & Norris 1991; Pinder et al. 2005; Strayer & Dudgeon 2006; Xenopoulos et al. 2005). Given the high costs and uncertain success of restoration efforts for degraded habitats, freshwater managers have been moving towards predictive and preventative approaches, in contrast to historically intuitive and reactive approaches (Zarkami et al. 2012).

Fisheries are a major provisioning freshwater ecosystem service, providing a daily food source for millions of people; with an estimated annual harvest of 14 million tonnes, freshwater fisheries are thought to employ 21 million fishermen and thus sustainable management of fish resources is vital (Gozlan & Britton 2013). Further economic activity is associated with recreational and sport fishing, generating large economic benefits (Holmlund & Manner 1999; Arlinghaus, et al. 2002). For example, in the UK, recreational fishing is thought to include 4 million regular anglers and generates £3 billion each year (Environment Agency 2004). Recreational fishing was

estimated to comprise 30 million days fished in 2005 by registered fishermen in the UK. Of this time, 88% was spent coarse fishing (a general term for the exploitation of mainly species of the Cyprinidae family), with the rest spent game fishing (when fishes of the Salmonidae family are exploited) (Mawle & Peirson 2009). When coarse fishing, a highly popular species for exploitation by anglers is roach *Rutilus rutilus*, especially in lowland rivers (Wintle 2011). Typically dominant in the fish community, they are a generalist species that tend to thrive in rivers which have been subjected to habitat alterations and nutrient enrichment, i.e. heavily modified rivers (Cowx & Broughton 1986).

1.4 The ecology of heavily modified lowland rivers

In comparison to upland rivers and streams, lowland rivers are generally warmer with reduced flow rates and increased turbidity, have greater proportions of fine sediment and have larger wetted-widths. They are also characterised by low hydraulic gradients and the relatively flat topography of the surrounding land (Schmalz et al. 2008). Lowland rivers are commonly found in areas with shallow groundwater, leading to intensive groundwater-river water interaction, with the natural, higher water balance being reduced by the construction of ditches, drainage pipes, canalisation and the alteration of river courses to become wider, deeper and straighter (Schmalz et al. 2008). In lowland rivers, the species of fishes, invertebrates and plants that are encountered tend to be more suited to reduced oxygen levels, and they tend to have broader temperature tolerances compared to species encountered in more upland rivers (Harper 1990; Downs & Thorne 2000). Many lowland rivers in Europe and the UK have been significantly influenced by anthropogenic activities, such as water abstraction, dredging, flood protection activities, inter-basin water transfer, land drainage and the construction of weirs and dams (EEA 1999; 2006). When such activities substantially alter natural conditions the water body is given the designation of 'artificial' or 'heavily modified' (EEA 1999; 2006). It is recognised that in many cases the societal benefits of the modifications needs retaining and so any alterations to the river processes, including river flow, species migration and transport of particulate material downstream, must be mitigated for but ultimately accepted (Acreman & Ferguson 2010).

Despite the impact of human activities on lowland rivers, they are still capable of supporting high densities and biomass of plant, invertebrate and fish species. In UK

lowland rivers, in-stream macrophytes are usually dominated by water lily (*Nuphar lutea*), common reed (*Phragmites australis*) and burreed (*Sparganium erectum*) which can grow sufficiently to affect local hydrology (Dawson 1989). Macrophyte growth is seasonal and coincides with key periods in the life-history processes of invertebrates and fish, which use in-stream macrophytes as sources of food and as refuges from flow (Harrod 1964; Merritt et al. 2010). The plants also provide cover from aquatic and terrestrial predators (Savino & Stein 1989; Brabrand & Faafeng 1993). Lowland rivers also contain a relatively high biodiversity of macro-invertebrates (Peterson 1962; Kaenel 1998; Bosco Imbert & Perry 2000; Wharton et al. 2006), with these invertebrates found occupying the both the riverbed substrate in association with aquatic macrophytes and the water column where they are present as drift (Brittain & Eikeland 1988; Peterson 1962; Kaenel 1998). Such drifting invertebrates can be of aquatic or terrestrial origin, with the terrestrial invertebrates entering the water column as a result of falling into the river, often from riparian vegetation or due to dispersal behaviour (Mason & Macdonald 1982; Adis & Junk 2002). Invertebrates of aquatic origin are found in or on the riverbed substrate, with a proportion of these entering the water column as drift; a result of either intentional dispersal behaviour or from being dislodged by water currents (Wilzback et al. 1988; LeRoy-Poff et al. 1991). Invertebrate drift density varies across different habitats as habitat characteristics influence the immediate invertebrate community and the movement of drifting invertebrates (Peterson 1962; Hemsworth & Brookers 1979). There is also temporal variation, with increased drift at dawn and dusk (Brittain & Eikelan 1988).

For an abundant lowland river fish species such as roach (Section 1.3), which are large enough to predate upon invertebrates, these benthic and drifting species represent a rich food source. The generalist diet and foraging behaviour of roach means they tend to target benthic invertebrates in the substrate rather than drift feeding as per species such as dace (*Leuciscus leuciscus*) (Hellawell 1974; Mann 1974) and species of the Salmonidae family (Railsback & Harvey 2002). Smaller roach (below 15 cm; (Papageorgiou 2006)) are less likely to predate upon benthic invertebrates as they are limited by gape-size and the increased energetic costs associated with foraging for macro-invertebrate prey (Mann et al. 1997; Hjelm et al. 2003). Therefore, these smaller roach are expected to consume a mix of zooplankton, plant matter and detritus (Mann et al. 1997; Hjelm et al. 2003). Consumption of zooplankton takes place through filter

feeding and as such, the intake rate is controlled though flow rate and gill-raker spacing (Van Den Berg et al. 1994). Compared to feeding on zooplankton, plant matter and detritus are relatively poor dietary energy sources and would normally be consumed incidentally in association with both filter feeding for zooplankton and targeted consumption of benthic invertebrates (Persson 1983).

Besides roach, lowland rivers in the UK also support a wide range of other species of the Cyprinidae family including dace (*Leuciscus leuciscus*), chub (*Leuciscus cephalus),* bream (*Abramis brama),* rudd (*Scardinius erythropthalmus),* tench (*Tinca tinca*) and gudgeon (*Gobio gobio*). The predominant aquatic predators are pike (*Esox Lucius)* and perch (*Perca fluviatilis),* which are predators of nearly all other lowland river fish species, subject to individual size limitations (Nilsson & Bronmark 2000; Dorner & Wager 2003).

1.5 Management and threats to heavily modified lowland rivers, and the Water Framework Directive

The biodiversity of even heavily modified rivers remains under threat from ecosystem stressors associated with anthropogenic activities that seek to further exploit provisioning ecosystem services (Dudgeon et al. 2006). As such, river managers face a conflict between stakeholder interests, human ecosystem services provision and biodiversity, especially in relation to assessment of ecosystem health (Degerman et al. 2007; Noble et al. 2007). Their fish communities, dominated by cyprinid fish generally and roach specifically, have high value for recreational fishing (including the economic value of riparian fishing rights) and also are important from the perspective of being relatively abundant secondary and tertiary consumers within lowland river food-webs (Holker et al. 2002; Bogacka-Kapusta & Kapusta 2007). Consequently, fishery managers seek to maximise the number of fish available for exploitation, as this should assist anglers being satisfied with their angling experiences. Given the importance of excellent recruitment for ensuring strong year-class strengths in roach cohorts and thus abundant populations in subsequent years (Mills 1981; Bystrom & Garcia-Berthou 1999; Nunn et al. 2003), river management practices should seek to promote juvenile roach recruitment, with this often being heavily influenced by their growth during early life stages where larger fish at age 1 year recruit more strongly (Nunn et al. 2010). Instead, however, the principal river management practices that are used in UK lowland

rivers tend to have the contrary effect. For example, the removal of in-stream macrophytes ensures channel navigability, and reduces siltation and flood risk, increases juvenile roach mortality and reduces their growth, negatively affecting the recruitment strength of the cohort (Garner et al. 1996; Nunn et al. 2010; Beardsley & Britton 2012). Consequently, in UK lowland rivers, there remains an outstanding requirement to better understand this apparent conflict between river management and fishery management to ascertain whether there are alternative approaches that could achieve more beneficial outcomes for both management perspectives.

This conflict in river management arises through issues such as the purposeful reduction in in-stream macrophytes also reducing the important egg-laying and nursery habitat occupied by larval and juvenile cyprinid fishes, increasing their risk of downstream displacement from increased flows, starvation through lack of food and predation through reduced refugia (Mills 1981; Copp 1997b; Nunn et al. 2003, 2007). Minimising the deleterious effects of these activities may be achieved through reducing the amount of macrophyte cutting and removal from water bodies. However, a compromise must be reached between maintaining or restoring ecological potential of the aquatic communities and the wider socio-economic considerations. The main potential compromises are to be found in the extent, timing or mechanism of macrophyte removal. Different patterns of macrophyte removal have been suggested to minimise the impact of management regimes on juvenile fish. Each relates to a reduction in the total amount of macrophytes removed in various patterns, for example, Garner et al. (1996) suggested only removing macrophytes from one side of the river, with this alternating each year. It has also been suggested to leave a small number of heavily vegetated areas, individual plants, or off-channel areas, solely as refuge or nursery habitats for juvenile fishes (Dawson & Haslam 1983; Copp 1997a,b). In terms of reduced management impacts through altered timings, it was suggested by Nunn et al. (2003) to only commence management schemes once the initial growth period of juvenile fishes was completed. By allowing more time for growth and development, juvenile fish would then be less vulnerable to both high flow rates and predation when the macrophytes are removed (Garner et al. 1996; Nunn et al. 2003). Finally, alternate mechanisms for controlling macrophyte density may be implemented, including influencing plant growth rates, for example by controlling direct sunlight and shade by altering riverbank height. Such factors can directly alter in-stream macrophyte cover,

providing an alternative or complimentary system to direct removal of macrophytes (Dawson 1979; Dawson 1989).

The other commonly enforced river management practice in UK lowland rivers is the regulation of river flow. Potential aims include reducing flood risk during periods of high flow and maintaining flow in connected systems during periods of low flow (Acreman & Ferguson 2010), or to divert water through hydropower schemes (Cowx & Gerdeaux 2004). In lowland rivers, flow is a major determining factor of the quality of physical habitat and this influences the abundance and distribution of aquatic communities, as well impacting the lateral and longitudinal connectivity of the river (Bunn & Arthington 2002). Indeed, lateral connectivity is particularly important in the provision of nursery areas for juvenile cyprinid fishes (Gregg & Rose 1985; Stromberg 2001). Flow rates can also affect fish directly through altered bioenergetic costs associated with swimming or keeping station (Ohlberger et al. 2006; Liao 2007). There is also the risk of displacement under periods of high flow, with smaller, juvenile fish being more vulnerable than adults (Mann & Bass 1997). Increased river discharge is also associated with increased turbidity (Goransson et al. 2013) which may impact foraging behaviour (Diehl 1988). Therefore, river managers ought to consider the potential impacts on river ecology and fish communities of flow rate regulation, either as a product of direct control over river discharge, or as a result of in-stream macrophyte removal (Garner 1996). As with macrophyte removal, negative consequences associated with changes to flow rate, especially acute increases in flow, could be mitigated though the use of refuge areas, by considering the timing and life-stages of fish, and by limiting maximum flow rate intensity and duration, informed by knowledge of its potential impacts (Mann & Bass 1997; Sagnes & Statzner 2009; Beardsley & Britton 2012).

The Water Framework Directive (WFD) is European Union legislation that centres on the status of water bodies, including transitional, costal, surface waters and groundwater (EU 2000). The WFD differs from other water policy legislation in that its assessment and focus is on 'ecological status'. Water bodies are assessed and given a rating using a five tiered system from High (undisturbed) to Bad (relevant biological communities absent). Member States are required to enhance and restore surface water bodies to at least Good ecological status (one below High) or suffer penalties deemed to be effective, proportionate and dissuasive (EU 2000). Those surface waters that are

interpreted as being sufficiently altered by anthropogenic activities that their restoration is not feasible - or even possible due to overriding socio-economic factors - are termed 'heavily modified'. For these surface waters, the WFD requires Member States to ensure they attain their maximum ecological potential.

The assessment methods used to monitor WFD compliance are based on three biological quality elements: biological, hydromorphological and physico-chemical. Of the biological quality elements, ecological status is assessed by surveillance of phytoplankton, other aquatic flora, macroinvertebrates and fish. However, in reality, it is often the case that only the biological quality element considered the most sensitive is monitored in a water body (Hatton-Ellis 2008). The fish faunal ecological assessments are based on assessment metrics that have been selected through their significant relationships between impact and increased human disturbance, usually in the form of a clear gradient of change (Schmutz 2004; Pont, et al. 2007; Schmutz et al. 2007). These assessment metrics are recorded at the site under investigation and then compared against pristine reference sites (type conditions). For example, where there is deviation away from the type-specific species and their predicted abundances in relation to their habitat, then ecological status is likely to fail and require remediation (Pont et al. 2007; Schmutz et al. 2007). Finally, abiotic variables are also recorded to ensure an accurate, type-specific comparison between the sites (Pont 2007). The metrics of the presence of type-specific species and their abundance in a site are crucial in determining fish ecological status. Thus, even in heavily modified surface waters, such as a managed lowland river, efforts are required to ensure that important species within the fish community are managed effectively, such as through ensuring habitat is available for each life-stage (for example, nursery areas for larvae and juveniles) and process (for example, areas suitable for species' reproduction). Where river management schemes impact upon fish population processes, such as recruitment, then this will affect subsequent population abundances and so potentially, the ecological status outcome for the fish community.

1.6 Project aims, model species, study site and objectives

1.6.1 Project aim

The research aim is to develop an individual based model with the ability to predict how a model fish population in a heavily modified lowland river responds to different scenarios of river management, centred on flow regulation and macrophyte control. The model will be developed, tested (validated) and then used to predict the outcomes of the scenarios on specific aspects of the model fish population that will be associated with key population processes, especially recruitment.

1.6.2 Model species

Given the potential use of predictive IBMs to ecosystem managers and their record of successful application to a wide range of actual ecosystems (Stafford et al. 2007; Railsback et al. 2009; Stillman & Goss-Custard 2010; Sibly et al. 2013; Liu et al. 2013), an IBM constructed and parameterised to simulate a generalist fish, in a typical lowland UK river, would represent a useful tool for informing river managers about the potential impacts of management decisions. In most UK lowland rivers, the ubiquitous species is roach. Whilst other cyprinid fishes might be present, it is rare these will be in greater abundance or biomass (Mann 1973). Moreover, they tend to be the dominant species within heavily modified lowland rivers in the UK, as they are tolerant of relatively low quality habitat and nutrient enriched waters, certainly when compared to species such as chub and dace (Beardsley & Britton 2012). Thus, roach have high utility as an ecological indicator due to their ubiquity allied to their range of ecological niches, high functional diversity and generalist diet (Olin et al. 2010). Moreover, they are also widely distributed within European lowland river systems and due to their dominance in many freshwater systems they meet many of the high physiological and ecological information requirements for an IBM (Holker et al. 2002). Their juveniles tend to inhabit marginal waters for nursery areas as there is greater macrophyte cover and associated lower flows (Garner 1996; Holker et al. 2002), providing refugia from predators and high flows, while also ensuring easy access to important food items such as algae and zooplankton (Copp 1997a,b). Thus, the influence of available refugia, food supply and flow rates are important determinants of the recruitment success of these fish which in turn influence their subsequent population abundance (Schmutz 2004; Beardsley & Britton 2012). As such, the ecological status of roach is a useful indicator

of ecosystem health and the impacts of river management schemes. Consequently, roach will be the model species used to meet the research aim. In the research, where data are deficient in the literature to parameterise the IBM, such as in their functional response, then experimental work will be completed to fulfil this requirement.

Given the advantages of modelling roach populations as an indicator of ecological status, management impacts and environmental health described above, previous examples of IBMs based on roach populations exist in the published literature (Holker & Breckling 2001, 2002, 2005; Holker et al. 2002). While some of the forager parameters estimated as part of this prior work were used to describe aspects of the roach foragers in this investigation (Table 5.1), it should be noted that this was limited to the bio-energetic characteristics of roach, which are not thought to differ between populations, outside of the degree to which they vary between individuals and as a result of known environmental factors (Holker & Breckling 2002). Furthermore, this investigation differs significantly from previously described roach individual-based modelling work, and still provides novel insight, given the emphasis on the important individual outcomes of growth and recruitment of juvenile roach in a common riverine environmental setting, highlighting the impact of routinely performed current management practices during the summer growth season.

The approach used in this investigation is further supported by the annual recruitment patterns of roach populations. In lowland rivers, their populations generally tend to be numerically dominated by one or two very strong year classes (out of up to 12 to 15 year classes present) that develop as a consequence of highly favourable environmental conditions (such as warm temperatures and low flows) in their first summer of life (Mills & Mann 1985; Nunn et al. 2003, 2007; Britton et al. 2004). The importance of these year classes is that they subsequently provide high numbers of both mature fish for reproduction and for anglers to exploit by catch-and-release angling when they reach sizes above 120 mm. These year classes can also persist in the population for over 10 years (Beardsley & Britton 2012). As such, successful recruitment is vital for riverine roach population abundance and thus ensuring that the annual recruitment of juvenile roach is maximised (subject to overriding climatic controls) through increased growth and reduced mortality could be interpreted as a sensible management practice to fulfil fish-based assessments of ecological status and

quality (Copp 1997a,b; Nunn et al. 2007; Noble et al. 2007). Poorly considered management practices that reduce the year class strength of a roach cohort would thus substantially reduce the recruitment rates of roach over time (Pinder 1997; Beardsley & Britton 2012). In a summer that would otherwise produce a strong year class through its warm temperatures and low flows, it could reduce the recruitment strength of the cohort from a 'strong' to an 'average' year class; in a summer that would be predicted to produce a weak class (e.g. cool temperatures, high rainfall and higher river flows; Nunn et al. 2007) this could result in the virtual elimination of that year class. Moreover, these reductions in year class strengths represent a strong deleterious effect on roach population abundance that could have consequences for assessments of ecological status in the Water Framework Directive (Pont et al. 2007).

1.6.3 Study site

Developing an IBM requires both a species to model and a site to model that species in. The study site selected is the River Stour in Suffolk, a heavily modified lowland river in which flow is regulated and, every summer, the abundant in-channel macrophytes are managed through removal by a weed-cutting boat, i.e. a very non-discriminatory approach that tends to drastically reduce the amount of in-stream macrophytes present (R. Wright, personal communication).

The River Stour marks the boundary between the counties of Suffolk and Essex in South-eastern England, and centrally occupies a low plateau of chalk bedrock covered with sand and clay (Bubb & Lester 1993). The River Stour forms from a water catchment area of $578km^2$ with average flows ranging from 0.9 m^3s^{-1} in headwater streams, to 6.0m^3s^{-1} in the lower reaches (Bubb & Lester 1993). During periods of low rainfall, flows are maintained from aquifers, sewage treatment outflows and water supplied by transfer schemes. Such a transfer scheme maintains a minimum flow at Wixoe, near the study site (Section 4.3.2; Figure 4.3) of 0.3m^3s^{-1} ensuring dilution of sewage effluents and safeguarding water quality (Bubb & Lester 1993). Public access to the river at the study site is limited, meaning little disturbance to the system besides the management activities performed by the Environment Agency and Wixoe pumping station activities. More information on the study site is provided in Chapter 4.

1.6.4 Research objectives

Following the setting of the research aim and definition of both the species to be modelled and the study site in which their population will be modelled, the research objectives can now be defined. Given some of the deficiencies in data to parameterise the model, the initial objective is to fulfil this outstanding requirement, the second objective then centres on collating the field data that the model is reliant upon, and the subsequent objectives involve model development, testing and utilisation. The objectives are thus:

O1. Under controlled conditions, describe and predict functional responses of roach under different ecological scenarios (e.g. turbidity, food size) in order to provide the forager parameters for the individual based model (Chapters 2 and 3);

O2. At the field site, describe the distribution, growth rate and recruitment process of the roach population (Chapters 4);

O3. Collect, analyse and compare data describing habitat conditions, roach growth rate, population size distribution and habitat preferences at the study site with similar data from two other heavily modified lowland rivers in Eastern England to identify common population patterns and processes (Chapter 4);

O4. Through the combination of O1 and O2, in conjunction with underpinning data from literature and O3, parameterise and validate an individual based model for roach (Chapter 5); and

O5. Use the IBM from O4 to predict the response of roach populations (e.g. in growth, recruitment, distribution) to river management scenarios (flow regulation and macrophyte removal schemes) and identify their influence on fish based ecological status assessments (Chapters 6 and 7).

1.7 Thesis structure

Given these research objectives, the thesis structure provides a series of chapters that initially collate the roach data for modelling, with these data then used to develop and validate the model, before being used to test scenarios of river management. As such, the sequence of chapters has been designed to provide two distinct components of the thesis: model data collection (Chapters 2, 3 and 4), and then model development, validation and utilisation (Chapters 5 and 6). As such there is no distinct 'Materials and Methods' chapter, with each chapter providing its own self-contained method section. The chapter titles are as follows:

Chapter 1: Introduction

Chapter 2: Experimental predictions of the functional response of a freshwater fish

Chapter 3: Habitat complexity and food item size modifies the functional response of a freshwater fish

Chapter 4: Data for building the roach individual-based model, with comparison of roach habitat association and growth across three UK lowland rivers

Chapter 5: Predicting growth and distribution of roach in lowland rivers: an individual-based modelling approach

Chapter 6: Assessing the impact on growth and recruitment of aquatic macrophyte management and flow rate regime using a roach individual-based model

Chapter 7: Discussion

This sequence of chapters thus provides a series of self-contained aspects of research that, when read in entirety, should provide a coherent perspective on the development and execution of an IBM for roach in a heavily modified lowland river that has the power to predict how aspects of river management impact their populations via key processes.

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2. Experimental predictions of the functional response of a freshwater fish

The aim of this chapter is to describe the initial behavioural experiments conducted on juvenile roach, in order to better understand their foraging behaviour and help in the development of the IBM constructed and validated in Chapter 5.

2.1 Introduction

Functional response models describe the relationship between the feeding rate of a forager and its prey density (Solomon 1949; Holling 1959) and are useful in describing the foraging performance of species (Baker et al. 2010). Functional responses are important ecologically as animals under resource restrictive conditions strive to maximise their energy intake, whilst minimising the costs associated with their searching and handling of prey (Stephens & Krebs 1986; Galarowicz & Wahl 2005; Oyugi et al. 2012a,b). Conversely, *ad libitum* resource conditions promote satisfying over optimal foraging behaviour (Myers 1983, Krebs & McCleery 1984, Stephens & Krebs 1986). Measuring the differential responses of animals to varying food availabilities also provides important explanatory information underpinning the tendency and ability to optimise foraging behaviour, as well as their associated levels of condition, growth and, ultimately, fitness (Mittelbach 1981; Werner et al. 1983; Galarowicz & Wahl 2005). Functional responses also provide important insights into the dynamics of consumer-prey systems (Buckel & Stoner 2000; Nilsson & Ruxton 2004) and can have consequences for population stability as it impacts higher trophic levels through its relationship with prey availability, with cascading effects on lower trophic levels (Koski & Johnson 2002).

Foraging studies on fishes are often restricted to estimating their feeding rates, for example calculating the number of prey taken per unit time (Caiola & de Sostoa 2005; Oyugi et al. 2012a,b). In considering fish functional responses, the Type I, II and III functional responses are often described (Holker & Breckling 2001; Galarowicz & Wahl 2005; Gustafsson et al. 2010). All are based on the foraging parameters of searching rate and handling time, but differ in how these parameters are treated. The Type I functional response assumes handling time is either negligible, or that searching

and handling can occur simultaneously (Jeschke et al. 2002). This results in a linear increase in feeding rate with prey density until it reaches a constant value at saturation and has only been reported in filter feeding species (Jeschke et al. 2004). Conversely, Type II responses assume that handling time and searching time are mutually exclusive (Kaspari 1990; Baker et al. 2010), producing a feeding rate that increases at a decreasing rate with prey density as it approaches a maximum value. As such, it typically describes the foraging behaviour of a species capable of handling only one prey item at a time and in environments of reduced complexity, without the influence of factors including capture success, learned behaviour and prey clumping (Real 1977; Abrams 1990). Finally, a Type III response produces a characteristic sigmoidal response (Nachman 2006) through factors that alter the probability of detection or attack of prey items, such as learned behaviour, prey item switching, capture success or prey item clumping (Murdoch 1973; Morgan & Brown 1996).

There are functional response models available for some fish species that directly incorporate searching and handling times, such as for walleye *Stizostedion vitreum* (Galarowicz & Wahl 2005), brown trout *Salmo trutta* (Gustafsson et al. 2010) and lake trout *Salvelinus namaycush* (Barnhisel & Kerfoot 2004). The time spent searching for food may be further divided into discrete foraging parameters, such as reaction distance and swimming speed, enabling further separation of the time spent foraging at specific prey densities. For example, Aksnes & Giske (1993) and Aksnes & Utne (1997) described the importance of visual range in determining fish foraging rates and Baker et al. (2010, 2011) split searching time into several discrete behaviours in the determination of the functional response of granivorous birds. For many fish species, searching times have not been split further due to the difficulty of separating searching into its discrete behaviours at a sufficiently fine scale. This has now become much easier to achieve as videography techniques have improved, enabling efficient video capture and post-experiment analysis (Kane et al. 2004, 2005) that use reference markers to accurately estimate distances moved by the foraging fish through validation processes (Hughes et al. 2003).

Consequently, the aim of this study was to test how the Type II functional response model could predict the observed functional response of a model fish species, when parameterised using directly observed behavioural parameters and was completed

through two research objectives. The first was to validate the accuracy of measurements of distances moved by the model fish within their experimental arena (tank aquaria), in response to food item exposure. The second was to parameterise a Type II functional response model using recorded behavioural parameters and then compare it to an experimentally-obtained observed functional response to determine its accuracy. The output was then also compared with a Type I model; note a Type III response was not also tested as the experimental design precluded the development of more complex foraging behaviours that would typically lead to this response. The Type II functional response used in the study was based on the Holling's Disc Equation (Holling 1959) which has been used extensively to determine functional response curves in a wide range of animals (Goss-Custard et al. 2006).

2.2 Methods

2.2.1 Ethical note

All animal work was conducted in accordance to national and international guidelines to minimize discomfort to animals. All regulated procedures completed under the Animals (Scientific Procedures) Act 1986 were licensed by the UK Home Office under project licence number PPL 30/2626. The Ethics Review Panel of the School of Applied Sciences of Bournemouth University approved this project licence.

2.2.2 Model species

The model species was roach *Rutilus rutilus*, a visual foraging fish (Diehl 1988) of the cyprinidae family widely distributed throughout Eurasia. While components of roach foraging behaviour have been described previously, this was through estimation from a functional response, derived from field data on energetic costs and growth rate (Johansson & Persson 1986; Persson 1986; Persson 1987; Holker & Breckling 2001), rather than through direct observation as per this study. Information on their functional response has also been determined from direct observation using live prey with individual fish (Winkler & Orellana 1992), where both Type II and Type III responses were described. Thus, their use here enables refinement of their functional response parameters under controlled experimental conditions and a different prey item.

2.2.3 Experimental species and arena

The foraging experiments used 36 roach of age 1+ years, (mean total body length +SE = 129 + 2.5 mm and mean body mass + SE = 20.5 + 1.3 g) of aquaculture origin that had been raised primarily on fishmeal pellets. Following transfer to aquaria (20 litre tanks of 0.46 × 0.31 × 0.39 m; 18°C; 12:12 hour light: dark cycle), the fish were acclimatised for 35 days before being paired for initial foraging trials. In these, their foraging behaviour appeared constrained and it was only when they were held in groups of three that their behaviour return to the normal state observed at higher densities during acclimatisation. Thus, for the actual foraging experiments, the fish were randomly divided into threes and placed across 12 experimental tanks, each with a volume of 20 litres.

To minimise external visual stimuli and disturbance to the fish to promote their natural behaviour, curtains were placed around the tanks and card was taped to the side and rear panels of the tanks. The card on the rear panel of the tank was also marked with a grid of 0.01m^2 lines (Figure 2.1) that assisted distance estimation during subsequent analyses. Identification of the individual fish was enhanced through a pelvic fin-clipping process that had been completed on the fish upon their arrival to the facility for the purposes of trophic analyses (unpublished data), with the three fish per tank comprising fish with a left-clip, right-clip and no-clip. [Note fin-clipping in this manner does not adversely affect fish behaviour, survival or growth (Gjerde & Refstie 1988; Pratt & Fox 2002).] To facilitate measurement of the distances moved by fish during experiments and to record growth over the experimental period; weight and total body lengths were measured every two weeks throughout the study. To test the changes in length and weight of the fish over the study period, only their initial and final data were used, however, to prevent pseudo-replication (Hurlbert 1984).

2.2.4 Video capture and validation of fish movement data

The foraging experiments were captured using a combination of two digital SD video cameras (Panasonic SDR-S26), with the video files subsequently transferred to a personal computer in .wmv format (640 × 480 pixels, variable bitrate at 25 frames per second). These cameras were attached to a movable frame that ensured their position, relative to one another, was consistent across all the experiments and tanks. One camera was positioned horizontally, facing the only uncovered side of the tank, with the second camera positioned vertically, above the surface of the water. Both cameras were

positioned at a distance of approximately 16 cm in the front of the tank and from the surface of the water. The movable frame was positioned so as to ensure the cameras were parallel with the pane of the tank and surface of the water, and that the entire tank was visible during each foraging experiment (Figure 2.1).

To subsequently analyse the video footage from both cameras, a purpose-built event-logger program (Event; Bournemouth University 2012) was used that allowed frame-by-frame viewing and recording of the on-screen position from the horizontal and vertical pixel count. The video footage from both cameras was also edited to place the vertical footage above the horizontal and rendering them together into a single file. The pixel co-ordinate information then enabled the position and movement of the fish to be determined in the tank. As fish movement was not always parallel to the horizontal camera, the angle of movement was considered by reading the angle of movement from the footage recorded on the vertical camera. This was expressed in degrees away from a direct across screen movement, i.e. 0° would be parallel to the front pane of the aquarium and directly across the screen when viewing footage from the horizontal camera (*cf.* Figure 2.1). The actual position or distance travelled by the fish was then calculated using trigonometry from the apparent position or distance travelled (horizontal camera) and angle of movement relative to the front pane of the aquarium (vertical camera).

This system was used to determine fish positions and distance of movement from pixel co-ordinates using two methods. The first was to relate the number of pixels to the $0.01m^2$ grid pattern printed on the card on the rear of the tank, that allowed the observed distance in pixels to be described in centimetres. The second was to compare the number of pixels from apparent distance to the number of pixels that make up the length of the fish. As the body length of the fish was known from their regular biometric measurements, this enabled conversion of pixel co-ordinates into cm. These methods were tested for accuracy by analysing video footage of the movements of an artificial 8 cm roach that was moved across 60 randomly assigned distances (5 to 45 cm) and angles (0 to 90°) by an independent operator. These were analysed in a blinded manner and the two different methods for estimating distance were compared to the known distance using linear regression. The most accurate method was identified by its lower value of the Akaike Information Criterion (AIC).
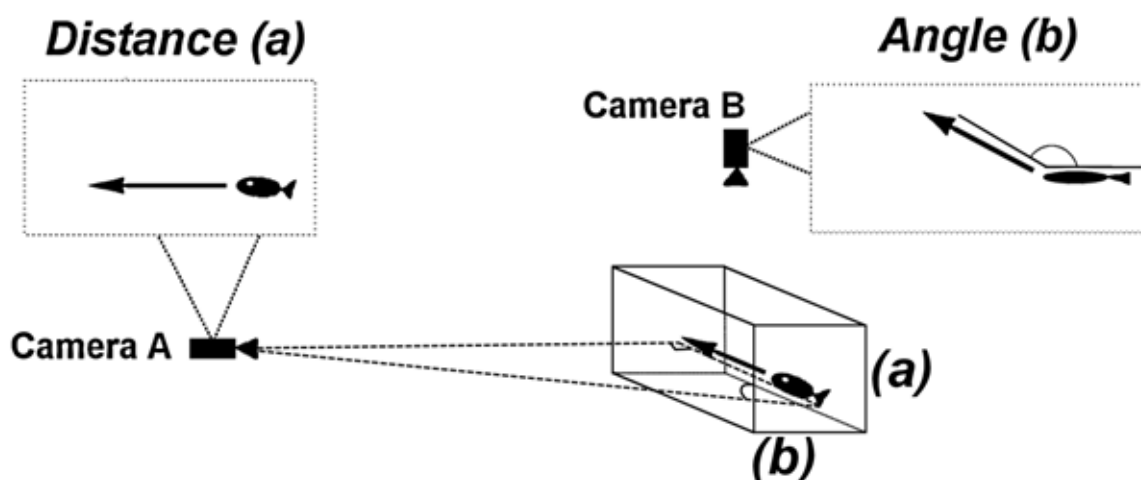
Figure 2.1 The experimental set up of cameras for estimating actual from apparent movement distance or position, where the horizontal camera (A) produces the apparent values *(a)* and the vertical camera (B) allows estimation of the actual values by providing information on angle of movement *(b)*. The estimated distance *(c)* is calculated using the trigonometric formula $c = a/cos\ b$.

2.2.5 Experimental design and data analysis

The experiment required two aspects of data collection from the video footage; (i) feeding rates of the fish at different food densities (**observed functional response**); and (ii) data on reaction distance, swimming speed and handling time of each fish in relation to food density, to enable parameterisation of the Type II functional response model (**predicted functional response**). Throughout the experiments, the food used was fish meal based pellets (1 mm diameter) as per their food source at the culture site. Moreover, cyprinid fish tend to respond well to fish-meal pellets in foraging experiments in tanks (Britton et al. 2012; Oyugi et al. 2012a,b). The foraging experiments were completed on alternate days, feeding on the day in between was on a daily maintenance ration of approximately 1.5 % body weight (approximately 75 pellets) that was calculated in accordance with the fortnightly weighing of the fish, with maintenance used rather than *ad libitum* to ensure feeding motivation on the experimental days, given that functional responses relate to optimal foraging. Thus, feeding on experimental days occurred 24 hours after the last exposure to the maintenance ration. It comprised of exposing a tank of roach to one randomly selected food density from 10, 25, 50, 100 or 150 pellets per tank, equivalent to 75, 187, 375,

750 and 1125 items m^{-2} respectively. Food items were introduced to the tank by being spread evenly over the surface of the water, after which they sank through the water column and settled on the bottom of the tank. On the release of the food, the filming of the foraging behaviour commenced for five minutes (Oyugi et al. 2012a,b). At the end of this period, all uneaten food was removed immediately using a siphon.

Each food density was used in every tank on two occasions, providing the potential for 72 individual data points per food density. In practice, the number of data points per food density was lower, as each experiment did not always produce three fish for each tank that displayed the foraging behaviours required to estimate reaction distance, swimming speed and handling time. In such cases, these fish were omitted from the analyses, reducing the available data. Furthermore, to reduce the effects of depletion at the lowest food density only the first fish to feed was considered in the analysis. In the video analysis, feeding rate was recorded during the time between the fish taking its first and fifth food item, and expressed as the number of items consumed per second.

To determine the observed functional response, the mean feeding rate was expressed as a function of food density. To predict the functional responses from foraging parameters, the video footage was analysed to estimate: (i) swimming speed (s) whilst searching for food, characterised by relatively slow swimming, with frequent changes in body orientation and leading to food item capture; (ii) reaction distance (d), determined as the distance a fish would travel in a straight line directly towards a food item, quickly followed by capture of the food item, often following a change in body orientation towards the food item; and (iii) handling time (h), determined as the time taken to move towards and consume a food item, and then be ready to consume a further food item. Handling time was determined on occasions when food items were captured in rapid succession and when no other behaviour was observed between food item capture.

These parameters were used to parameterise the Type I and Type II functional response models:

The Type I model was:

$$F = \begin{cases} aD & \text{if } D \leq \dfrac{1}{ah} \\[2ex] \dfrac{1}{h} & \text{if } D > \dfrac{1}{ah} \end{cases} \qquad \textbf{(Eqn 2.1)}$$

The Type II model was Holling's Disc Equation (Holling 1959):

$$F = \frac{aD}{1 + aDh} \qquad \textbf{(Eqn 2.2)}$$

Where F = feeding rate (items s^{-1}), a = searching rate (i.e. search area per unit time) (m^2 s^{-1}), D = food density (items m^{-2}) and h = handling time (s) (Holling 1959).

In both cases a was defined as:

$$a = 2ds \qquad \textbf{(Eqn 2.3)}$$

Where s = swimming speed (ms^{-1}) and d = reaction distance (m). This equation assumes that fish consumed prey on the bottom of the tanks and detected prey at up to twice the observed reaction distance i.e. the fish can search over the same distance on either side around their search path, multiplied by the distance travelled. Thus, a was derived directly from the foraging behaviour parameters. This is an approach frequently used to describe searching rate in birds (Baker, Stillman & Bullock 2009) but not before in fish. Note that 'searching rate' also includes the success rate of a predator capturing prey. Typically, Type I and Type II functional responses include probability of discovery (i.e. of detecting prey) but here the probability of discovery was equal to 1 so was omitted. Equation 2.3 describes fish as searching for prey in two dimensions, although the recorded foraging behaviour enabled description of movement to be measured in three dimensions. A simplified approach was used as this reflected the

foraging behaviour of the fish as they generally consumed food items only once they were on the tank bottom. Meanwhile h was measured directly from video footage. As per Hjelm & Persson (2001), the data were combined from across all of the fish to parameterise the above equations, rather than predicting a functional response for each individual fish. The rationale for this was that at the individual level, there was often a low number of data points per fish resulting from, for example, only one fish being used per tank at the lowest food density.

To quantify the ability of these parameters to predict the functional response, they were used in Equations 2.1, 2.2 and 2.3, with the predicted Type I and Type II functional responses compared to the observed functional response. The parameters were also directly compared to previously described behavioural parameters for roach (Persson 1987). All statistics and testing was completed in R (R version 2.12.2) (R Development Core Team 2011).

2.3 Results

2.3.1 Validation of data from video capture

Both of the methods for converting pixel co-ordinates into actual distances accurately estimated the distances moved by the artificial fish, independent of the angle and distance moved (Figure 2.2). Significant relationships were obtained between known and estimated distances for both the grid (linear regression: adjusted $R^2 = 0.84$, $F_{1,56} = 315.1$, $P < 0.01$) and body length method (linear regression: adjusted $R^2 = 0.51$, $F_{1,56} = 62.2$, $P < 0.01$). Akaike's Information Criteria indicated that the grid method provided the most reliable estimates of distance moved (AIC: grid: 83.5; body length: 149.9) and so was used for all subsequent analyses.
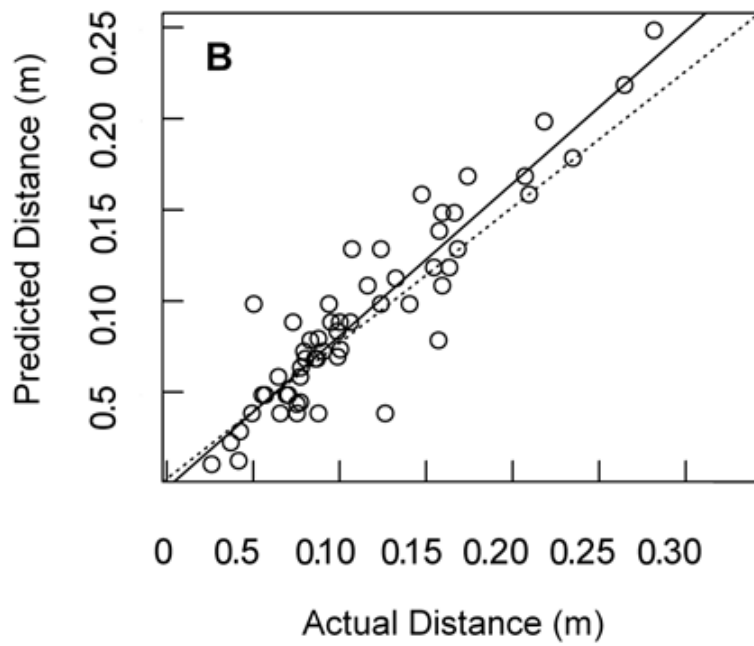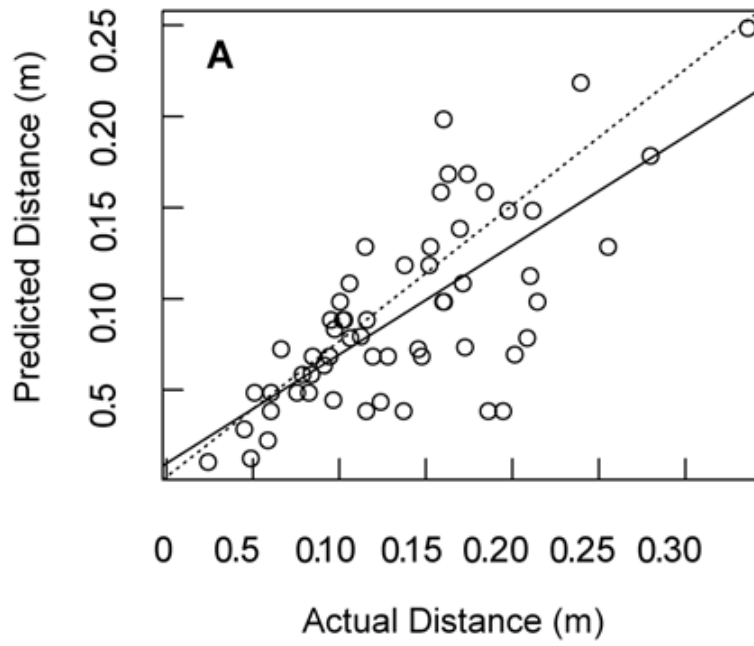
Figure 2.2 Relationships between actual and estimated movements of an artificial roach comparing the output of (A) the number of pixels moved to number of pixels in body length; and (B) the number of pixels moved to number of pixels in 0.01m^2 grid. Solid Lines are fitted Linear Regression equations; Dotted lines are 1:1 relations between estimated and actual distances.

2.3.2 Fish length and body weight over the study period

The two-weekly measuring and weighing of the fish over the study period revealed minimal growth in the fish. Comparison of their initial and final lengths and weights also revealed that no significant increase in length or weight had occurred (paired t-tests: length $t_{1,35}$ = -1.269, P > 0.05; weight: $t_{1,35}$ = 3.296, P > 0.05).

2.3.3 Functional response

Of the functional response parameter values, handling time (Figure 2.3A) and swimming speed (Figure 2.3B) showed no overall relationship with food item density, and whilst reaction distance (Figure 2.3C) showed some indication of a negative relationship with food density, this was not significant (handling time: adjusted R^2 = -0.01, $F_{1,161}$ = 0.78, $P > 0.378$; swimming speed: adjusted R^2 = -0.02, $F_{1,37}$ = 0.01, $P > 0.917$; reaction distance: adjusted R^2 = 0.16, $F_{1,14}$ = 3.91, $P > 0.067$). As handling time and swimming speed did not change significantly with food item density, these parameter values were derived from data collected at all experimental densities. Conversely, although reaction distance was not significantly related to food density, there is reason to expect that reaction distance will decrease with food density as more food items are likely to be closer to the fish, as per experiments in birds (Stillman & Simmons 2006; Smart et al. 2008; Baker, Stillman & Bullock 2009; Baker et al. 2011). Thus, at higher densities, reaction distance is likely to be underestimated as fish forage optimally by moving to food items well within their maximum reaction distance. Therefore the reaction distance parameter value was derived from data collected only during feeding experiments at the lower three of the six food item densities.
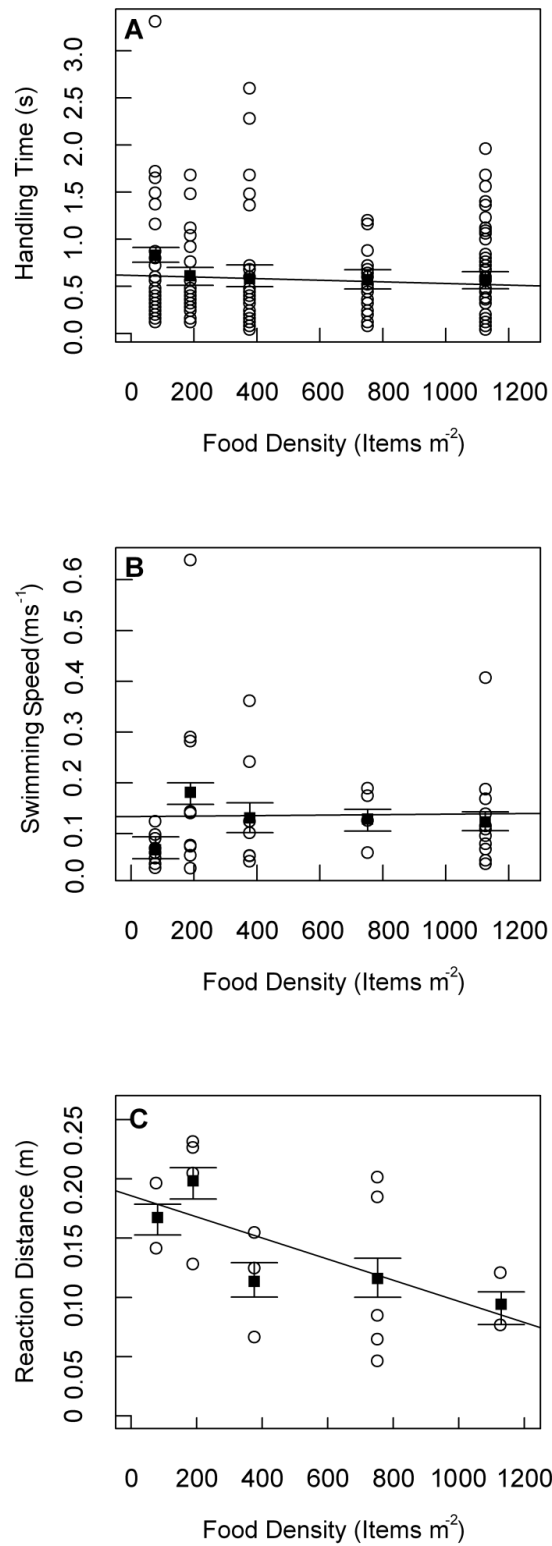
Figure 2.3 Observed relationships between behavioural parameters and food density for (A) handling time; (B) swimming speed; and (C) reaction distance. Open circles are observed values, while filled squared are means for each food density with associated 95% confidence intervals.

The observed functional response of the roach was best described by a Type II functional response. The feeding rate significantly increased at a decelerating rate with increasing food density (adjusted $R^2 = 0.94$, $F_{1,3} = 48.22$, $P < 0.01$; Figure 2.4). The lowest feeding rate was measured at the lowest tested food density, with this then increasing almost fivefold at the highest food density (Figure 2.4). The increase in foraging rate between the food densities of 75 and 750 m^{-2} food density was significant (linear regression adjusted $R^2 = 0.95$, $F_{1,3} = 13.39$, $P < 0.05$), with the rate then decelerating to 1125 m^{-2} (Figure 2.4). The observed parameters of searching rate, reaction distance and handling time were then fitted to Equations 2.1, 2.2 and 2.3 to obtain the predicted functional response. The predicted Type II functional response provided a strong fit with the observed across all food densities (RSS +SE = 0.0002+0.00781, $P < 0.05$; Figure 2.4). A mean value for handling time (h) was observed at 0.605 seconds, compared to 0.75 ($\pm$ 0.19) reported by Persson under similar artificial conditions and temperature (18ºC). A one-way ANOVA showed no significant difference between the values of handling time ($F_{1,165} = 0.230$, $P = 0.632$). Similarly the value of searching rate (a) (equal to instantaneous search rate or attack coefficient as reported in Persson 1987) was calculated at 4.45 in this study based on direct observation of swimming speed and reaction distance (Eqn 3), compared to a value of 5.10 ($\pm$ 2.41) reported by Persson. This is again reflected in a one-way ANOVA showing an non-significant difference between the values ($F_{1,2} = 1.256$, $P = 0.379$).
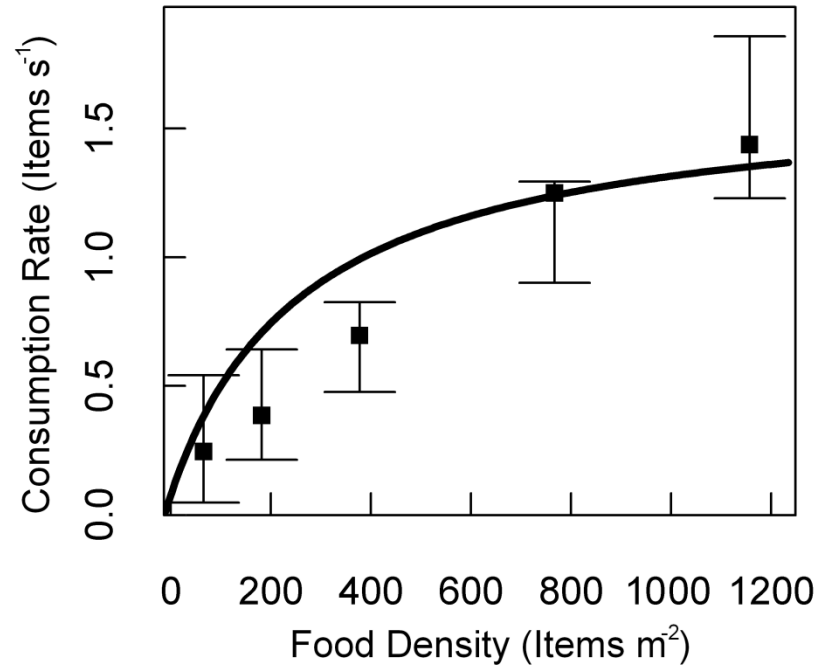
Figure 2.4 Comparison of observed and predicted functional responses, showing mean observed feeding rates (filled squares; 95% confidence intervals) and the predicted functional response (solid line).

Given the significant increase in foraging rate at the lower food densities (Figure 2.4), the Type I and II functional responses were then compared (Figure 2.5). This revealed that the predicted Type I functional response was a poor fit compared with the observed functional response (adjusted R^2 = 0.12, $F_{1,3}$ = 1.59, P > 0.05) as it overestimated consumption rate over most food densities (Figure 2.5). It was also a poor fit of the data when compared to the Type II predicted functional response, as reflected in the relative goodness-of-fit of the models versus the observed, where the lowest AIC was in the predicted Type II (AIC = -941.98) compared to the predicted Type I functional response (AIC = -560.79).
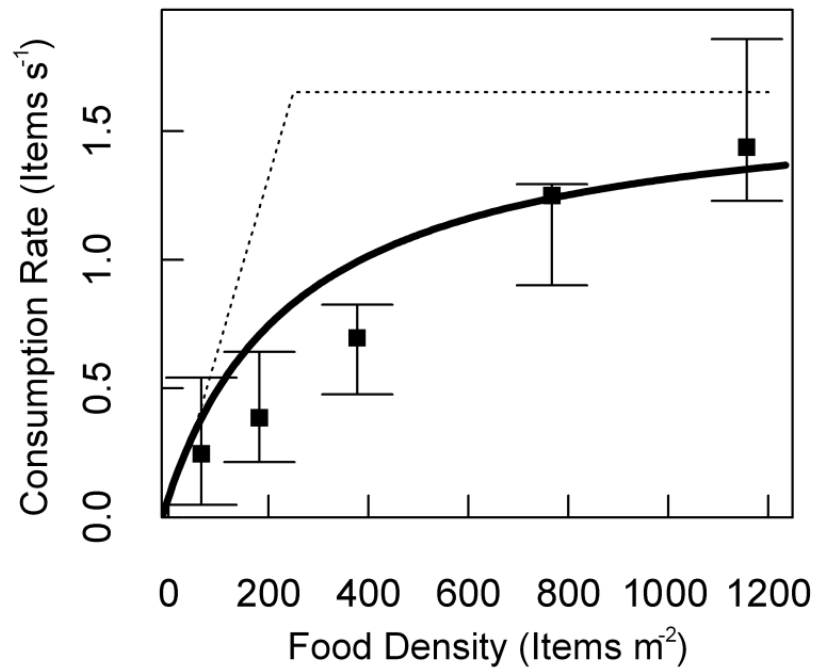
Figure 2.5 Comparison of observed and predicted functional responses, showing mean observed feeding rates (filled squares; 95% confidence intervals) and the predicted functional responses (Type II solid line and Type I dashed line).

2.4 Discussion

The study demonstrated that the foraging behaviours of a visual foraging fish could be measured under controlled conditions and, through analysis of their behaviour in three dimensions, their distance of movement and swimming speeds were accurately estimated. This enabled handling time, swimming speed and reaction distance of the fish to be estimated in relation to their exposure to different food item densities and enabled parameterisation of a Type II functional response model (Holling's Disc Equation). This predicted functional response matched the directly observed functional response, and was shown to be superior to the Type I functional response model.

Holling's disc equation assumes that at high food densities, the feeding rate is limited by the handling time of the individual rather than the time taken to locate food (Baker et al. 2010). Whilst this appeared true in the roach of this study, other studies have shown this is not always apparent. For example, Caldow & Furness (2001) described kleptoparasitic behaviour where handling time was seen to vary with host abundance. Moreover, as food density increases, an increase in food selectivity may also be observed. Individuals may selectively targeting only the most attractive food items, reducing the number food items consumed per unit time with a trade-off of an increase in food quality (Magnhagen & Wiederholm 1982). Another effect of increased food density is the confusion effect, whereby excessive numbers of evasive prey can reduce attack rates and/or capture efficiencies, especially in cases of visual predators with mobile prey (Ioannou et al. 2007; Tosh et al. 2009). Similarly, the rate at which the digestive system can process food may also be below that determined solely by the handling time (Jeschke et al. 2002). In the current study, however, handling time did appear to determine the asymptote of the functional response. This may be related to the food item being a pellet of consistent size and quality, and so selectivity with food item density was negligible. Similarly, there would be the absence of a confusion effect as the food items lacked evasive behaviour or mobility. Furthermore, as the foraging experiments ran for a maximum of five minutes, there was little opportunity for individual fish to be satiated. Indeed, some recordings showed some of the fish going on to consume over 10 food items within the 5 minutes. Thus, the short-term functional response of roach was described here, rather than the longer term, daily functional response when time is also allocated to non-feeding activities (Mills 1982; Henson &

Hallam 1995). In addition, the non-significant increases in fish length and weight over the study period confirmed their feeding regime was a maintenance diet and, thus, their behaviours would have been optimal foraging behaviours rather than feeding to satisfaction as per feeding *ad libitum* (Myers 1983, Krebs & McCleery 1984, Stephens & Krebs 1986).

Reaction distance (*d*) was defined here as the distance a fish would travel in a straight line directly towards a food item, immediately before its capture. It was uncertain at the start of the study as to whether this type of behaviour could be measured with sufficient accuracy. However, during the video analysis, a clear change in behaviour was observable in each roach when moving towards a food item that aligned to the *d* definition. Applicability of this method to other fish species is dependent upon the foraging behaviours of the fish concerned. In the wild, roach tend to be zooplanktivorous and herbivorous (Garcia-Berthou 1999) and their feeding rate appears to be very low when compared to species such as common carp *Cyprinus carpio* (Oyugi et al. 2012a,b). Thus, roach behaviours tend to be relatively easy to observe and interpret as they are relatively slow and deliberate. For fish species such as walleye, for which functional response data is available (Galarowicz & Wahl 2005), their piscivorous feeding may mean their reaction distance is much more difficult to interpret, as their foraging strategy is likely to be quite different (e.g. ambush predation). Similar issues have been noted in determining the reaction distance of different bird species (Caldow & Furness 2001; Stillman et al. 2002). Alternatives exist, for example, estimating reaction distance can be completed by correlating reaction distance with time, the number of paces or by being estimated from their general behaviour (Stillman & Simmons 2006).

When fish forage optimally, their reaction distance may decrease with higher food densities. This was not, however, observed here although this may relate to low statistical power due to the sample sizes used. With increased power, this relationship may be significant, either as a linear or non-linear relationship. Thus, future work should consider greater replication, although this should be in the number of individual fish and tanks used rather than repeated measures of the same fish to avoid pseudo-replication (Hurlbert 1984). Increasing the number of individuals used in experiments may also be useful given that optimal foraging behaviour has been shown to have a

significant heritability coefficient (Morris & Davidson 2000; Gibbons et al. 2005). Consequently, this provides high potential for individual variation in foraging parameters that are ultimately linked to fitness. The constraints of sample size already outlined prevented the prediction of individual functional responses here that might have revealed this individual variability and so increasing the sample size should be considered in future studies.

The functional response of other animals may display increased complexity including different foraging behaviours that were not considered in this study, such as the influence of interference competition (Elliot 2003; Vahl et al. 2005) and the trade-off between vigilance and foraging (Baker et al. 2010; Bartosiewicz & Gliwicz 2011). Habitat structure may also impact foraging behaviour and thus the functional response In both aquatic and terrestrial environments, macrophyte cover may influence food item visibility and/ or movement costs (Butler et al. 2005; Stillman & Simmons 2006). Consequently, considering the predicted functional response of roach in more complex experimental systems, or more natural systems, may require measuring and accounting for other factors that influence their foraging, such as water turbidity and temperature, prey types and predation pressures. This would enable the prediction of foraging outcomes in relation to environmental and biological changes, in situations where direct observation was not possible. The degree to which these influencing factors can be investigated depends upon how they may be replicated under laboratory conditions, although both water turbidity (Vollset & Bailey 2011) and temperature (Oyugi et al. 2012a,b) effects should be feasible in the current system.

The functional response of roach has also been previously described as a Type II functional response, based on an estimated functional response using data gathered on metabolic costs and food availability in a eutrophic lake system (Johansson & Persson 1986; Persson 1987). The functional response of roach from direct observation has also been previously described (Winkler & Orellana 1992), although this was based on zooplankton feeding experiments with individual fish, rather than groups of three as per this study. In that study, a Type III response was described, (Winkler & Orellana 1992), a likely consequence of the evasive behaviour of the zooplankton prey and the developing of searching behaviours in the fish. Here, a Type II response was the best fit of the foraging data, suggesting that the functional response of roach is context

dependent and reinforces the requirement to develop complexity into functional response experiments

Recording and measuring behavioural movements on a small scale is often necessary but can be prohibitively expensive, requiring specialist hardware or software (Gingras et al. 1998; Delcourt et al. 2006). Furthermore, this type of videography often relies upon reference markers which may influence a subject's behaviour, limit the scope of the investigation or be avoided altogether (Hughes & Kelly 1996). Previous work on terrestrial organisms which rely upon recording pace length (Poole et al. 2006) for measuring d assume that this is constant or, as in the case of fish, cannot be measured at all (Stillman et al. 2002). The use of single camera systems also precludes description of distances in all planes of movement (Laurel et al. 2005). The methods described in this paper however, overcame these issues. The software used is freely available and was user-friendly. When using the grid lines as reference markers, the system was unobtrusive and avoided having to use fish lengths as a way of measuring distances. Movement and position was also described in all planes using a simple two-camera videography system. Thus, by using manual over automated analysis, the foraging behaviour of roach was able to be quantified using more rigorously defined behavioural parameters than previously.

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3. Habitat complexity and food item size modifies the functional response of a freshwater fish

The aim of this chapter is to describe further behavioural experiments conducted on juvenile roach, in order to better understand the impact of abiotic factors on foraging behaviour and to help with the development of the IBM, constructed and validated in Chapter 5.

3.1 Introduction

The functional response is the relationship between the feeding rate of a forager and its prey density, and is used to describe and model foraging behaviour (Solomon 1949; Holling 1959; Holling 1966). It is an ecologically important metric as under conditions of limited resource availability, individuals will attempt to maximise their energy intake whilst minimising the costs associated with prey searching and handling (Galarowicz & Wahl 2005; Oyugi et al. 2012a,b; Section 2.1). Consequently, measuring how animals respond to variations in food availability helps the understanding of how individuals optimise their foraging behaviour (Werner et al. 1983; Galarowicz & Wahl 2005; Murray et al. 2013; Section 2.1). This provides knowledge to assist interpretation of the effect of prey availability on consumer condition, growth and fitness (Werner et al. 1983). Moreover, functional responses provide insights into the mechanics of consumer-prey relationships that can have cascading effects through the food web (Koski & Johnson 2002). They have considerable ecological applications with, for example, their use as important parameters within individual-based models (Stillman 2008) and as explanatory variables in the success of invasive species (Bollache et al. 2008; Dick et al. 2013).

Due to how consumers can influence the structure and stability of their prey populations (Alexander et al. 2013), it is ecologically important to distinguish the type of functional response being exhibited (Section 2.1). There are three major function response types: I, II and III (Hassell et al. 1977). Type I describes a linear increase in feeding rate with prey density until it reaches a constant value at saturation (Jeschke et al. 2004) whereas the feeding rate of the Type II response increases at a decreasing rate

with prey density until it reaches it maximum value (Holling 1959; Section 2.1). Type II is thus inversely density-dependent and so for the prey population, mortality risks decrease with increasing density (Jeschke & Hohberg 2008). The Type III response describes a sigmoidal, density-dependent relationship, where an initial increasing risk of prey mortality switches to a decreasing risk of mortality as the prey density increases above a threshold level (Real 1979; Morgan & Brown 1996).

It has long been known that, despite their apparent simplicity, functional responses are not fixed within the predator–prey relationships of pairs of species, conversely under different contexts, foraging and anti-predator behaviours can shift and significantly alter the form of the response (Holling 1959; Alexander et al. 2013). This may involve subtle changes in, for example, the ability of the consumer to detect and respond to the presence of prey items, or may even involve a shift in the functional response type should there be, for example, a substantial increase in the time spent foraging (Abrams 1982). Environmental variables that have been found to influence functional responses include, temperature and light levels (Lipcius & Hines 1986, Koski & Johnson 2002), and also habitat structure (Alexander et al. 2012). Indeed, habitat structure and complexity has been found to both alter the search ability of the consumer (Savino & Stein 1989, Heck & Crowder1991) and the refuge area of their prey (Gotceitas 1990; Warfe & Barmuta 2004; Alexander et al. 2012). Prey body size might also be important in determining the values of foraging parameters, given trade-offs between the ease of detection of larger items versus their increased handling time (Bean & Winfield 1983; Oksanen & Lundberg 1995).

The aim of this chapter was to determine the effects of habitat complexity and prey item size on the foraging parameters and functional response of a model freshwater fish whose foraging behaviour, when not filter feeding (Hjelm et al. 2003; Bogacka-Kapusta 2007), is reliant on visual cues, namely, roach *Rutilus rutilus* (Diehl 1988; Section 1.6.2, 2.1). This is a freshwater fish species that is ubiquitous to many temperate European freshwaters (Lappalainen et al. 2008) and invasive in others (Elvira & Almodovar 2001; Winfield et al. 2011). Their ecological importance includes their potential for invoking cascading effects on freshwater ecosystems through their high zooplankton grazing rates (Jeppesen et al. 2010) and thus understanding the context-dependency of their foraging behaviours and functional responses can be ecologically significant. Whilst previous

studies have indicated *R. rutilus* can exhibit a Type II (Johanson and Persson 1986; Persson 1987; Section 2.3.3) and Type III (Winkler & Orellana 1992) response, these studies were based on a range of field and experimental approaches, making comparisons difficult. Consequently, here we build on the work described in Section 2, where highly controlled experimental conditions were used to reveal that in a simple environment *R. rutilus* demonstrated a Type II response. Here, we tested the predictions that with altered habitat complexity and food item size, there will be significant consequences for the foraging parameters. Namely that the presence of substrate will reduce reaction distance and consumption rate and increase the searching time of foraging roach; with increased turbidity producing a similar effect. Finally, increasing food item size will increase handling time, thus reducing consumption rate of food items, while increasing reaction distance. With the influences of these environmental conditions affecting consumption rate and thus the functional response of roach.

3.2 Materials and Methods

3.2.1 Experimental design overview

Replicated groups of three *R. rutilus* individuals per experimental arenas were used, with each group being exposed to different numbers of prey items (10, 25, 50, 100 or 150) and their foraging behaviours recorded, using a two-camera videography system. Whereby one camera was positioned horizontally, facing the side of the tank, with the second camera positioned vertically, above the surface of the water. The actual positions and distances moved by the fish were calculated using trigonometry based on footage from both cameras (Section 2.2.4). The specific details of the experimental arena, video capture, validation of fish movement data, and the use of the Hollings Disc equation for the Type II functional response are detailed in sections 2.2.3; 2.2.4; 2.3.1 and 2.2.5 respecively. In summary, there were 12 behavioural arenas (fish aquaria of $0.46 \times 0.31 \times 0.39$ m) in the experiments that were maintained at 18°C on a 12:12 hour light/ dark regime. Three randomly selected roach from a batch of 84 fish (mean length 129 mm $\pm$ 2.5 mm; age 1+ years) were introduced into each arena and allowed to acclimatize to the tanks for 14 days prior to the start of the experiments. Throughout this and the experimental period, the food items used were pelletized fish-meal ('pellets'). This was due to: (i) the experimental fish were originally farmed fish that had been reared on

pellets and so were used to consuming them; (ii) cyprinid fish (such as *R. rutilus*) tend to respond well to such pellets in foraging experiments in tanks (Britton et al. 2012; Oyugi et al. 2012a,b); (iii) as a non-motile 'prey' item that can neither actively select a refuge area, nor display evasive behaviour, measuring the effect of habitat complexity on the consumer would not be confounded by changes in the behaviour of their prey; and (iv) pellets are available in different sizes so food item size could be easily and accurately manipulated. However, the use of pellets, compared to live prey, precludes the display of more complex foraging behaviour, under certain conditions, prey mobility has been shown to influence feeding rates both negatively, through the confusion effect (whereby large numbers of evasive prey can reduce attack rates and/or capture efficiencies) (Ioannou et al. 2007; Tosh et al. 2009), or positively with the movement of prey items increasing predator reaction distance, especially in turbid environments (Utne-Palm 1999).

During the experimental period, feeding trials were conducted every other day, with feeding on the day in between comprised of a maintenance ration of approximately 1.5 % body weight. A maintenance ration was used rather than *ad libitum* to ensure feeding motivation on the experimental days, given that functional responses relate to optimal foraging and therefore behaviour seeking to maximise net energy gain should be promoted. Thus, feeding on experimental days occurred 24 hours after the last exposure to the maintenance ration. Each feeding trial consisted of exposing each tank of fish, in turn, to one randomly selected food density of 10, 25, 50, 100 or 150 pellets per tank (equivalent to 75, 187, 375, 750 and 1125 items m^{-2} respectively). By discounting a food density previously used in a tank, eventually each of these food item densities was used across all 12 arenas with the process then being repeated once more (i.e. each food item density was used twice in each tank). During the trials, the pellets were introduced to the tank across the entire surface of the water with all pellets sinking through the water column and settling on the base of the tank, with pellets being taken by the fish both as they fell through the water and once they had settled on the bottom of the tank. On the release of the food, the filming of the foraging behaviour commenced for 10 minutes (Oyugi et al. 2012a,b). At the end of this period, all uneaten food was removed immediately using a siphon.

Each food density was used in every tank on two separate occasions, potentially providing 72 individual data points for each forager parameter per food density and treatment (Section 3.2.2). In practice, the number of data points was lower, as each experiment did not always produce three fish from each tank that displayed the foraging behaviours required to estimate the forager parameters. In such cases, these fish were omitted from the analyses, reducing the available data. This was also true of the experiments using the lowest food item density, whereby, in order to account for the effect of depletion, only the first fish to feed was considered in the analysis. As before (Section 2.2.3), identification of individual fish allowed the number of datapoints used in estimating forager parameters collected from each fish to be accounted for and limited, controlling for the potential impact of pseudo-replication (Hurlbert 1984).

3.2.2 Experimental treatments

To test the effect of habitat complexity and food item size on the foraging parameters and the functional response, the manipulated parameters were substrate complexity, water turbidity and food item size. The effect of substrate complexity was tested first and then turbidity and food item size.

To test the effect of substrate complexity, the treatments were (1) arenas with no substrate (i.e. simply the glass bottom of the arena) (n = 6) and (2) arenas with a layer of dark aquarium gravel (2 to 5 mm) of approximately 10 mm depth on the arena bottom to represent the complex substrate (n = 6). Other than the change in substrate, the arenas were identical regarding water turbidly (clear) and food item size (1 mm pellets). These trials were completed separately to the trials of water turbidity and food item size, and used different fish.

To test the effect of water turbidity and food item size, a two-factor experimental design was used as it enabled testing of the influence on foraging of both factors and their interactions. These two factors were used together as their interactions will be important in more natural systems where habitats are already complex and their interactions are likely to have sympathetic effects on a visual forager. Across the 12 arenas, 6 were used with clear water and 6 with water turbidity being increased through addition of a fine powder of bentonite clay to the arena (1g ± 0.1g) 5 minutes prior to the experiments commencing. This was as per Vollset & Bailey (2011) who

demonstrated the method had no harmful effects to the fish. At the end of each feeding trial, the water turbidity of each arena was quantified through measurement with a turbidity meter (Hanna Instruments, HI 93703 Micro processor, www.hannainst.co.uk), mean turbidity in the increased turbidity areas being recorded as equal to 3.41 ± 0.5 FTU. As the clay settled out of solution in approximately six hours, it was then able to be removed by siphoning. The arenas used as clear and turbid water treatments remained constant throughout the experiments.

Across these 12 tanks of varying turbidity, two different sizes of sinking pellets were used: 1 mm and 2 mm; the numbers released across the trials were as per the substrate experiment (*cf*. Section 3.2.1). Whilst this meant at a given food density, the biomass of food being introduced would differ between the sizes of pellet, this was justified through functional response analyses generally being based on the consumption rate according to food item density. During each experimental food exposure, the density of food items used was selected randomly for each tank. Once each density had been tested, the trials were later repeated, i.e. each food item density was tested twice in each tank, for both pellet sizes. The actual size of pellet used alternated from one experimental food exposure to the next.

3.2.3 Data capture

The recorded footage of each feeding trial in both sets of experiments was analysed using a purpose-built event-logger program (Event; Bournemouth University 2012). This allowed frame-by-frame viewing and estimation of the position of objects in three dimensions, enabling parameter estimates of fish foraging behaviour to be measured that formed the basis of the functional response equations (Holling 1959; Section 2.2.5). These parameters were: (i) swimming speed (*s*) whilst searching for food, characterised by relatively slow swimming, with frequent changes in body orientation and leading to food item capture; (ii) reaction distance (*d*), determined as the distance a fish would travel in a straight line directly towards a food item, quickly followed by capture of the food item, often following a change in body orientation towards the food item; and (iii) handling time (*h*), determined as the time taken to move towards and consume a food item, and then be ready to consume a further food item. Handling time was determined on occasions when food items were captured in rapid succession and when no other behaviour was observed between food item capture. Other parameters recorded, but not

used in the functional response equations were: (iv) Consumption rate, which was estimated directly, taken as the time between a fish taking its first and fifth food item, and expressed as the number of items consumed per second (Section 2.2.5). By repeating across the range of food densities, the shape of functional response was able to be described; and (v) Searching time, recorded as a percentage proportion of the total foraging time that was spent actively searching. This was used to gain insight into the level of risk-taking behaviour displayed by the fish. When perceived risk is reduced, it has been shown that fish will spend a greater proportion of their time searching for food as a compromise between energy intake and potential risks (Milinski & Heller 1978; Oksanen & Lundberg 1995).

3.2.4 Data analysis

Across the feeding trials in both experiments, there were insufficient data points related to forager parameters collected for each individual fish to enable analyses of their foraging behaviour at that level. Consequently, for the parameters of swimming speed, reaction distance and handling time, separate mean parameter values were calculated for each food density and treatment, whilst limiting the number of data points collected for each parameter from any one fish to four, limiting the potential impact of pseudo-replication (Hurlbert 1984). Any further potential impact on the experimental outcomes through familiarisation and learning of optimum feeding behaviour at the experimental food item densities was limited by the use of maintenance rations and time between trials of the same density. Given that the effect of substrate was being tested separately to turbidly and food item size, its effect on the foraging parameters used repeated measures ANOVA. When two factors were being tested (turbidity and food item size experiment) then linear mixed effects models (LMEM) were used, with either food item size or turbidity as a random effect (depending on the test). When comparing the proportion of time spent searching (as a percentage of total experimental time) binomial generalised linear models (GLM) were used.

The foraging behaviour parameters were used to parameterise both a Type I (Jeschke et al. 2002; Jeschke et al. 2004; Section 2.2.5) and Type II (Holling 1959; Section 2.1, 2.2.5) functional response equation. These used the same variables of attack rate (derived from swimming speed and reaction distance) and handling time, together with food item density, differing only in how these parameters were treated. Note that the

selection and parameterisation of the functional response models, and the estimation of the foraging parameters, are described in more detail in Section 2.2.5. The Type I model was:

$$F = \begin{cases} aD & \text{if } D \leq \dfrac{1}{ah} \\ \dfrac{1}{h} & \text{if } D > \dfrac{1}{ah} \end{cases}$$

(**Eqn 3.1**)

The Type II model was Holling's Disc Equation (Holling 1959):

$$F = \frac{aD}{1 + aDh}$$

(**Eqn 3.2**)

Where F = feeding rate (items s^{-1}), a = searching rate (i.e. search area per unit time) (m^2 s^{-1}), D = food density (items m^{-2}) and h = handling time (s) (Holling 1959). In both cases a was defined as:

$$a = 2ds$$

(**Eqn 3.3**)

Where s = swimming speed (ms^{-1}) and d = reaction distance (m).

Thus, the outputs provided the predicted functional response of the fish according to Type I and II equations. These were then compared to the observed functional response that was produced from the observed consumption rate data, taken directly from the recorded footage. The best fit between predicted models and observed functional response was then determined by its lower value of the Akaike Information Criterion (AIC) using linear regression models, with each factor (substrate, turbidity and food item size) being tested separately.

Finally, to assess the relative influence of all three factors on the consumption rate and the foraging parameters, as the experimental conditions were the same across both sets of experiments, the data were combined for further testing using linear mixed effects models. To test the relative effects of the factors on each foraging parameter; food density and body length of individual fish were the covariates and experimental

arena number was set as a random effect (to account for the fact that different experimental arenas were used across the two experiments). Depending on the model, consumption rate and foraging parameters were the dependent variables and were fitted through systematic removal of non-significant terms according to non-significant P values. All statistics and testing were completed in R (R version 2.15.1) (R Development Core Team 2012).

3.3 Results

3.3.1 Substrate complexity

The effect of increasing the complexity of the substrate on the foraging behaviours was a significantly decreased reaction distance between the no-substrate (mean 13.2 ± 5.5 cm) and substrate treatment (mean 7.3 ± 3.9 cm) (ANOVA: $F_{1,18} = 6.75$, $P < 0.05$). There was also a significant difference in searching time, with fish in the substrate treatment searching longer (mean 91.0 ± 3.7 %) than the no-substrate treatment (mean 28.5 ± 3.1 %; GLM: $F_{1,67} = 97.11$, $P < 0.01$). By contrast, there were no significant differences between the treatments for swimming speed and handling time (ANOVA: $F_{1,28} = 0.91$, $P > 0.05$ and $F_{1,10} = 0.28$, $P > 0.05$ respectively).

The effect of substrate complexity on the consumption rate of the fish was significant, with reduced rates in the substrate treatment (ANOVA: $F_{1,16} = 6.21$, $P < 0.05$; Figure 3.1). Comparison between observed functional response and that predicted by the foraging parameters fitted to equations 3.1, 3.2 and 3.3 revealed that a predicted Type II response was the better fit in both substrate and non-substrate treatments (adjusted $R^2 = 0.94$ $F_{1,3} = 48.84$, $P < 0.01$ and adjusted $R^2 = 0.96$, $F_{1,3} = 64.86$, $P < 0.01$ respectively) compared to a Type I functional response (adjusted $R^2 = 0.92$, $F_{1,3} = 53.55$, $P < 0.01$; adjusted $R^2 = 0.94$, $F_{1,3} = 72.52$, $P < 0.01$). Similarly, the Type II functional response was a better fit when compared to a simple linear increase (adjusted $R^2 = 0.91$, $F_{1,3} = 68.65$, $P < 0.01$; adjusted $R^2 = 0.92$ $F_{1,3} = 77.87$, $P < 0.01$). Lastly, the predicted Type II functional response was a better fit than Type I for both the substrate and non-substrate treatment according to AIC (predicted Type II: substrate AIC = -51.15; non-substrate AIC = -44.96; predicted Type I: substrate AIC = -31.42; non-substrate AIC = -14.97).
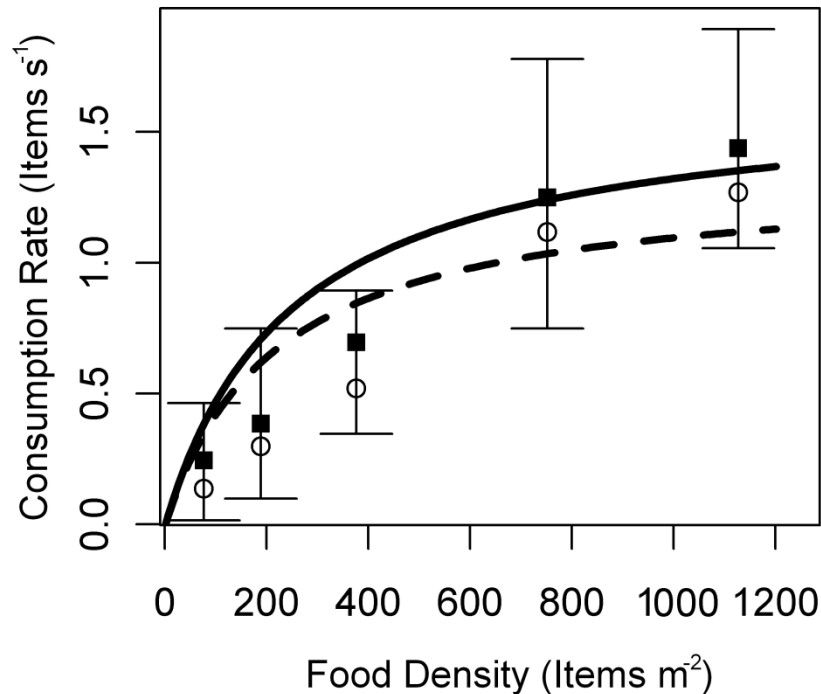
Figure 3.1 Comparison of observed functional responses for the no-substrate (filled squares) versus substrate treatments (clear circles), where the lines represent the modelled Type II functional response from Holling's Disc Equation parameterised using observed foraging parameters under the no-substrate (solid line) and the substrate treatments (dashed line).

3.3.2 Water turbidity and food item size

When controlling for the effect of food item size, the effect of increased water turbidity was a significant increase in searching time, with fish searching significantly longer (mean 85.0 ± 3.2 %) than in the clear treatments (mean 25.0 ± 2.9 %) (GLM: $F_{1,69} = 56.72$, $P < 0.01$). Its effect on consumption rate was also significant, with reduced rates in turbid conditions (LMEM: $t_{1,74} = -4.37$, $P < 0.01$; Fig. 2). There were, however, no significant differences for swimming speed, reaction distance or handling time between the turbid and clear conditions (LMEM: $t_{1,48} = 1.43$, $P > 0.13$; $t_{1,89} = -2.92$, $P > 0.06$; $t_{1,87} = 0.149$, $P > 0.88$ respectively).

When controlling for the effects of turbidity, increasing food item size resulted in a significant reduction in consumption rate (LMEM: $t_{1,74} = 2.51$, $P < 0.02$; Fig. 3). There was, however, no significant effect on searching time, swimming speed, reaction distance or handling time (GLM: $F_{1,69} = 2.13$, $P > 0.05$; LMEM: $t_{1,48} = 1.22$, $P > 0.18$; $t_{1,89} = 2.90$, $P > 0.06$ and $t_{1,87} = -1.57$, $P > 0.11$ respectively).
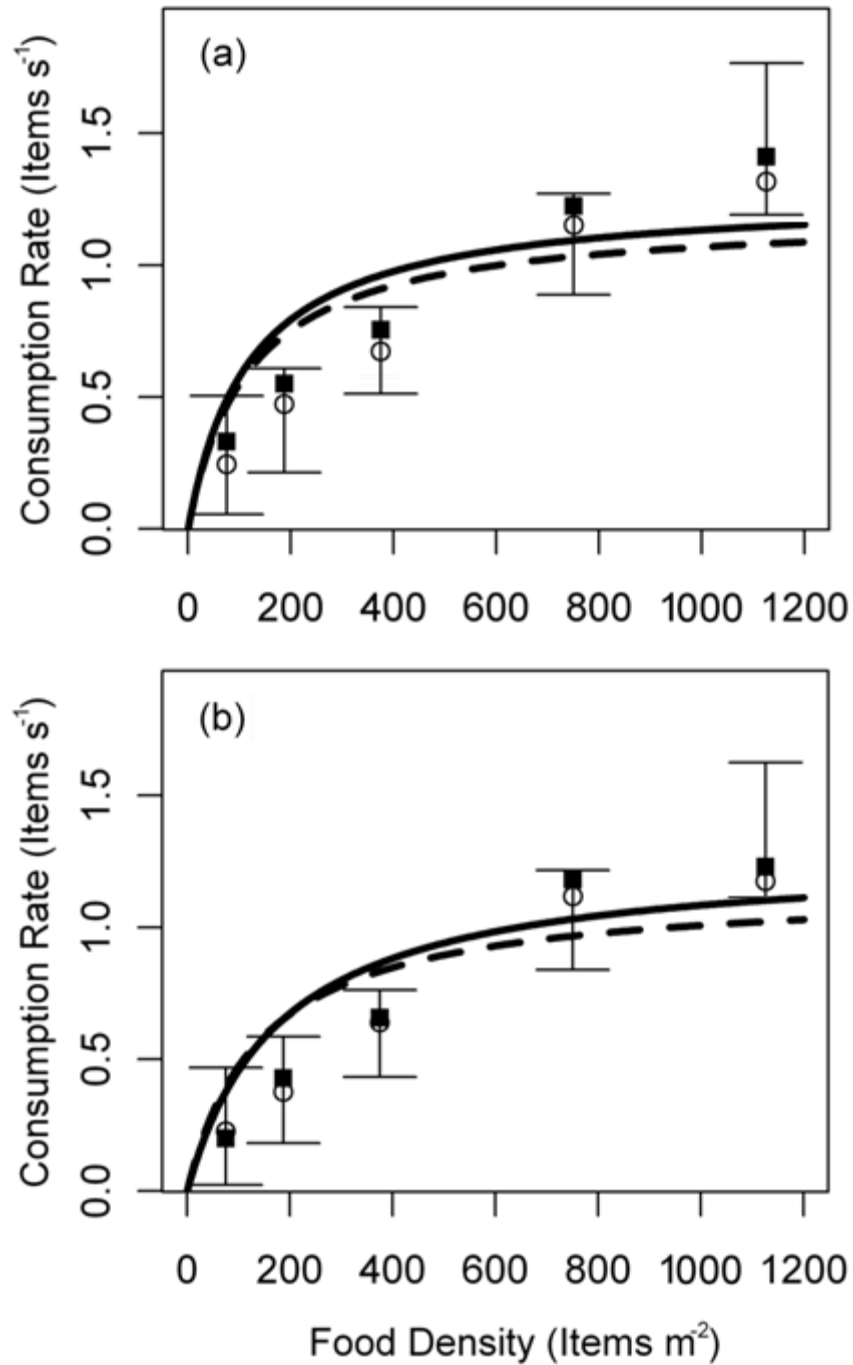
Figure 3.2 Comparison of observed functional responses for clear water (filled squares) and turbidity treatments (clear circles) using (a) 1 mm pellets and (b) 2 mm pellets. The lines represents the modelled Type II functional response from Holling's Disc Equation parameterised using observed foraging parameters, under clear (solid line) and turbid treatments (dashed line).
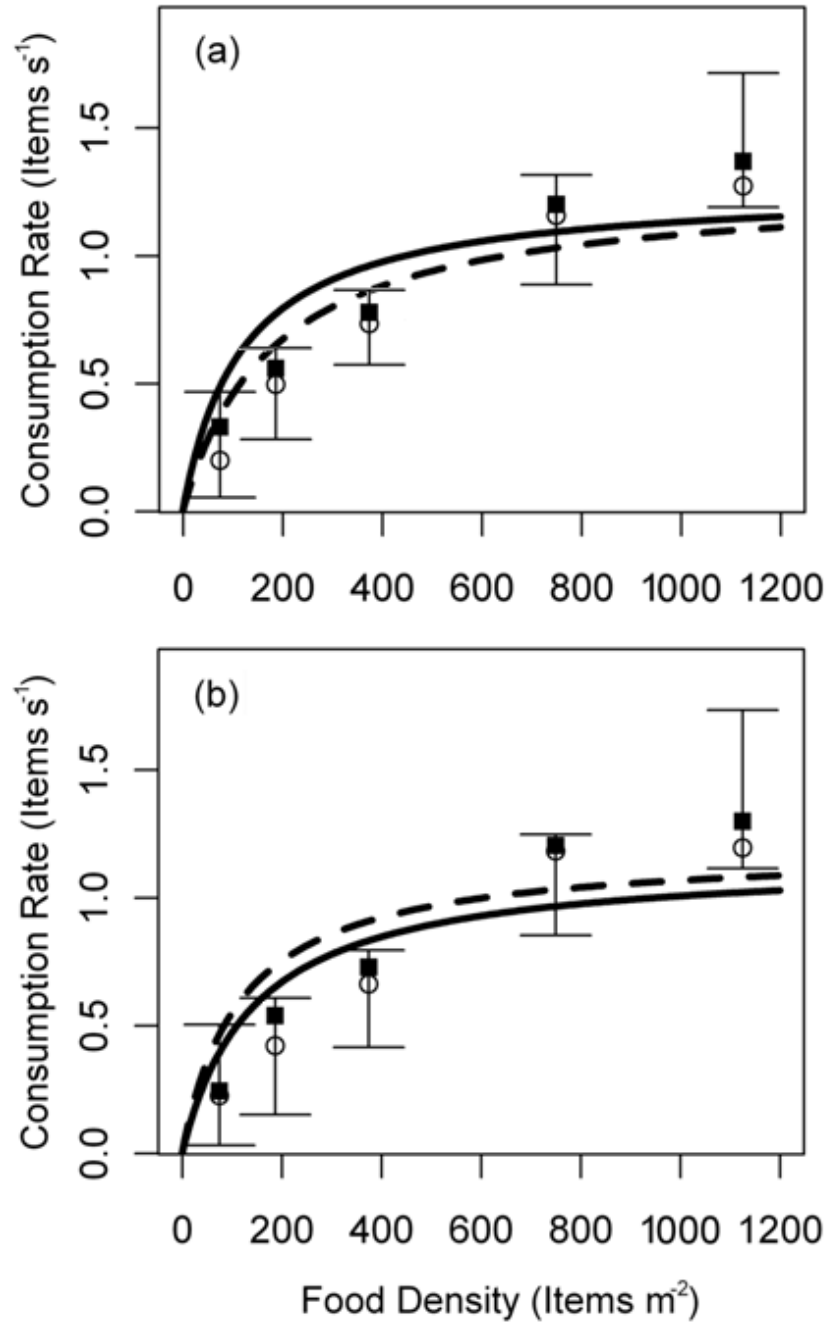
Figure 3.3 Comparison of observed functional responses for differences in food item size, where filled squares represent 1 mm pellets and clear circles 2 mm pellets under (a) clear conditions and (b) turbid conditions. The lines represents the modelled Type II functional response from Holling's Disc Equation parameterised using observed foraging parameters, under 1 mm food item size (solid line) and 2 mm food item size treatments (dashed line).

Table 3.1 Outputs of the Linear Regression and AIC values, testing the fit of each
predicted model against the observed functional response. Model selection was based
on the AIC scores with tests performed separately for each factor.

Turbidity	Food Item Size	Model	df	R^2	F	P	AIC
Turbid	1 mm	Type II	66	0.93	60.76	<0.01	-30.26
Turbid	2 mm	Type II	62	0.95	43.65	<0.01	-18.68
Turbid	1 mm	Type I	66	0.91	65.94	<0.01	-20.65
Turbid	2 mm	Type I	62	0.91	46.59	<0.01	-13.89
Turbid	1 mm	Linear	66	0.92	38.30	<0.01	-5.65
Turbid	2 mm	Linear	62	0.91	26.10	<0.01	-4.45
Clear	1 mm	Type II	59	0.93	34.71	<0.01	-8.23
Clear	2 mm	Type II	69	0.97	66.01	<0.01	-3.17
Clear	1 mm	Type I	59	0.90	38.36	<0.01	11.47
Clear	2 mm	Type I	69	0.92	72.60	<0.01	13.84
Clear	1 mm	Linear	59	0.91	49.20	<0.01	15.29
Clear	2 mm	Linear	69	0.95	26.10	<0.01	16.38

The effect of turbidity on functional response was analysed separately for both food
item sizes. Under turbid conditions, the functional response closely matched a Type II
response using both 1 mm and 2 mm pellets (Table 3.1). Furthermore, the Type II
functional response was a better fit compared to a Type I functional response for both
food item sizes in the turbidity treatment (Table 3.1). Similarly, the Type II functional
response provided a better fit when compared to a simple linear increase (Table 3.1).
Lastly, the predicted Type II functional response was seen to be a better fit than Type I
through lower values using Akaike's Information Criterion (Table 3.1).

Under clear water conditions, the functional response for both food item sizes closely
matched a Type II response in both food item size treatments (Table 3.1). Furthermore,
the functional response was a better fit when compared to a Type I functional response
and a simple linear increase (Table 3.1). When the models were compared, the lower

AIC values were always for the predicted Type II response rather than predicted Type I (Table 3.1).

3.3.3 Factors influencing observed behaviour

The linear mixed effects model (LME) output revealed that substrate and food item size tended to have the greatest consequences for the foraging parameters (Table 3.2). The most significant effect on consumption rate was food item size ($F_{1,123} = 8.36$, $P < 0.01$), and for reaction distance and handling time it was substrate complexity ($F_{1,50} = 12.3$, $P < 0.01$) and ($F_{1,96} = 5.20$, $P < 0.05$) respectively. Within the model, the effects of turbidity on the foraging parameters were not significant.

Table 3.2 Outputs of the linear mixed effects models testing the effect of food item size, substrate presence and increased turbidity on consumption rate and foraging parameters. Fixed effects listed by the significance of their effect on each dependent variable. F = consumption rate; d = Reaction Distance; h = Handling Time and s = Swimming Speed.

Dependent:	df	1st Factor:	F	P	2nd Factor:	F	P	3rd Factor:	F	P
F	123	Food Item Size	8.36	<0.01	Substrate	0.13	0.73	Turbidity	2.75	0.87
d	50	Substrate	12.32	0.01	Food Item Size	0.53	0.81	Turbidity	-	-
h	96	Substrate	5.20	0.02	Food Item Size	2.16	0.11	Turbidity	0.01	0.97
s	101	Food Item Size	2.55	0.07	Substrate	0.28	0.86	Turbidity	1.73	0.18

3.4 Discussion

The experiments demonstrated that changes in habitat complexity and food item size had significant consequences for the foraging parameters and functional responses of *R. rutilus*. Thus, aspects of their foraging were dependent on their environment and food resources, and this requires consideration in any study that measures foraging behaviours and functional responses. These responses to changing conditions are likely to relate to their foraging being strongly reliant on visual cues (Diehl 1988; Podolsrky, Uiblein & Winkler 1995; Wanzenbock et al. 1996; Aksnes & Utne 1997). Regarding the type of functional responses elicited by *R. rutilus*, the best fitting functional response model in each experiment was always Type II. This is a similar outcome to most other studies on *R. rutilus* (Johanson and Persson 1986; Persson 1987; Section 2.3.3). The only exception is Winkler & Orellana (1992) where Type III functional response was measured, with this likely to relate to the role of capture probability as a result of evasive behaviour displayed by the live prey.

Testing of how water turbidity impacted the foraging parameters whilst controlling for the effect of food item size revealed that consumption rate and reaction distance were reduced as turbidity increased, with this likely to be a result of visual foraging behaviour in roach. It was not considered likely that it was related to changes in olfactory cues as bentonite clay is considered odourless (Zamor & Grossman 2007; Vollset & Bailey 2011), plus the role of olfaction (compared to visual cues) is limited in roach foraging (Wanzenbock et al. 1996). This outcome is in contrast to findings in three-spined sticklebacks *Gasterosteus aculeatus* whose reaction distance and attack rate actually increased as turbidity increased (Vollset & Bailey 2011). This outcome was related to the altered conditions; both reducing the perceived conspicuousness of the stickleback to potential predators and increasing prey item contrast in the water column, increasing their visibility (Vollset & Bailey 2011). Notwithstanding, as the attack rate of *G. aculeatus* increased their capture success actually decreased, resulting in the consumption rate actually remaining the same and the energetic costs of foraging increasing (Vollset & Bailey 2011). The use of pelletized fish meal in our study meant that there was a much more limited role for capture success in shaping the outcome of

the foraging as evasion behaviour is negligible in this experiment and prey refuge was not available as a gravel substrate was not used.

The presence of a gravel substrate within the experimental arenas detrimentally impacted the majority of the foraging parameters. Within this experiment, the selection of pellets was due to them being a non-motile food item. This was to eliminate the potential confounding effect of the food items actively seeking refuge in more cryptic environments that could result in any shifts in the foraging parameters being due to prey rather than fish behaviour. Indeed, other studies have revealed that functional responses are significantly affected when the refuge area for live prey is increased as this provides greater opportunities for prey avoidance (Gotceitas 1990; Warfe & Barmuta 2004; Alexander et al. 2012). Nevertheless, in this study, our observations on the reduced foraging performance of the *R. rutilus* in the substrate treatment indicated that the reduced consumption rate was largely due to the increased difficulty of the fish being able to detect the pellets once they had settled on the gravel, as the size of pellets allowed a proportion to settle into relatively inaccessible areas (i.e. they provided a 'prey' refuge).

The outcomes of this study highlight the respective roles of prey item visibility and environmental conditions in determining the foraging behaviours and parameters of a visually foraging fish (Utne-Palm 1999; Sweka & Hartman 2003). In natural environments, these dynamic relations are important considerations in habitat selection and optimal foraging given that foragers will always seek to maximise their energy intake whilst minimising energetic costs and risk of predation (Chick & McIvor 1997). Frequent changes in the environmental conditions of lowland riverine habitats (where the presence of *R. rutilus* tends to be ubiquitous across their range) are common, in response to prevailing weather conditions or more general shifts in lowland river management. This latter aspect is important given that many lowland river management techniques that are aligned to flood management works substantially modify fish habitats through, for example, removal of instream macrophytes that tend to increase turbidity, decrease refugia and increase flow rates (Gregg & Rose 1985; Copp 1997; Allouche & Gaudin 2001; Grenouillet & Pont 2001). This suggests that works such as these are likely to be detrimental in the perspective of *R. rutilus* foraging performance,

with adult roach switching to less productive filter feeding behaviour in response to environmental challenges, including increased flow rates and water turbidity (Van Den Berg et al. 2004; Bogacka-Kapusta & Kapusta 2007; Nurimen et al. 2010) in association with habitat refugia (Garner 1996), and so potentially has substantial implications for fishery and fish population management.

In conclusion, the investigation revealed that foraging parameters and functional responses of *R. rutilus* are modified by changing conditions, with increased complexity tending to decrease aspects of their foraging performance. While increased turbidity, substrate presence and larger food items were seen to reduce the consumption rate of food items. In combination, these outcomes suggest that the foraging performance of this species is context-specific, being subject to prevailing conditions and food item availability, and this requires consideration in all relevant applications of their foraging behaviour.

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4. Data for building the roach individual-based model, with comparison of roach habitat association and growth across three UK lowland rivers

This chapter describes the environmental and forager data collected at the study site that will be used in subsequent chapters as part of model construction, validation (Chapter 5) and scenario testing to predict how aspects of river management influence the roach population (Chapter 6). The study site is the River Stour (Suffolk, England), from which data on the roach population is collated and compared with two other lowland rivers in Eastern England, the Great Ouse and the Wensum, to ascertain how representative the Stour population is of lowland river roach populations generally. The chapter has five principal sections: (1) the study site; (2) collection and analysis of environmental data; (3) collection of invertebrate data; (4) collection and analysis of 0+ roach data; and (5) collection and analysis of 1+ roach data. For each of the environmental data, invertebrate, 0+ roach and 1+ roach data sections, the methods used to collate the data are described, the results presented and the application of these data to the modelling process discussed. For the juvenile (0+) and adult (≥1+) roach, comparison is also made on the growth, recruitment and habitat associations across the three rivers. It should be noted that data collected and analysed in the Chapter were done so to primarily provide outputs suitable for model parameterisation, validation and scenario testing, rather than research that tested specific ecological hypotheses.

4.1 Introduction

4.1.1 MORPH individual based model

The research develops the MORPH individual based model (IBM) for predicting the response of roach to river management scenarios. MORPH is a spatially-explicit model, composed of parameters and rules which describe animal physiology, bioenergetics and foraging behaviour, and the distribution and abundance of resources required by the forager-prey system, in which individuals behave in order to maximize their perceived fitness (Stillman 2008). Within MORPH, the following entities are required: (*i*) global parameters applied throughout the modelled system, (*ii*) patch parameters describing mesohabitat-specific variables, and (*iii*) forager parameters describing foraging animals within the system, consuming diets and assimilating components (Chapter 5).

Therefore, global, patch and forager parameters, specific to the study site, were obtained through the completion of field studies completed at the study site on the River Stour, Suffolk, England (Section 4.1.2).

The methods for collecting and using global and patch environmental variables at the study site are described in Section 4.3, with the methods for collecting macro-invertebrate data comprising Section 4.4, while forager variables are described in Sections 4.5 for 0+ roach and 4.6 for adult roach. Before IBMs can be used for real world applications, they must first be validated; a pattern-oriented modelling approach is used here (Grimm & Ralisback 2005) (Section 5.2.3). This requires information on observed patterns at the study site, specifically distribution at the stretch level of adult roach (age 1+ fish are used here, hereafter referred to as '1+'; Section 4.6.4), and specific growth rate (SGR) of juvenile roach (fish in their first year of life, hereafter referred to as '0+') and 1+ roach (Section 4.5.7; Section 4.6.5). Section 4.6.5 also analyses aspects of the roach population dynamics at the study site and compares them with the other datasets (Section 4.1.2).

4.1.2 Datasets used in the study and this chapter

To develop an individual-based model that is capable of predicting the response of a fish population to environmental change the field study site must be representative of a typical lowland river where cyprinid fishes, such as roach, are dominant. The river selected was the River Stour, Suffolk (Section 4.2). To ensure that the model has utility beyond the study site, it was ascertained whether the roach population of the site were similar in characteristics (for example, in patterns of growth rates, recruitment and habitat associations) to other lowland river roach populations in Eastern England. This was completed using four datasets from three rivers:

1. The River Stour study site was used throughout, with data collected in 2011 and 2012 specifically for developing the model (*cf*. Section 4.2). This is then the only dataset that is used in subsequent chapters for model development and scenario testing.

2. The upper River Stour, the same river as (1) but incorporating more sites and sampled for adult fish every three years by the Environment Agency between 1998 and 2007 (National grid reference TL690487).

3. The River Wensum, a lowland river in the east of England (National grid reference TG250078) where fish and environmental data were collected between August 2007 and November 2008.

4. The River Great Ouse is a large lowland river, located in eastern England (National grid reference TL360712). Data were collected from a number of sites on the lower river (Copp 1992; Garner 1995).

Wherever data from datasets 2 to 4 are used in this chapter, this will be made apparent in the relevant sub-section, with a rationale provided for their inclusion. Wherever the term 'study site' is used in this chapter, it refers to (1) River Stour, the site in which data were specifically collected for model development in this research (Section 4.2).

4.2 The River Stour study site

4.2.1 The Suffolk Stour

The study river was the River Stour in Suffolk, England (Figure 4.2). The rationale for its use was that it is a typical lowland, slow-flowing river in Eastern England, with a fish community dominated by fish of the Cyprinidae family and roach in particular. Moreover, the river is important for flood risk management and for an Essex-Suffolk water transfer scheme. Correspondingly, in the summer months, the heavy macrophyte growth that results from the slow flow is managed by the Environment Agency through weed cutting. A weed-cutting boat typically carries this out in a relatively indiscriminate manner, raising fishery management concerns that it results in a deleterious effect on the juvenile fish of the river, although there is little empirical evidence currently supporting this. The water transfer scheme means that even during a dry summer, flow rates can be variable as water is moved between catchments and, similar to weed cutting, the effect of increased flow rates has been raised as a concern in its damaging effect on the juvenile fishes (Garner et al. 1996; Ohlberger et al. 2006; Nunn et al. 2007).

The River Stour has a catchment area of 478 km^2, where the principal land use consists of agricultural land, although the catchment also contains the major urban centres of Haverhill, Sudbury and Harwick, with a regional population of 681,000 people. The river rises at Eastern Cambridgeshire, North of Haverhill, then flowing for 76 km before entering the sea at Harwich. The elevation of the river is 115m at source, giving the river a low gradient.

The study site was a 230m stretch of the Stour (Figure 4.3). At 51m elevation, it was the highest site in the catchment that is monitored by the Environment Agency for its fish populations (Grid Reference TL710429), located approximately 40 kilometres from the source. The site was characterised by its slow flow rates, substrate of silt and mud, and the presence of submerged and emergent macrophytes, dominated by water lily (*Nuphar lutea*), common reed (*Phragmites australis*) and burreed (*Sparganium erectum*) (Figure 4.1). The site was located immediately downstream of a water abstraction point used for a water transfer scheme and terminated before a weir that acted as a blockage to fish migration.

Figure. 4.1. The study site, facing downstream on the left hand back of the River Stour.
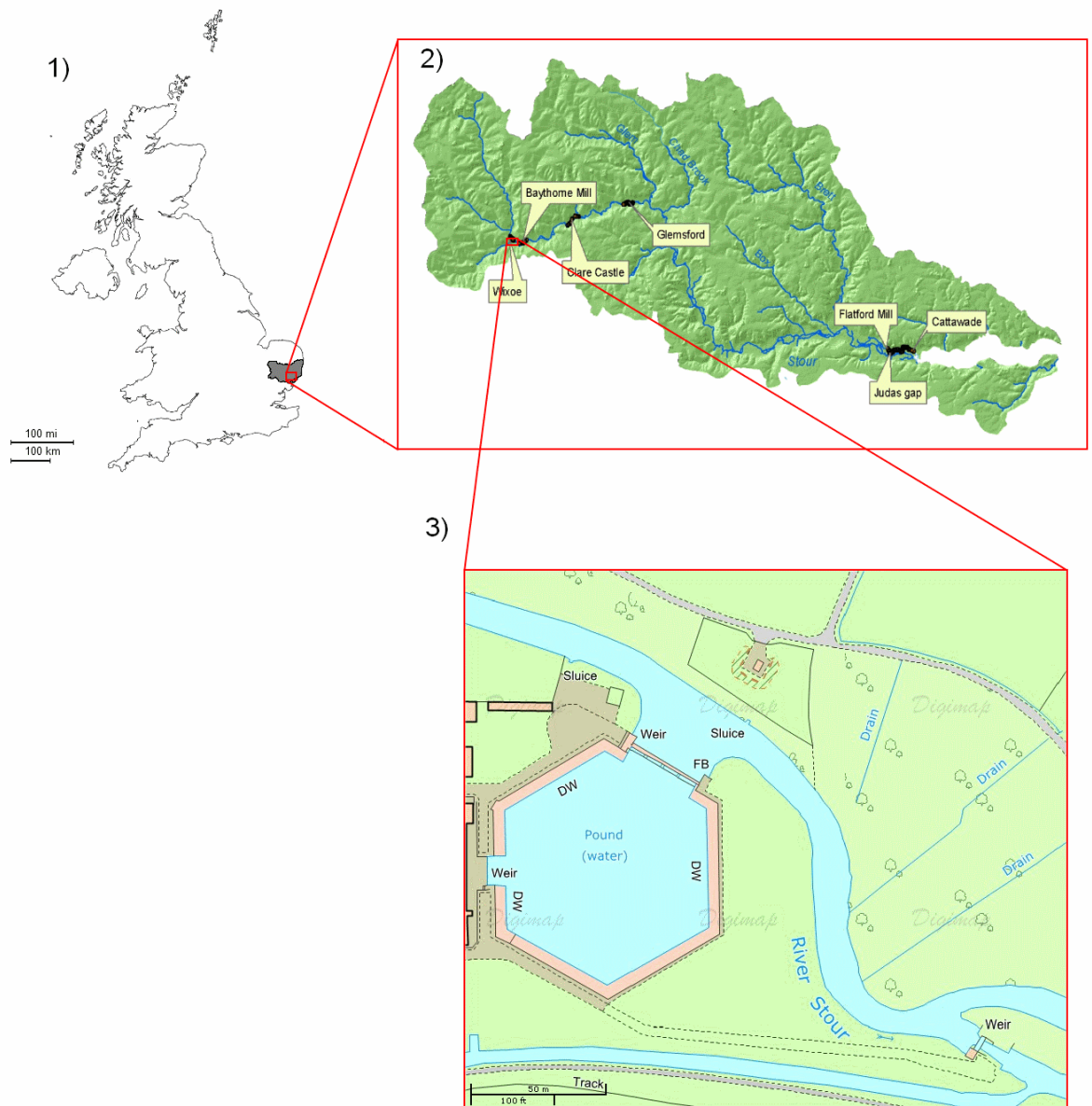
Figure. 4.2. Map of the UK showing; 1) Suffolk and River Stour catchment area location. (© 2007 World Trade Press) 2) River Stour catchment area with Wixoe site location. (© Environment Agency) and 3) Study Site details. (© Digimap).

4.2.2 Stretch and Patch Selection

The collection of data on global and patch parameters for MORPH requires information to be obtained at two spatial scales, stretches and patches. It is then within these stretches and patches that the environmental and biological characteristics are recorded, including ecological aspects of the fish populations (Section 4.4 to 4.6).

Correspondingly, prior to any data collection on the environmental and biological characteristics of the river, the study site was separated into a series of stretches and the stretches were then separated into patches. These corresponded with the macrohabitat (stretch) and mesohabitat (patch) units simulated in the model (Figure 4.3).

Within the site, five stretches were mapped out, at approximately 50 m intervals, and marked with wooden stakes placed in the riparian zone. Each stretch consisted of a section of river that comprised of roughly similar habitat characteristics (for example, in width, macrophyte cover, flow and depth). The patches were then smaller units of habitat, of which between 8 and 10 made up a stretch (Table 4.2), and were marked out approximately every 10 m using smaller, colour-coded wooden stakes, with each patch consisting of homogeneous habitat characteristics (for example, in their macrophyte, flow rate and depth). Most patches covered the entire width of river, but where one side of the river differed markedly from the other, they were separated into two patches.

River Stour

Stretches = 5
Patches = 34

Total Length = 230m
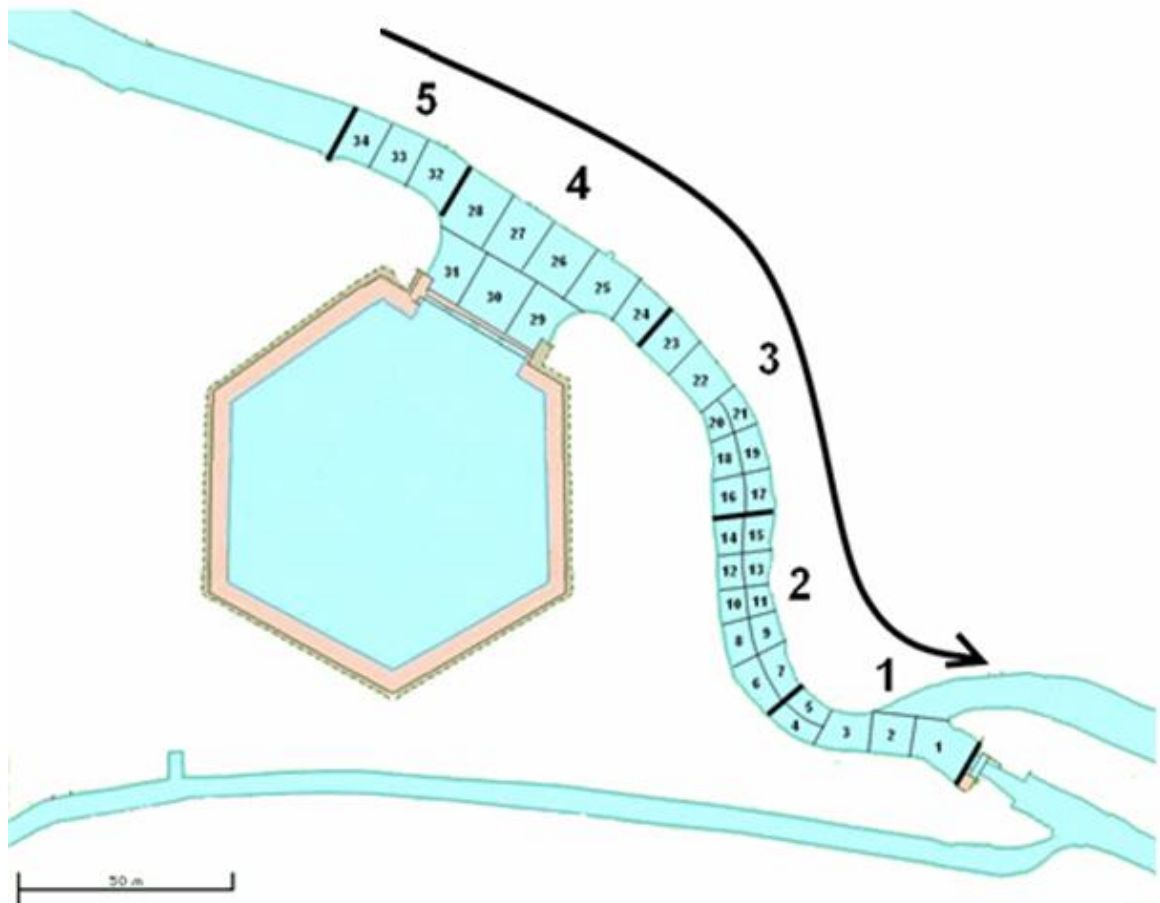
Figure 4.3. The Study site, showing the layout of stretches (1 to 5) and patches (1 to 34) (Section 4.2.2). The direction of flow is from left, to right along the orientation of the illustration.

4.2.3 Data collection

The study period at the site was between July and October 2011 when data were collected from the stretches and patches on the environmental parameters, invertebrate communities, juvenile (0+) fish and adult fish (≥1+). The sampling dates and the data collected on those dates are provided in Table 4.1. Note that data were not collected

before July as roach are a species that tend to aggregate in specific habitats for spawning between May and June (Mills 1981; Copp 1992), and so it was assumed by July the adult fish would have completed spawning and be occupying their typical summer habitats. Moreover, their assimilated energy would now be used primarily for somatic growth rather than gonadal growth and recovery from spawning activities, and the percentage weed cover and flow rate in the study stretch was also assumed to vary much less between July and October than, for example, May to October. In May, the macrophytes would only just be starting to recommence their growth following the winter months; precipitation and high ground water from the previous winter would still be affecting flow rates.

Table 4.1 Sampling dates on the study site, with an overview of data collection activities on those dates.

Date	Global/Environmental	Invertebrate	0+ roach	≥1+ roach
11/07/2011	✓			
09/08/2011				✓
10/08/2011				✓
11/08/2011		✓		
12/08/2011				✓
16/08/2011			✓	
18/08/2011	✓			
18/09/2011	✓			
19/09/2011				✓
20/09/2011				✓
23/09/2011	✓			
26/09/2011	✓	✓		
20/10/2011			✓	

4.3 Environmental data

Following the delineation of the stretches into their patches, the environmental parameter values within each patch had to be recorded. The objective of this section is to describe the environmental parameters collected, the methodology used, analyse the environmental data and discuss their application to the IBM.

4.3.1 Environmental data collection

To accurately calculate the area of each patch, the differential Global Positioning system (dGPS) (Leica 500, Leica Geosystems (http://www.leica-geosystems.co.uk)) was used to record each boundary; by combining the relevant patch areas, the stretch area could also be calculated. Calculation of the combined areas was possible to within the accuracy of the dGPS apparatus (+/-0.25m).

The environmental parameter values recorded in each patch were turbidity, flow rate, water depth, macrophyte cover and temperature (Table 4.2, 4.3). Given the nature of the study site, these data had to be collected through use of a boat. Within each patch, 2 areas were sampled; one selected at random from within the area of the patch containing macrophytes and one selected at random from within the area clear of macrophytes. The proportion of macrophyte cover (%) was estimated by eye to the nearest 5%. Turbidity (FTU) was recorded through measurement of water samples collected in each of the two random areas in each patch and assessed using a turbidity meter (Hanna Instruments, HI 93703 Micro processor, www.hannainst.co.uk). Flow rate (ms^{-1}) was recorded in two locations per patch using a Valeport 'Braystoke' model 002 current flow meter, fitted with a 50 mm diameter/100 mm pitch impeller (http://www.valeport.co.uk), with readings normalised over 60 seconds, recorded approximately 10cm below the water surface, 10cm above the riverbed and the middle of the water column. Concomitantly, depth (m) was recorded using a measuring rule.

Temperature data were used to model the water temperature in each patch of the virtual environment over the entire simulation period. In order to do this, two high frequency temperature loggers (Tiny Tag data loggers; Gemini Data Loggers, Chichester, UK, http://www.geminidataloggers.com) were positioned in the study site under typical shaded and sunlight exposed patches, with data recorded every three minutes throughout the entire data collection period (Table 4.1, 4.2). In order to measure any potential difference in water temperature between the patches, water temperatures were recorded at surface level in each patch at two random locations using an electronic temperature probe (EcoScan Temp 5; Thermo Scientific, Landsmeer, The Netherlands http://www.eutechinst.com) at midday on each environmental data collection day (Table 4.1). This approach allowed the water temperature in each patch to be estimated through calibration against the high-frequency water temperature data collected by the data loggers. In order to estimate the water temperature at the patch level beyond the end of the study period and prior to the data collection, a site-specific relationship was calculated in comparison to the Hadley Centre Central England Temperature (HadCET) dataset (http://www.metoffice.gov.uk/) (Section 4.3.4). In order to estimate water temperature in each patch, a conversion between the Central England Temperature and the water temperature at the study site was made, based on the data

from the temperature loggers, using a conversion of 1.072 air temperature to water temperature. This conversion matches described relationships between air and water temperature (Kothandaraman & Evans 1972).

For each environmental parameter, values were analysed across the patches and stretches, and where mean values are provided in all subsequent sections, error around the mean represents standard deviation.

4.3.2 Environment data outputs

Patch area varied between the five stretches, with a mean area of 86.7 m^2 (range 31.4 to 179.1 m^2). The reason for this relatively great variation in mean patch area was through variation in the wetted-width of the river (Figure 4.3). The widest section was in Stretch 4, and so patches tended to cover only half the wetted-width of the river (Figure 4.3). The patches that comprised Stretch 2 also tended to cover only half of the wetted-due to the depth differences across the river width. Thus, mean patch area was higher in Stretch 4 and relatively low in Stretch 2 (Table 4.2). The number of patches was relatively similar between each of the 5 stretches (Table 4.2), with the exception of Stretch 2, where more patches were designated due to the difference in the morphological features of the river arising from the meander (Figure 4.3) and Stretch 5 that was relatively short. Stretch 5 was also limited by presenting different habitat characteristics to Stretch 4 downstream and by access further upstream (a fence and surface net designed to catch debris from an upstream construction site).

The environment parameters at the stretch level are provided in Table 4.2 and the patch level in Table 4.3. Across the five stretches, mean water temperature was 14.2°C, with a range across the study period from 13.2 to 19.1°C. Mean flow was 0.053 ms^{-1} with a range from 0.001 to 0.204 ms^{-1}. Given the physical structure of the river, especially the meander in Stretches 1 and 2 (Figure 4.3), water depth varied at the patch and stretch level (Table 4.2, 4.3); mean depth of the study site was 0.76 m with a range from 0.07 to 1.57 m. The stretches with the greatest mean depths were Stretches 1 and 5, with stretch 2 the shallowest (Figure 4.3; Table 4.2). In-stream macrophyte cover varied markedly between both patches and stretches (Table 4.2, 4.3); mean cover was 25% with a range from 5 to 80 % between patches. Stretch 5 had the highest macrophyte cover, with less variation observed between the other stretches (Table 4.2).

Table 4.2 Mean values of environmental variables for each stretch calculated from data recorded in each patch within the study site.

Stretch Number	Number of Patches	Mean patch area (m^2)	Mean flow (Open Channel ms^{-1})	Mean flow (Bank-side Channel ms^{-1})	Mean depth (m)	Mean Macrophyte (%)	Mean Temperature (°C)	Mean Turbidity (FTU)
1	7	90.7	0.49	0.06	0.83	7.8	14.2	5.96
2	10	57.9	0.74	0.24	0.72	6.5	14.3	5.25
3	7	65.7	0.79	0.26	0.81	5.0	14.2	3.76
4	7	140.4	0.37	0.11	0.78	6.4	14.0	3.67
5	3	96.7	0.70	0.50	0.83	15.0	14.1	2.52

Table 4.3 Mean values of environmental variables for each patch calculated from data recorded in each patch within the study site.

Patch Number	Mean patch area (m²)	Mean flow (ms⁻¹)	Mean depth (m)	Mean Macrophyte Cover (%)	Mean Temperature (°C)	Mean Turbidity (FTU)
1	64.6	0.12	1.40	30	14.2	3.06
2	136.7	0.05	1.10	20	13.8	4.34
3	175.7	0.04	1.39	35	14.0	4.19
4	73.8	0.04	1.15	25	14.0	5.74
5	76.3	0.08	1.36	30	14.2	7.80
6	51.4	0.05	0.63	25	14.1	10.91
7	56.4	0.01	0.94	35	14.2	5.66
8	85.3	0.04	0.34	25	14.3	7.82
9	65.3	0.06	0.87	25	14.3	6.40
10	71.4	0.01	0.33	20	14.1	6.00
11	31.4	0.05	1.20	20	13.8	4.19
12	76.5	0.04	0.32	20	14.1	11.14
13	64.0	0.08	1.32	20	13.9	3.68
14	41.9	0.15	0.36	20	14.4	6.12
15	51.9	0.04	1.43	20	14.0	2.41
16	44.8	0.06	0.40	15	14.1	2.47
17	47.3	0.03	1.35	20	14.1	2.27
18	53.1	0.01	0.90	40	14.2	1.53
19	38.1	0.04	1.27	10	14.1	2.94
20	92.0	0.12	1.02	40	14.0	8.64
21	57.0	0.05	1.42	25	13.9	3.63
22	70.4	0.13	1.41	20	14.1	4.46
23	64.7	0.03	1.17	20	14.2	3.50
24	85.0	0.04	1.41	40	14.0	1.60
25	136.4	0.08	1.14	25	14.0	4.00
26	155.0	0.05	0.84	20	14.1	6.33
27	154.1	0.12	0.88	25	14.4	3.61
28	197.1	0.05	0.84	25	14.5	1.92
29	89.35	0.01	0.55	20	14.3	3.29
30	109.9	0.04	0.79	20	14.5	5.35
31	159.3	0.04	0.63	15	14.5	1.22
32	106.0	0.04	0.87	25	14.3	4.11
33	108.6	0.03	1.04	20	14.4	1.15
34	75.6	0.01	1.11	25	14.4	2.30

4.3.3 Application of the environmental data to the IBM

The environmental data collected at the field site was sampled at a spatial and temporal scale that enabled a relatively full description of the physical conditions at the study site during the growth season of roach (Barbour et al. 1999). This meant they were applicable for use as a basis of model construction and validation (Chapter 5), and for comparisons with the Rivers Wensum and Great Ouse (Sections 4.5.5; Section 4.6.5) and in relation to the roach populations (Section 4.5; 4.6). In IBM development, the study site environmental data are used to create global parameters (Section 5.2.6) and patch parameters (Stillman 2008; Stillman & Goss-Custard 2010; Section 5.2.7) so that the virtual system is representative of the study site. Once combined with the forager parameters for roach, this enables model validation by comparing model output patterns to patterns observed in roach from the study site (Railsback 2001a,b; Kramer-Schadt 2007).

The environmental data collected shows that the study site presented no extreme abiotic conditions, including depth, flow or macrophyte (Bubb & Lester 1994). The section of the River Stour chosen also represents the type of river that is subject to river management, particularly in-stream macrophyte removal (Section 4.2.1). Such management is usually performed to improve channel navigability, bank-side access and as flood risk mitigation (Stanford 1996; Downs 2000). The site also contains a water impoundment facility used to maintain flows in adjoining river systems during periods of drought (Section 4.2.1). Given the impacts of reduced growth, reduced invertebrate food availability, increased turbidity and increased risk from predation or displacement caused by high flow rates and removal of in-stream macrophyte on juvenile cyprinid fish (Bean & Winfield 1983; Copp 1997), understanding the consequences of such river management strategies is vital. As such, the study site was well chosen to be represented in the IBM (Section 5.2.2) and the patterns described in the model may be applied to similar lowland river systems throughout the UK and globally (Boisclair 2001; Hollowed et al. 2009).

4.4 Invertebrate data collection

4.4.1 Benthic macro-invertebrate data in the IBM

The amount of food resources available to the roach population at the stretch level is a fundamental component of the IBM as not only is diet a fundamental aspect of modelling behaviour (Durell et al. 2006; Stillman 2008); given that energy budgets are fundamental to a foraging species' behaviour (Holker 2006; Haertel & Eckmann 2002), it is also a key factor in the growth and therefore survival of juvenile roach (Dijk van et al. 2002; Beardsley & Britton 2012). Furthermore, energy intake is often given primacy when reproduction and predation risk are reduced or absent, as is the case in the simulated environment (Section 6.2.8). Finally, sensitivity analysis performed on the completed model indicated that the model output was sensitive to changes in the amount of energy available to the foragers (Section 5.3.4). This pattern is similar to that observed in previous MORPH-based IBMs, simulating populations of dace (*Leuciscus leuciscus*) as well as salmonid fish and overwintering shorebirds (Durell et al. 2006; Stillman 2008).

4.4.2 Macro-invertebrate data collection: calculating the proportion of benthic invertebrates

In order to create the parameter describing the benthic macro-invertebrate prey energy resource available to the simulated foragers, the amount of energy available in each stretch in the form of benthic invertebrates had to be estimated from the drifting macro-invertebrates surveyed at the study site. Invertebrate drift densities had to then be converted into energy, relative to the area searched. At the stretch level, the body-size and species diversity of the drifting macro-invertebrates was assessed using drift nets (250 μm mesh). Sampling was performed in each stretch, three times during each day of sampling (dawn, midday and dusk) (Table 4.1), with linear interpolation between the points allowing estimates of drifting macro-invertebrate densities for the periods between the sampling points to be made; this approach made the least assumptions about potential changes in macro-invertebrate densities during the intervening time. A relationship of 23.5% of recorded drift invertebrate densities to available benthic invertebrate prey was used (Diamond 1967; Herpher 1988; Haertel & Eckmann 2002; Holker et al. 2002), allowing an estimation of the number of benthic invertebrates in

each stretch, based on drift sampling and patch area. This information on benthic macro-invertebrates was converted to potential energy resources for each captured invertebrate of aquatic origin by analysis to determine their average dry mass (mg), energy density (KJ g^{-1}) and energy content (J) using published length-mass, mass-energy relationships (Cummins & Wuycheck 1971; Ganihar 1997; Benke et al. 1999; Sabo et al. 2002). These data were the final benthic macro-invertebrate resource energy densities used in the model (Section 5.2.25) described in terms of energy (KJ) for each area searched (m^2) (Table 4.4).

Table 4.4 Mean values of drift and benthic resource variables for each stretch calculated from data recorded at the study site.

Stretch Number	Number of species	Mean length (mm)	Mean dry mass (mg)	Proportion aquatic/ terrestrial	Mean energy content per prey item (J)	Mean available benthic energy per m^2 (KJ)
1	14	4.7	3.0	0.9	68	2.9
2	11	4.6	3.2	2.3	71	2.5
3	14	4.7	2.7	2.1	60	3.4
4	14	5.6	4.0	2.0	88	3.3
5	13	6.9	5.7	0.9	129	2.5

4.4.3 Application of the invertebrate data to the IBM

By sampling at a sufficiently fine spatial and temporal scale, it was possible to describe the macro-invertebrate community at the study site in relation to the foraging behaviour of juvenile roach (Mann et al. 1997; Hjelm et al. 2003; Bogacka-Kapusta & Kapusta 2007). As such, this information was used during the IBM construction in order to create patch parameters describing the energy available to roach foragers in different patches (Section 5.2.7), with this reflecting the availability of benthic macro-invertebrate prey. Such availability is usually a result of the river substrate characteristics, although it is also influenced by other factors, including flow rate and macrophyte cover (Tolonen et al. 2003; Wharton et al. 2006). The macro-invertebrate

data collected shows that the study site is representative of heavily-modified lowland rivers as they tend to have relatively low macro-invertebrate diversity (Hatton-Ellis 2008).

4.5 Juvenile roach (0+ roach)

4.5.1 Overview

During the period of data collection in 2011 (Table 4.1), two aspects of the roach population were studied, fish in their first year of life, spawned in May/ June and referred to a 0+ roach, and fish in at least their second year of life, referred to as adult roach, albeit age at maturity in roach is plastic and no dissections were performed here to assess maturity (Weatherley 1986; Copp & Kováč 1996; Kováč & Copp 1996). The reason for analysing these two components of the roach population separately is because the biology and ecology of juvenile (0+) freshwater fishes generally have been recognised as quite different from their adult conspecifics, arising from their rapid ontogenetic development from larvae to juveniles, specific habitat use, and growth and high mortality rates that are influenced by environmental parameters such as flow, temperature and macrophyte cover (Nunn et al. 2002, 2007). The small body size of 0+ roach, often below 30 mm for much of the summer, also means their sampling methods are quite specific, incorporating point-abundance electric fishing (Copp 2010), a method that is unsuitable for sampling larger fishes. Consequently, the IBM requires data on the performance of both the juvenile roach and the adult roach.

The objective of this section is to outline the data collected and analysed for the 0+ roach, with discussion of their application to the IBM. The focus is on their biometric data and their habitat utilisation in relation to environmental parameters. Both aspects are completed for the study site and the habitat analyses are completed for the study site and the Rivers Wensum and Great Ouse, enabling comparison between the three rivers to identify common patterns. Whilst the IBM also requires specific growth rates (increase in mass per day) for the 0+ roach, there was no available methodology to accurately record their growth rate during the study period and so values for specific growth rates of 0+ roach were collected from published literature (Cryer et al. 1986; Soleimani et al. 2012; Dijk et al. 2002).

4.5.2 Factors affecting 0+ fish recruitment in lowland rivers

In lowland cyprinid fish communities, fish populations tend to be dominated by specific strong year classes (cohorts) whose survival was high in their first year of life and resulting in disproportionately high numbers recruiting into the adult stock (Mills & Mann 1985; Mann 1991; Cowx & Frear 2004). In a typical roach population where fish are present up to 8 or 10 years old, there will be typically two or three strong year classes of fish present, with the other year classes being in low abundance due to their relatively weak recruitment (Britton et al. 2004).

Consequently, the recruitment of 0+ fish is a key process regulating the number of adult fish that are subsequently present in the population and it is determined by the number of fish surviving their first year of life. In this time, there will be 'critical periods' (such as episodes of flooding) that are deleterious to their abundance as these periods increase their displacement and mortality rates, and so affect the number of surviving fish (Nunn et al. 2003, 2007). The physical habitat characteristics (e.g. flow rates) and environmental conditions (e.g. extent of refugia, such as macrophyte cover) of rivers are thus often limiting factors for 0+ fish survival rates; a lack of cover and high flow rates tend to result in high mortality rates (Souchon 1994; Lamouroux et al. 1999). Good areas of habitat for the juvenile life stages of riverine cyprinid fish tend to be areas of slack water that provide areas of refuge from flow and predation, even for rheophilic species like European barbel *Barbus barbus* that only tend to seek faster water flows once body lengths above 50 mm are achieved (Britton & Pegg 2011). Correspondingly, should an episode of elevated flow occur, with it resulting in the elimination of the slack water areas and if there are no alternate refuge areas available, then increased displacement and mortality of the 0+ fish is likely to occur. These episodes are more likely to impact recruitment when they occur during the larval stages of the fish, as their swimming abilities will be low (Catteneo et al. 2001; Grenouillet et al. 2001; Nunn et al. 2003, 2007a; Piffady et al. 2010).

4.5.3 0+ fish in lowland rivers and river management schemes

The relationship between 0+ fish and their habitat preferences are important in the context of not only environmental conditions and river flow regimes, but also river management. For example, long-term flood management methods tend to involve

channel straightening that has the general effect of reducing the area of favourable larval and juvenile habitat in the littoral areas, with this often compensated by increasing the availability of connected off-channel refuges (Nunn et al. 2007b, 2010; Janac et al. 2010). In some rivers, such as the study river, excessive macrophyte growth in the main channel elevates flood risk and so weed cutting programmes are executed, despite their utility as a source of refugia for 0+ fish (Jurajda 1995; Copp 1997). For example, weed cutting on the River Great Ouse in Eastern England can have substantial consequences for the river biota generally as well as the 0+ fish specifically (Garner et al. 1996). In the river, a significant relationship between 0+ cyprinid fish, macrophyte cover and zooplankton density was found in macrophyte presence, with elevated densities of zooplankton and fish in the macrophyte zone. The removal of the macrophytes through mechanical cutting resulted in a rapid decline in the mean densities of zooplankton present and in the 0+ fish, resulted in their increased downstream displacement, predation and starvation. This caused in reduced growth rates in the surviving fish as their diet shifted from zooplankton to the less nutritious detrital aufwuchs (Garner et al. 1996). Thus, river management schemes, such as those that reduce flood risk through channel straightening and weed removal, can be a significant factor influencing 0+ fish survival rates and so also upon the recruitment success of their year classes.

4.5.4 0+ roach data collection at the study site

The 0+ roach were sampled in the study site using point abundance sampling by electric fishing (PASE) (Cowx et al. 2001). Note all electric fishing and associated data collection and fish handling/ procedures were completed in conjunction with the Environment Agency, Anglian Region, Eastern Area. PASE surveys were completed on two separate occasions (Table 4.1) in order to gather information on the 0+ fish at the patch level (Copp 2010). The rationale of sampling at the patch rather than stretch level was that the 0+ fish, due to their small size, tend to show high fidelity to specific areas of habitat within the patches, whereas older, larger fish are mobile and have less fidelity to patch specific habitat features and so measuring their distribution is more appropriate at the stretch level. PASE was completed using battery powered electric fishing equipment (Smith-Root LR-24 Backpack http://www.smith-root.com, with 50 MHz pulsed DC at approximately 2 Amps) from a boat. The equipment was operated for a

standardised 10 second period in a random location within each patch, with all immobilised fish within the electric field removed using a hand net (Copp 2010). Their processing, consisting of identification of captured fish to species level, counting the number sampled at each point, and recording of their lengths (fork) (mm) and weights (g), was completed once all patches had been sampled. After each point was sampled, the following habitat variables were measured: patch location (GPS), flow rate, macrophyte cover (%), depth and water temperature.

4.5.5 0+ roach data collection at the River Wensum and Great Ouse

River Wensum

To determine the habitat requirements of 0+ roach in the River Wensum, the Environment Agency completed point abundance electric fishing in the summers of 2007 and 2008 in 5 stretches of the river in a 40 km stretch between Bintree (52°46'57.05"N, 0°57'37.94"E) and Hellesdon (52°38'25.49"N, 1°14'58.03"E). The electric fishing gear was specifically adapted to catching 0+ fish (Copp & Garner 1995), with adaptations including a 10 cm diameter anode ring and a large 20 metre long cathode to reduce energy loss. Current was supplied by a Honda EU 10i, 1.0 KW electrofishing generator via an Electrocatch control box that produced approximately 0.5 to 1.0 amps of Pulsed Direct Current at 50 Hz. This enabled an effective fishing area around the anode of approximate radius 0.5 m. The surveys were generally conducted monthly between July and November and comprised the fishing in each stretch of 60 random points in the littoral areas of the river, as these habitats tend to be favoured by 0+ roach (Copp & Garner 1995; Copp 2010). Each point was fished for a standard period of 10 s and all fish immobilized within the electric field were captured with a hand net. These fish were then identified to species, counted and measured (fork) (mm), and the environmental variables of depth (m), flow (ms^{-1}), estimated macrophyte cover (%) and location (GPS) were then recorded.

River Great Ouse

Habitat requirements of 0+ roach in the River Great Ouse were assessed by Garner (1995) using data collected by Copp (1992) using point abundance electric fishing conducted weekly between early August and late September 1990 across 130 sites of the river. 2800 point samples were taken at an approximate density of 1 point per 100m^2

using battery-powered electric fishing equipment adapted for catching 0+ fish (Copp & Garner 1995), with adaptations including a 10 cm diameter anode ring (Copp 1992), this enabled an effective fishing area around the anode of approximate radius 0.071 m^2 (Garner 1995). Each point was fished for a standard period of 10 s and all fish immobilized within the electric field were captured with a hand net and preserved in 4% formaldehyde. These fish were then identified to species, counted, measured (fork) (mm) and categorised in three intervals related to crucial developmental events: young larvae, older larvae and the juvenile period (Copp 1992). Finally the environmental variables of depth (m), flow (ms^{-1}) and location were then recorded.

4.5.6 Data analyses

Length-mass relationship

Fork length (mm) and body mass (g) were recorded for 0+ roach captured using PASE at the study site, this data was used in constructing the IBM, in the form of forager parameters (Section 5.2.8). A parameterised length-mass relationship was also developed (Equation 4.1) for the 0+ roach, in conjunction with data from the adult roach also survey at the study site (Section 4.6.4).

$$Y = 2.44\,X^{3.606} \qquad (\textbf{Eqn 4.1})$$

Where *Y* equals body weight in g and *X* equals fork length in cm.

This relationship (Eqn 4.1) takes the form of the standard description of a weight; length relationship in fish (Froese 2006), although the specific form used is similar to that of a roach-specific length-mass relationship detailed by Papageorgiou (1979), which was seen to agree with the relationship described in the fish sampled from the study site.

Habitat Suitability Indices and binomial logistic regression of habitat utilisation

To assess the habitat preferences of 0+ roach in the study site specifically (so as to inform the IBM) and lowland rivers generally (to assess the applicability of the IBM beyond the study site), data from the PASE surveys for the three rivers were used. The data used for the analyses was their presence ($\geq 1 \times 0+$ roach captured at the sampling

point) and absence (0 ×0+ roach captured at the sampling point), along with the recorded habitat data at each point. These data were used initially to construct habitat suitability indices. These are univariate habitat associations that calculate the suitability of a specific habitat variable over their range of recorded variables for 0+ roach. Habitat suitability indices have been widely used in fisheries management and ecological restoration studies, benefiting from general applicability and relative simplicity in construction, and model calibration and validation (Brooks 1997; Tian et al. 2009). These were calculated for the study site and River Wensum for macrophyte cover (%), flow rate and depth, with each of these variables divided into 5 categories (Table 4.5), with data recorded as per Section 4.3 and section 4.5. The habitat suitability indices for the River Great Ouse were already available from Garner (1995).

Table 4.5 Range of physical habitat variables assessed using habitat suitability indices and the categories used to describe the riverine habitats of the Stour and Wensum.

Category	1	2	3	4	5
Depth (cm)	0-5	6-10	11-15	16-20	>20
Flow (ms^{-1})	0-0.02	0.03-0.05	0.06-0.08	0.09-0.1	>0.1
Macrophyte cover (%)	0-19	20-39	40-59	60-79	>80

For each habitat variable category, the frequency of occurrence in non-null samples (i.e. when roach were present) was divided by the frequency of occurrence in all samples (i.e. including instances of sampling when no roach were captured). The calculated value for each category was then divided by the total produced in all 5 categories, for each habitat variable, producing a proportional value for each habitat suitability indices (Figure 4.4a,b to 4.6a,b,c).

The final habitat analysis was to analyse the habitat preferences of 0+ roach using multivariate data. This was completed on only one dataset, selected on the basis of the proportion of points in which 0+ roach were sampled and the similarity of its habitat suitability indices with the other two rivers. As the raw data to complete these calculations were not available for the Great Ouse, then this resulted in the River Wensum data set being applied to binomial logistic regression and enabled predictions

to be made on the presence/absence of roach in response to the different combinations of habitat characteristics. The initial model tested the probability of capturing one or more roach in a point sample (measured as binary presence (1)/ absence 0)), against each explanatory habitat variable. As some degree of co-correlation might have been expected between the habitat variables (e.g. increased areas of flow tend to be shallower and have less macrophyte cover) then this was described as part of the binomial logistic regression in the form of a correlation matrix.

4.5.7 Data outputs for 0+ roach

Body length and mass

In the study site, the mean 0+ roach fork length and body mass was 33.4 ± 12.5 mm and 2.6 ± 8.2 g respectively (Table 4.6). The specific growth rate (SGR) of 0+ roach, taken from published literature (Cryer et al. 1986; Dijk et al. 2002; Soleimani et al. 2012) was 0.99 ± 0.16 % body mass per day (Table 4.6). Whilst only 0+ fish were captured and described using PASE, the SGR of larger, older roach captured by alternative sampling methods at the stretch level (*cf*. Section 4.6) are included here for comparative purposes (Table 4.6).

Table 4.6 Mean, minimum and maximum length (fork) and mass of 0+ roach at the study site, along with their mean specific growth rate (% body mass per day) for roach of age classes 0+ to 3+, for comparison, with their data sources (*cf*. Section 4.6).

	Length (mm):	Body Mass (g):	Age (Years):	Mean SGR (% Body Mass per day):	Source:
Mean 0+ roach:	33.4	2.69	0+	0.998	Literature*
Minimum value:	4.8	0.20	1+	0.622	Section 4.6
Max Value:	46.0	35.50	2+	0.431	Section 4.6
Standard Deviation:	12.5	8.19	3+	0.293	Section 4.6

* Cryer et al. (1986); Dijk et al. (2002); Soleimani et al. (2012)

Habitat suitability indices

Across the three rivers where PASE was employed, a total of 4016 point samples were surveyed, producing 3476 points with no 0+ roach and 540 where at least one 0+ roach was recorded; of these 540 points, 28 were from the study site, 134 were from the River Wensum and the remainder were from the Great Ouse. Roach preferentially occupied areas of increased macrophyte cover (Figure 4.4), reduced flow rate (Figure 4.5) and depth greater than 6cm but less than 20cm (Figure 4.6). While the same general patterns of habitat preference were seen across all three rivers, there were a few subtle differences. Roach were seen to more frequently occupy the most heavily vegetated areas in the study site, compared to the River Wensum, where more roach were seen in the next most heavily vegetated habitat category (Figure 4.4). Similarly, slight differences in the habitat preferences between the rivers were seen in the outputs for flow rate and water depth. While a general preference for habitats of low flow and median depth was observed, the relative proportion of fish seen to occupy habitats of higher flow and both higher and lower water depths was seen to vary between the rivers. Finally, the Great Ouse differed in that macrophyte cover was not recorded as part of the survey.
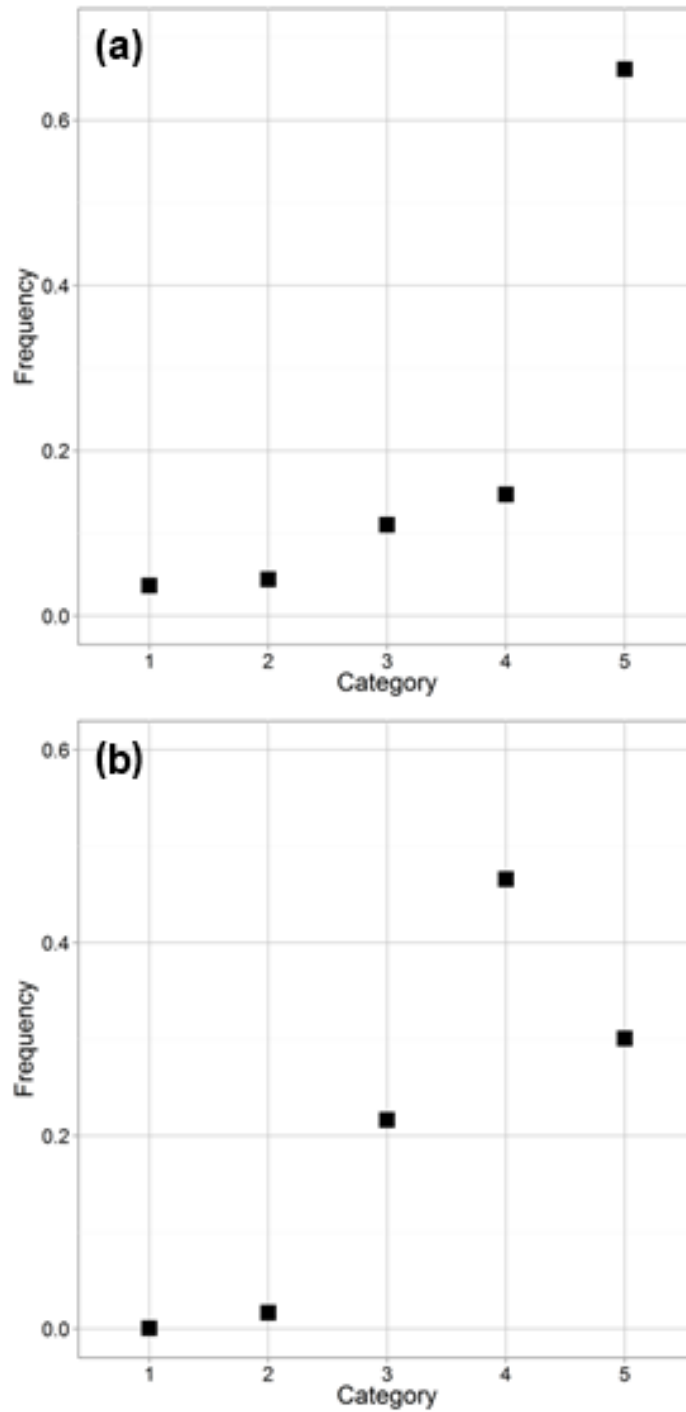
Figure 4.4 Habitat suitability index outputs for macrophyte cover for (a) the study site and (b) the River Wensum. Note the Y-axis of frequency of sites occupied by 1 or more roach differs between plots for ease of comparison between the habitat categories within each plot.
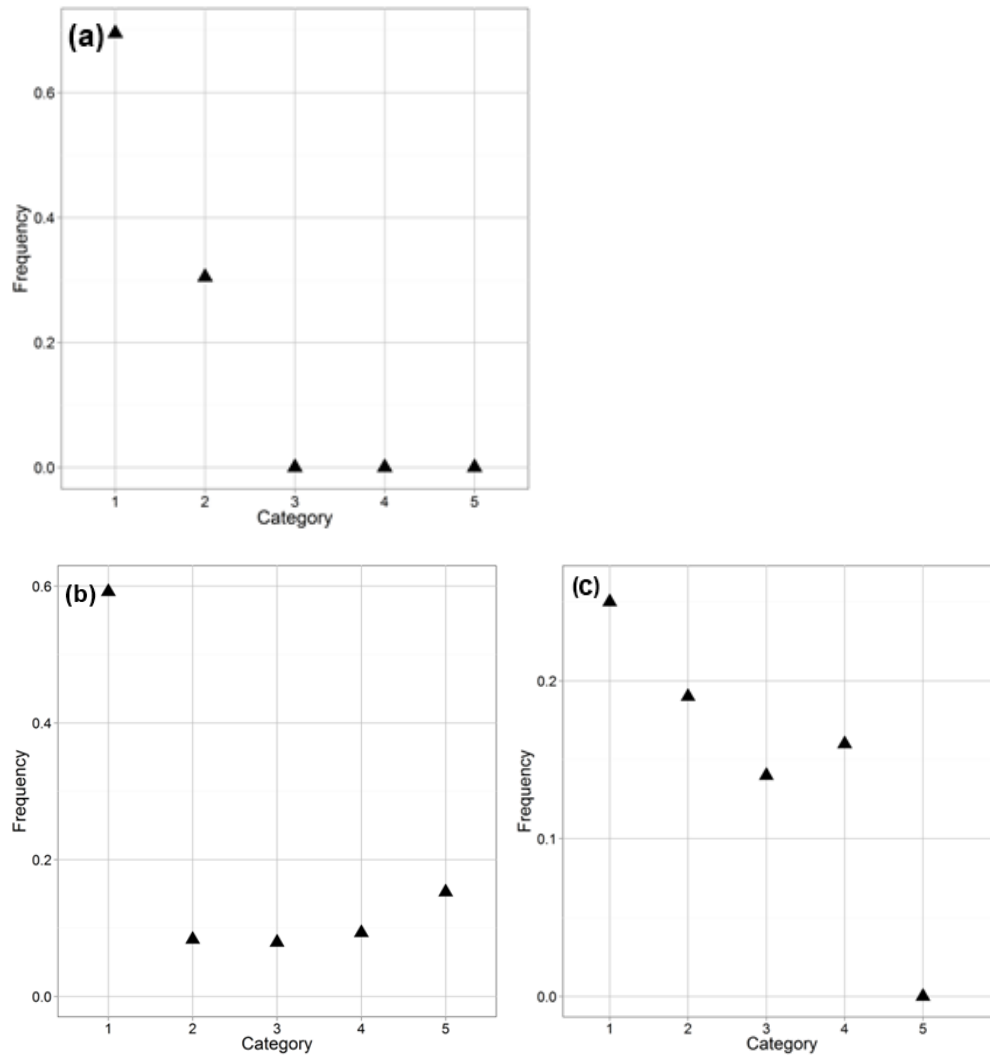
Figure 4.5 Habitat suitability index outputs for flow rate for (a) the study site; (b) the River Wensum; and (c) the River Great Ouse. Note the Y-axis of frequency of sites occupied by 1 or more roach differs between plots for ease of comparison between the habitat categories within each plot.
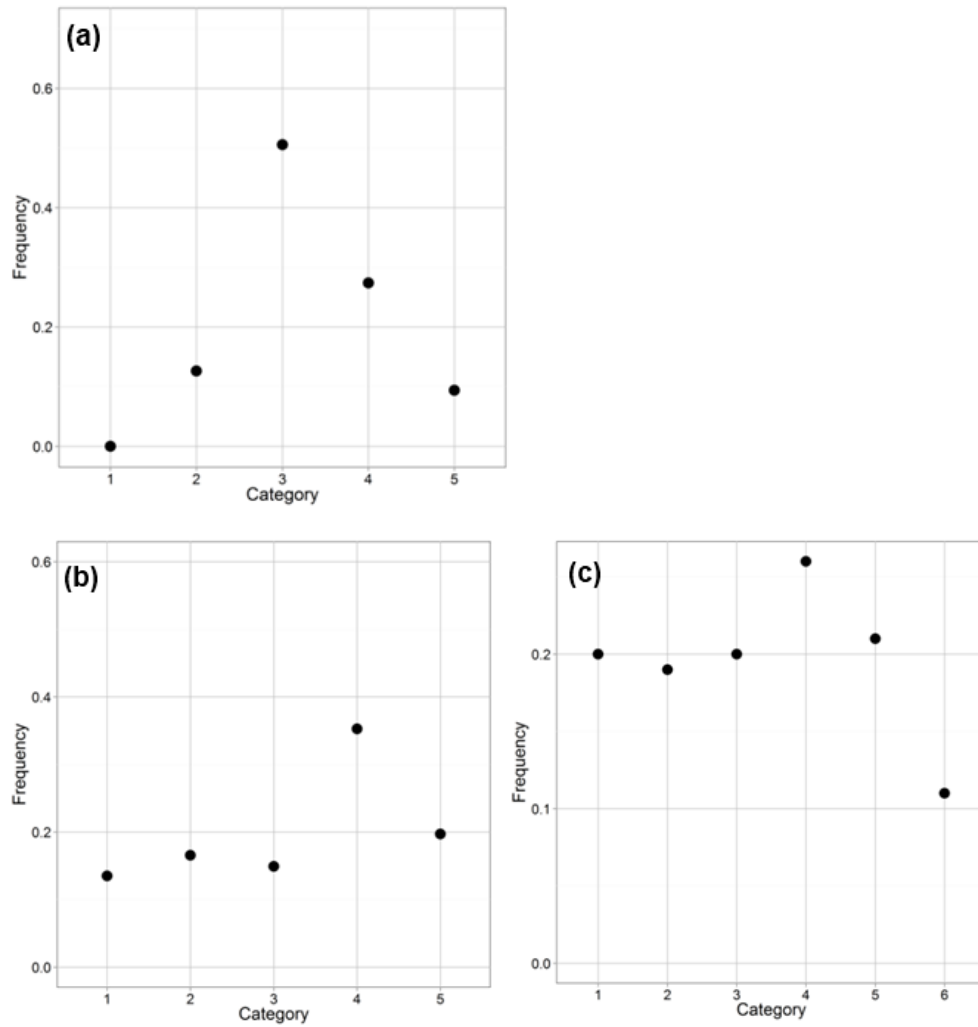
Figure 4.6 Habitat suitability index outputs for water depth for (a) the study site; (b) the River Wensum; and (c) the River Great Ouse. Note the Y-axis of frequency of sites occupied by 1 or more roach differs between plots for ease of comparison between the habitat categories within each plot.

Binomial logistic regression

The River Wensum dataset was used here in preference to that of the study site due to the greater number of point samples recorded (n = 2162), the number of points where 0+ roach were recorded (n = 134) and the total number of 0+ roach sampled (n = 703, albeit these were not used in the analyses). The presence or absence of roach within the points was thus described as a function of the explanatory habitat variables in the logistic regression model. This revealed that macrophyte cover was a significant factor in the model predicting the presence of roach within a point (76% correlation, Binomial logistic regression Z = 2.855, P = <0.01) while depth and flow were not (5% correlation, Binomial logistic regression Z = -0.663, P = >0.05; -9% correlation, Binomial logistic regression Z = -0.604, P = >0.05 respectively). The habitat explanatory variables themselves were also co-correlated, with flow being positively associated with depth and negatively associated with in-stream macrophyte, whilst depth was positively associated with macrophyte presence (Table 4.7).

Table 4.7 Binomial logistic regression *correlation* matrix for roach in the river Wensum. Influence of each explanatory variable on the presence of roach and the other explanatory variables, along with associated binomial logistic regression statistical output.

	Roach presence	Flow:	Depth:	Macrophyte:
Flow:	-0.099	—	—	—
Depth:	0.054	0.067	—	—
Macrophyte:	0.769	-0.067	0.138	—
Z statistic of explanatory variable:	N/A	-0.604	-0.663	2.855
P value of explanatory variable:	N/A	0.54	0.51	<0.01

4.5.8 Discussion for 0+ roach

Data collected at the study site on 0+ roach lengths and mass were in the region of those recorded in other populations of 0+ roach in both lakes and lowland rivers (Persson 1983; Holker 2006; Nunn et al. 2007). This indicates that this component of the roach population of the study site is relatively typical of a lowland river in the UK. This is important, given the key role length, and to a lesser extent body mass, plays in the life history of 0+ fishes, with body size directly influencing swimming ability, foraging ability, growth, recruitment, habitat selection and survival rates (Papageorgiou 1979; Mann & Bass 1997; Mann 1997; Holker & Breckling 2002; Holker 2003; Nurminen et al. 2010).

These data collected for the 0+ roach will thus be used to parameterise the forager variables in the model (Section 5.2.8). Furthermore, the specific growth rate derived from literature values will be used in model validation. The specific growth rate of 0+ fish captured using PASE could not be assessed at the study site as opportunities to collect data suitable for its calculation were not possible, for example mark-recapture as

the fish were too few and too small for identification tagging and too young to have formed the growth rings used in scale back-calculation (Figure 4.7).

Habitat association was analysed using habitat suitability indices (Brooks 1997) in the case of all three rivers and binomial logistic regression of presence/ absence data in the case of the River Wensum. In all cases, the outputs corresponded with other studies on habitat preferences of 0+ roach, namely an affinity for in-stream macrophytes, relatively deep water and reduced flow rate (Garner 1995; Persson & Eklov 1995; Schulze et al. 2006; Bond et al. 2010). Similarly these habitat characteristics are co-occurring, in-line with expected relationships between macrophyte and flow rate, water depth and flow rate as well as water depth and macrophyte presence (Gurnell et al. 2006). These habitat associations will be used to assist understanding of the natural behaviours that should be emulated by virtual foragers in the IBM and to understand the mechanisms behind predicted river management impacts on juvenile roach (Mann & Bass 1997; Pinder 1997). This is important, as it was apparent from the point sampling on all rivers that only a small proportion of the littoral areas of the river provide suitable nursery habitat for 0+ roach (low flow, high macrophyte cover) and so any habitat disruption, such as weed-cutting, would be a concern from a recruitment perspective. Despite its deleterious consequences for both invertebrate and 0+ fish populations, indiscriminate weed cutting that leaves only small buffer areas remains common and so its effects on recruitment need to be better understood.

4.6 Adult roach (≥ age 1+ years)

4.6.1 Overview

This objective of this section is to outline the data collected and analysed for the adult roach, with discussion of their application to the IBM. The focus is on their somatic growth rates and, for the River Stour, the temporal recruitment patterns and the significant factors that influence annual recruitment. For somatic growth rates, data for the River Stour are compared with both the Rivers Wensum and Great Ouse to identify whether patterns are similar across the three rivers. The IBM also requires specific growth rates (increase in mass per day) for the adult roach and the methodology and outputs for this are outlined. Thus, the research objectives of the section are to (1) describe the age range and somatic growth rate of adult roach in the study site and river, and compare these to the Rivers Wensum and Great Ouse; (2) calculate the SGR of a representative component of the adult roach population for subsequent use in the IBM; and (3) determine and evaluate the temporal recruitment patterns of roach in the River Stour.

4.6.2 Importance of roach growth rates as an ecological indicator and IBM parameter

Foragers displaying fitness maximising behaviours will seek to increase their energy stores, resulting in growth. The rates of growth achieved by cyprinid fishes in UK lowland rivers tend to be density-independent, being most heavily affected by environmental factors (Nunn et al. 2010; Beardsley and Britton 2012). An example of an environmental influence on the abundance and growth of lowland riverine fish climate, with this being reflected by the primary growth period displayed by roach during the warmer summer months, prior to cooler winter conditions where little growth is expected; in mature individuals, warmer periods in early summer are also associated with spawning behaviour (Mills 1981; Koch et al. 1992). As such, broad-scale climatic effects represent a strong underlying influence on the growth and recruitment of juvenile fishes (Grenouillet et al. 2001; Nunn et al. 2003). The influence of climate varies spatially and temporally, highlighting that significant shifts in these variables may cause significant impacts to potential growth rates (Nunn et al. 2003, 2007). The value of understanding changing fish growth rates is reflected in the popularity of growth meta-analyses, which use latitude to estimate temperature in order to explain

patterns of variability in growth rates of fish across their distribution ranges (e.g. Lappalainen et al. 2008; Cucherousset et al. 2009; Benejam et al. 2009). In general, faster growth rates tend to occur in more southerly habitats as a result of increased water temperatures providing longer and warmer growth seasons (New et al. 1999; Lappalainen et al. 2008). The foragers simulated in the model have their growth rates directly mediated through net energy gain, as such, besides temperature, growth rate is also influenced by environmental factors such as flow rate, food item availability, turbidity, light levels, substrate type as well as by forager parameters including reaction distance, swimming speed, body size, gape size, metabolic costs and associated bioenergetic processes (Table 5.1).

Given the importance of growth rate in ensuring survival and recruitment of juvenile roach, (Nunn et al. 2010; Beardsley & Britton 2012) and its fundamental relationships with the factors simulated in the modelled system, it provides a useful and representative model output for validation of the model under a pattern-oriented approach (Railsback, 2001b; Grimm & Railsback 2012). This was achieved by pairing the simulated growth rate outputs with growth rate data from the study site collected through scale back-calculation (Section 4.6.4). Finally, in terms of management recommendations; the model predictions seek to promote juvenile roach recruitment, due to the importance of recruitment for ensuring strong year-class strength in roach (Mills 1981; Bystrom & Garcia-Berthou 1999; Nunn et al. 2003; Section 4.6.3). As such, the model predictions will inform how this process will be indirectly impacted by river management with this being heavily influenced by growth during early life stages (Nunn et al. 2010).

4.6.3 Importance of adult roach data for measuring recruitment success

In freshwater fish populations, the recruitment strength of each year class in a population tends to be calculated using 'year class strengths' (YCS) (Cowx & Frear 2004). As outlined in Section 4.5, recruitment success in temperate riverine cyprinid fishes is not consistent annually but instead varies over time. These annual variations in YCS have been attributed to temperature differences between years (Mills & Mann 1985; Mann 1995) and other biotic and abiotic factors, such as flow rates and fish

growth in their first year of life, as this assists over-winter survival (Paxton & Winfield 1999; Cowx 2001; Nunn et al. 2003).

As it is a relative measure of recruitment strength, calculating year class strengths requires data on the component of the fish population that has already recruited, i.e. the adult fish. In riverine cyprinid fish populations, this tends to be taken nominally as above age 1 years, although sexual maturity might not occur until the fish are older, usually from 2 to 3 years in male roach and 3 to 4 years in female roach (Papageorgiou 1979; Davies et al. 2004). This enables the use of year class strength indices to be used on adult fish population data using methods such as those described by Cowx & Frear (2004) where year class strengths are derived through the construction of life tables for each year class, with subsequent comparison of the number in each year class at time zero. This method is advantageous as: (1) it is relatively simple and can be based on one sample of the adult fish population only, thus the need for intensive surveying on an annual basis is not necessary; and (2) the temporal patterns in year class strength output can then be related to factors affecting each year class in its first year of life, such as temperature, flow regime and length achieved at the end of the first growth year (Beardsley and Britton 2012). As such, the use of year class strength indices provides a useful metric for describing the recruitment strength of current and previous year classes of fish in relation to known biotic and abiotic conditions (Goldspink 1978; Mills & Mann 1985).

4.6.4 Data collection and analysis

Adult fish population data

Electric fishing was used to assess the abundance, distribution and biometrics of the adult fish populations at the study site. Due to the increased mobility, reduced patch-fidelity and greater total numbers of adult fish, two-pass depletion electric fishing was used (Bozek & Rahel 1991; Lockwood & Schneider 2000). This was performed in early August and mid-September 2011 during the study period (Table 4.1), providing population density estimates (Section 4.6.5), scale samples for subsequent age and growth rate analyses, information on roach distribution at the stretch level (Figure 5.3a) and data on roach biometrics to parameterise a length-mass relationship (Section 4.5.6).

In these surveys, each stretch was 'closed' prior to fishing by placing stop nets across channel at the up-stream and down-stream boundaries (bold lines in Figure 4.3). Electric fishing was then completed from a boat using a generator (Honda, 500 KVA), supplying an Electra-catch electric fishing control box that transformed the current into pulsed DC (200 V) that was transmitted through the water via twin anodes and a single cathode. A two-pass depletion fishing method was used whereby fish were netted and removed from the stretch being fished, before being stored in aerated holding containers. The stretch was initially fished once, before a second pass was performed. The relative numbers of fish caught in the first pass and second passes was used to estimate the total stretch population. Firstly the probability of capturing a fish was calculated, followed by the estimate of total population numbers for each stretch following equations from Seber & Cren (1967):

$$P(capture) = \frac{P_1 - P_2}{P_1} \qquad \textbf{(Eqn 4.2)}$$

Where *P(capture)* is the probability of catching a fish during the electric fishing in a stretch of the river; P1 is the number of fish caught during the first pass; P2 is the number of fish caught during the second pass.

$$N = \frac{P_1}{P(capture)} = \frac{P_1^2}{(P_1 - P_2)} \qquad \textbf{(Eqn 4.3)}$$

Where *N* is an estimate for the total number of fish in the stretch being surveyed.

$$va(N) = \frac{P_1^2 P_2^2 (P_1 + P_2)}{(P_1 - P_2)^4} \qquad \textbf{(Eqn 4.4)}$$

Where *va(N)* is the variance in population estimate for the stretch being surveyed.

If the depletion was poor i.e.(there was little difference in the number of fish caught in the second pass, compared to the first pass), the probability of capture would be described as low, indicating low confidence in the population estimate (Seber & Cren

1967). Poor depletion using electric fishing could be caused by several factors, including difficult environmental conditions (e.g. high velocity or depth), inexperienced electric fishers or low population abundance. The electric fishing team consisted of experienced practitioners from the Environment Agency fisheries team and Bournemouth University, making poor depletion due to inexperience practitioners unlikely. As such, poor depletion (P(capture) < 0.2), was not observed during fieldwork at the study site.

The captured fish in each stretch were identified to species level, counted, measured (fork length, nearest mm), weight (nearest g), and scales were removed for subsequent age and growth rate determination (3 scales per fish).

Specific growth rate

Forager growth rates were calculated as specific growth rates according to Equation 4.5.

$$SGR = \frac{\ln(W_{tn}) - \ln(W_{t0})}{t_n - t_0} * 100 \quad \textbf{(Eqn 4.5)}$$

Where *SGR* is the specific growth rate, w_{t0} is the initial mass of a forager at survey time (t_0) and w_{tn} is the subsequent mass of a forager at survey time (t_n), finally t_n-t_0 is the number of days between surveys. SGR was calculated based on body length data (converted to weight) estimated from scale samples (see next sub-section).

Fish age and growth analysis from scales

Scales were viewed under a projecting microscope (×24, ×48, depending on scale size) and ages determined through identifying and then counting the annual growth checks (annuli) that are formed each year on the scales as a result of periods of faster and slower growth (Figure 4.7; Bagenal & Tesch 1978).
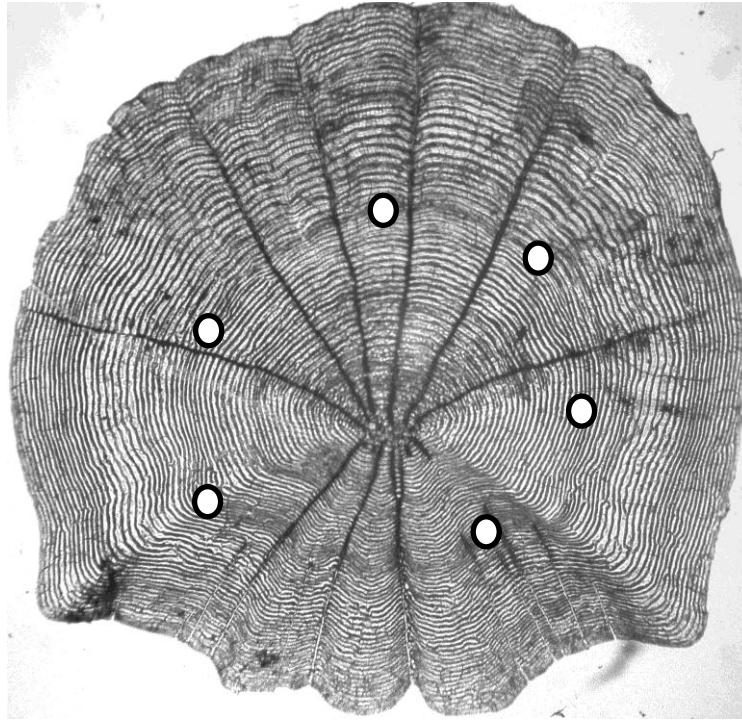
Figure 4.7 Scale removed from an age 1+ 82 mm roach from the survey site, captured during the second electric fishing boat survey. The white circle marks the annulus.

Following age estimation, through counting the number of annuli, the distances from the centre of each scale (scale focus) to the scale edge (i.e. the scale radius) and to each annulus were measured. For each fish, this enabled a comparison between the length at each age to the length at time of capture, and thus the growth increment produced during each growth year, in a process of back-calculation (Francis 1990; Horppila, & Nyberg 1999; Ibáñez et al. 2008). The back-calculated lengths were specifically determined using the body proportional equation (Dahl-Lea's method), as described in Francis (1990) in order to describe the relationship between body and scale size. While this provides an under-estimate of estimated length at age, due to the lack of a correction factor applied for the fish being of length when scales are formed, this was not an issue here as incremental growth rates (i.e. between age 1 and 2, 3 and 4 etc) were being used in subsequent analyses.

$$L_N = (S_N/S_T{}^{-1}) \, L_F \quad \text{(Eqn 4.6)}$$

Where L_N = Fork length of fish when annulus was formed, L_F = Fork length of fish when scale sample was taken, S_N = radius of annulus (at fish length L_N), S_T = total scale radius.

Adult roach distribution at the stretch level

The stretch level distribution is a measure of the distribution of the roach between the stretches as a proportion of the total in all five stretches at the field site. Stretch level proportional distribution was only available for adult fish of age class 1+ or greater, as smaller fish were sampled using PASE (Section 4.5), due to their higher fidelity to specific areas of habitat within the patches and the use of a smaller anode, designed to capture the smaller 0+ fish. The calculations were completed using Equation 4.7.

$$\text{Proportion}_{Strech(i)} = \frac{number \quad individuals \quad in \quad stretch_i}{total \quad number \quad individuals \quad in \quad stretch_{all}} \quad \text{(Eqn 4.7)}$$

Where i is the stretch being analysed and *all* is all the stretches in the virtual environment.

Estimation and analysis of roach growth rates in three lowland rivers

To assess patterns in the age and growth rates of populations of roach in three lowland rivers, the Suffolk Stour, Wensum and Great Ouse (Section 4.1.2) were used. For the study river, data from the study site were available from the surveys completed in 2011, and then for the upper River Stour generally (Section 4.1.2) for 2001, 2003, 2006 and 2009. These latter surveys were completed by the Environment Agency using the same electric fishing survey methodology as outlined in this section. For the River Wensum and Great Ouse, roach growth data were also obtained from the Environment Agency who collected these data in the same years and using similar methodologies as per the River Stour. The data available for each river were thus the age of each individual fish sampled, its year class (i.e. year of birth, calculated from year the sample was collected minus fish age), the back-calculated lengths at age, and the growth increment between each age.

To compare the growth rates of the roach across the three rivers, the initial step was to plot the back-calculated length at the last annulus of each fish (due to their sampling during their growth season) against its age on a scatter plot to identify the extent of the variability in the lengths at age across the study period. In assessments of back-calculated fish growth rates, statistical complications (e.g. auto-correlation, pseudo-replication) often occur through using repeated measurements from individual fish in the same test (i.e. all growth increments gained from back-calculated lengths). This was avoided here by the use of two methods: (1) comparison of the back-calculated length at the last annulus; and (2) the length increment produced between age 1 and 2 years.

Comparison of the back-calculated lengths at the last annulus across each river was completed through plotting the back-calculated lengths and ages of all roach from all surveys and all rivers, and fitting linear and quadratic models to the data; the best model was selected based on the smallest value of Akaike's information criterion (AIC) (Lappalainen et al. 2008); this was a 2nd order polynomial curve. The standardized residual of each individual fish was then stored and were compared across the three rivers, using a generalized linear model (GLM). This was used as it enabled the effects of year class (i.e. a temporal function) and age (in case of slower growing fish living longer than faster growing fish (i.e. Lee's Phenomenon (Stanley 1980)) to be controlled in the model. Outputs were the estimated marginal means of the standardized residuals for each river, their standard error, and the mean differences in the standardized residuals according to pairwise comparisons with Bonferroni adjustments for multiple comparisons. The rationale for then analysing the growth increment between age 1 and 2 years was that roach are generally immature at these ages and so energy resources for growth are used primarily for somatic growth, rather than gonad growth (in contrast to fish of age > 2 years) (Beardsley and Britton 2012). Thus, the growth increment of this component of the roach population was analysed by taking the mean increment and standard deviation of all fish from all surveys and all rivers, and then calculating the standardized residual for each individual fish. The standardized residuals were then compared across the three rivers using a GLM as described above.

Temporal recruitment patterns

Annual recruitment success was analysed for each roach sample collected from the River Stour (2001, 2003, 2006, 2009 and 2011) using the year class strength method of Cowx & Frear (2004). This comparative index of YCS was generated based on mortality in >1 year old fish:

$$N_0 = N_t \exp Z_t \qquad (\textbf{Eqn 4.8})$$

Where Z = Total mortality rate; N_0 = Numbers in starting population; N_t = Numbers at time t; and t = time. Year class strength was then calculated as the number of fish recruited divided by the mean number recruited from all year classes, multiplied by 100. Where a year class was present in more than one survey, the mean YCS value was calculated along with their standard error.

As year class strengths represent the relative recruitment strength of each analysed year class, the influence of factors affecting the year class when they were in their first year of life can be analysed (i.e. at 0+) (Nunn et al. 2003; 2007). Three factors were assessed here:

- Mean flow days above basal rate: this is a measure of the extent to which 0+ fish mortality and/ or downstream displacement could have been affected by high flow events (Nunn et al. 2003);
- Degree-days above 12°C in 0+ roach, years of higher air and water temperatures often result in stronger year classes through increased growth rates and greater food resources (Britton et al. 2004; Nunn et al. 2007); and
- Mean length at the end of the first growth year: larger body sizes at the end of the first growth year for 0+ fish are theorized as increasing over-wintering survival rates as they enhance the ability of the fish to hold station in elevated flows through fish swimming ability being positively correlated to body length (Nunn et al. 2003; Beardsley and Britton 2012).

Data on mean daily flow rates were available for the upper River Stour from the Environment Agency's flow monitoring station at Kedington (TL708450),

approximately 2.5 km upstream of the study site. The mean daily flow between June 1st and October 31st of all years was calculated to represent the basal flow rate. For each year, the number of flow days was then calculated using only days when flow exceeded the basal rate and was determined in two steps: (i) for each day between June 1st and October 31st, calculate whether flow exceeded the basal rate through Mean daily flow rate – basal flow rate; then (ii) Sum the total number of flow-days for each year using the data from (i).

Data on daily mean water temperatures were available using the water temperature data recorded in the study site by the TinyTag data recorders and their relationship with the Central England Temperature (CET) record (Section 4.3.1, 4.3.2). This enabled the daily water temperatures in the study site to be reconstructed using the CET data. For each year, the number of degree-days above 12 ^{o}C was calculated using two steps: (i) for each day in the first year of life of the year class, calculate whether the mean water temperature exceeded 12 ^{o}C, through Mean daily temperature – 12°C; then (ii) sum the total number of degree-days for the year using the data from (i). Data on the mean length at age 1 of each year class was available from the scale ageing and back-calculated length data already outlined.

4.6.5 Data outputs for roach ≥ age 1+ years

Fish abundance, biometrics and growth rates recorded at the study site

The number of fish and roach at the study site and in each stretch was estimated using two-pass depletion electric fishing (Section 4.6.4). The mean total abundance of roach from 2 separate electric fishing surveys (Table 4.1) was 238 roach of age ≥1 years. These roach were unequally distributed between the 5 stretches (Stretch 1, 18%; Stretch 2, 13%; Stretch 3, 43%; Stretch 4, 21% and Stretch 5, 5%). Specific growth rates were estimated through back-calculation of scale samples taken from fish captured at the study site (Section 4.6.4). This was performed for each year class of roach captured (1+ 0.62 % body mass day^{-1}; 2+ 0.43 % body mass day^{-1}; 3+ 0.29% body mass day^{-1}; 4+ 0.19% body mass day^{-1}; 5+ 0.16% body mass day^{-1}; 0.08% body mass day^{-1} and 7+ 0.04% body mass day^{-1}). At the study site, the mean 1+ roach length and body mass was 128.7 ± 21.8 mm and 37.2 ± 8.2 g respectively (Table 4.8).

Table 4.8 Mean, minimum and maximum length (fork) and mass of 1+ roach at the study site, the mean specific growth rate (% body mass per day) for 1+ roach is reported in Table 4.6 and not repeated here for the sake of parsimony.

	Length (mm):	Body Mass (g):
Mean 1+ roach:	128.7	37.2
Minimum value:	91.9	12.2
Max Value:	176.4	121.1
Standard Deviation:	21.8	8.2

Comparison of growth curves and incremental growth rates of roach across three UK lowland rivers

The data collected by the Environment Agency on roach age and lengths-at-age provided data on growth produced between 1995 and 2005 in 204, 782 and 261 roach across the Wensum, Stour and Great Ouse respectively. For the analysis of back-calculated length at last annulus, the standardized residuals from the 2nd order polynomial function (Figure 4.8) were used in the GLM. The model was not significant

(Wald Chi-square = 5.49, P = 0.06), with the effects of river, age and year class on length at the last annulus not being significant (P > 0.05 in all cases). The mean adjusted standardized residuals revealed no significant differences in length at the last annulus between the three rivers (Figure 4.9). For the growth increments produced between age 1 and 2 years, the GLM was not significant (Wald Chi-square = 5.31, P = 0.07), with the effects of river, age and year class on growth increments not being significant (P > 0.05 in all cases). The mean adjusted standardized residuals revealed no significant differences in length at the last annulus between the three rivers, although the difference between the Great Ouse and River Wensum was P = 0.06 (Figure 4.9).
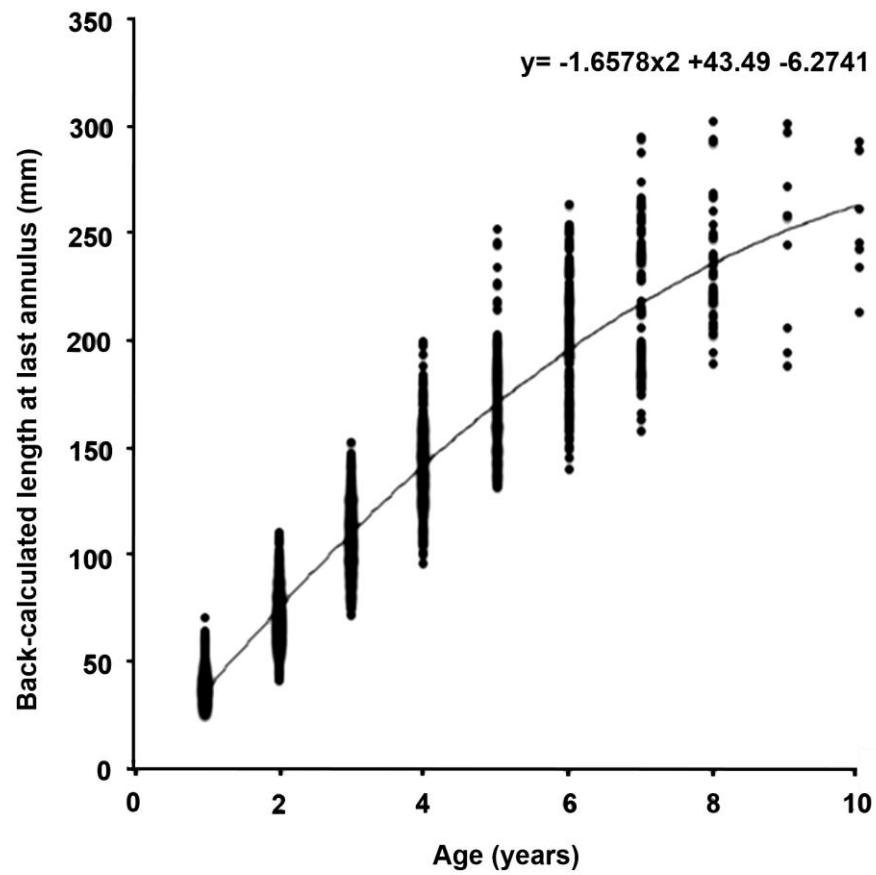
Figure 4.8 Back-calculated lengths at the last annulus for all roach sampled from the Rivers Great Ouse, Wensum and River Stour (filled circles; n = 1261), where the solid line is the second order polynomial curve and the equation in the top right of the plot is the equation describing the curve.
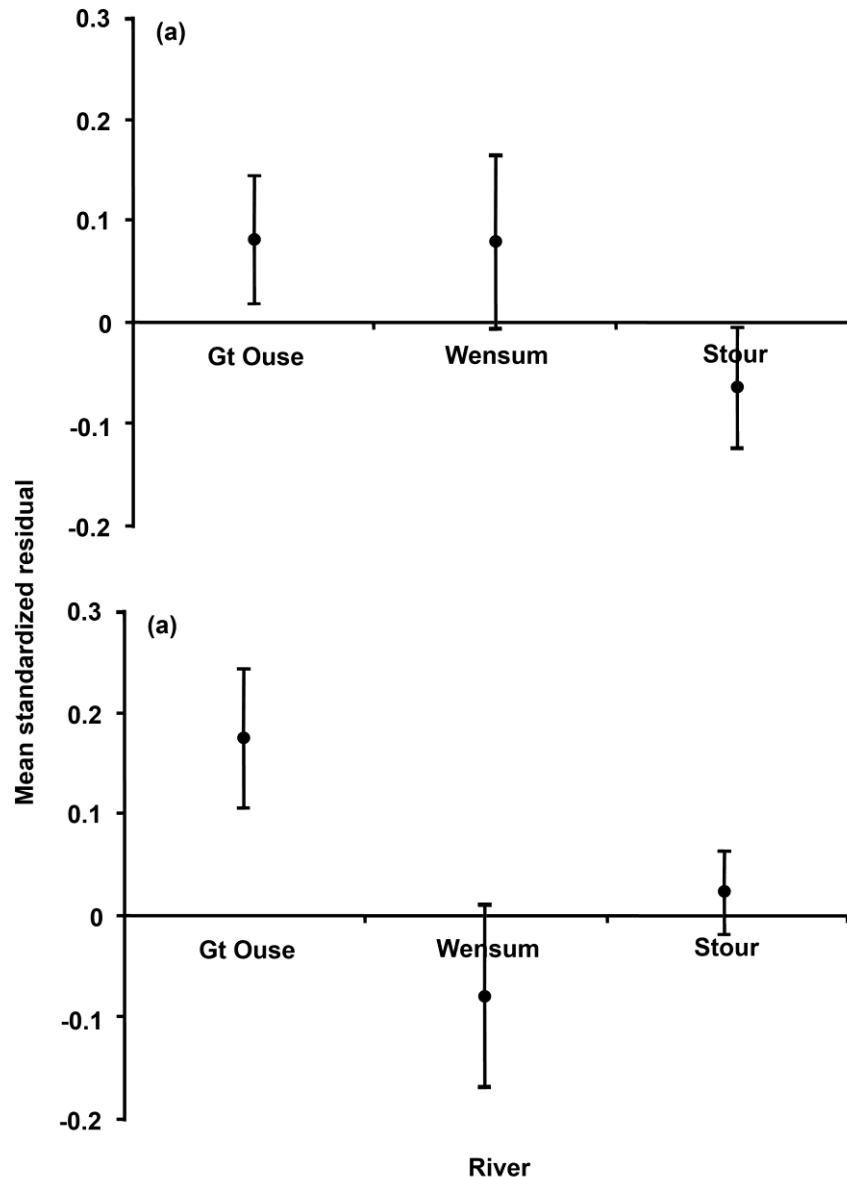
Figure 4.9 Mean standardized residuals, controlled for the effect of fish age and year of capture in a generalized linear model, and their standard error, for (a) lengths at the last annulus, and (b) length increment between age 1 and 2. Differences between the mean values were all non-significant (P > 0.05)

Temporal recruitment pattern

Between 1984 and 2009, year class strengths indicated strong periods of recruitment of roach in the River Stour were during the late 1980s and very early 1990s, the mid 1990s (especially 1996) and then 2004 to 2006 (Figure 4.10). Periods of poor recruitment were 1984 to 1987, 1993 to 1994, 2000 to 2003 and 2007 to 2009 (Figure 4.10). The

relationships between year class strengths and flow days above basal rate, degree-days above 12 $^{\circ}$C and mean length at age 1 were all significant according to linear regression (Flow: $R^2 = 0.29$, $F_{1,24} = 5.31$, $P < 0.04$; degree-days $>12^{\circ}$C: $R^2 = 0.22$, $F_{1,24} = 6.61$, $P < 0.02$; mean length at age 1: $R^2 = 0.34$, $F_{1,24} = 6.98$, $P < 0.02$; Figure 4.11). For mean length at age 1, the regression equation (YCS = [13.615 x mean length at age 1] − 397.36) indicated that a decrease in mean length of the year class of 0.5 mm decreased the year class strength by a value of 6.
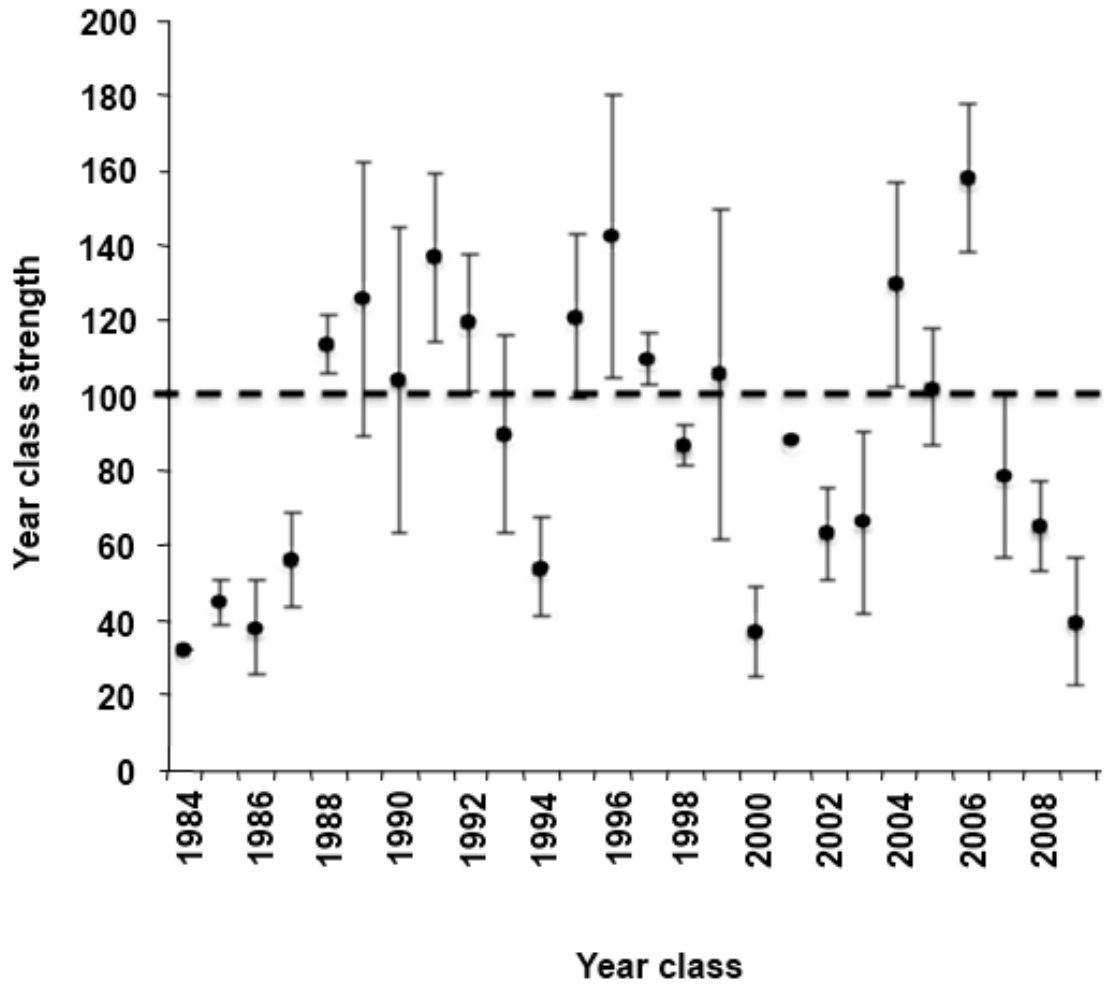
Figure 4.10 Year class strengths of roach in the River Stour, where a value above 100 represents strong recruitment for that year class with this marked by the horizontal dashed line.
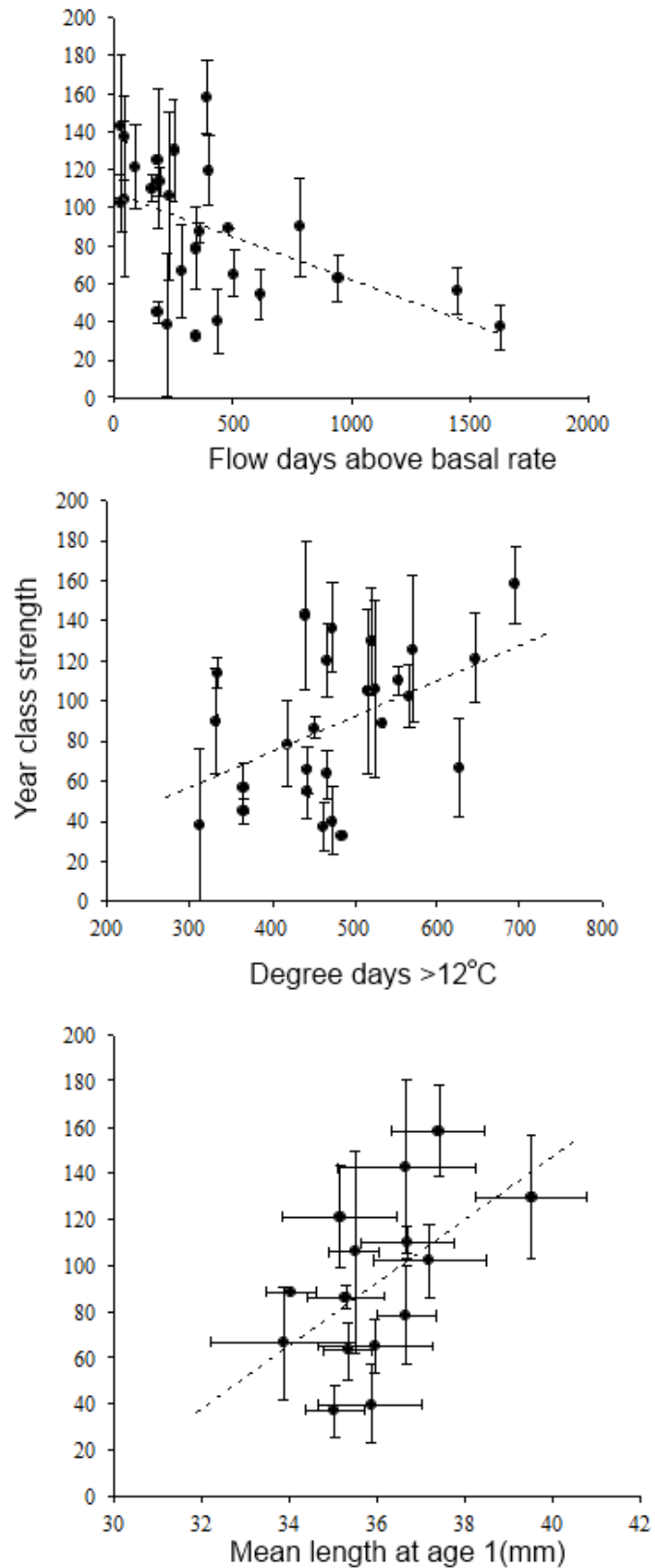
Figure 4.11 Relationship between year class strengths and flow days above basal rate, degree-days > 12 ^{o}C and mean length at age 1. The dashed line is the significant relationship between the variables according to linear regression.

4.6.6 Discussion for roach ≥ age 1+ years

Table 4.9 provides an overview of the data collected at the study site and described in this Chapter that will be used in Chapters 5 and 6 in order to construct and validate the roach IBM, simulating both 0+ and 1+ roach. This data were used in conjunction with the data collected on roach both at the study site and from the Wensum and Great Ouse which were also used to create forager variables for the IBM (Section 5.2.8), such as initial body mass and length, specific growth rate and variables derived from these values, such as swimming speed, reaction distance and various energetic parameters (Section 5.2.8; Table 5.1). While roach of greater age class than 1+ were recorded, the data collected was only used to describe population patterns such as growth curves (Figure 4.8) and to understand the population ecology of the study site. As such, only 0+ and 1+ roach were modelled, given the objectives of this investigation i.e. the emphasis on recruitment success and the period during which the greatest mortality occurs (Mills 1981; Bystrom & Garcia-Berthou 1999; Nunn et al. 2003). Furthermore, given the use of specific growth rate as a pattern for model validation, by concentrating on the age classes that represent the juvenile life-stage, recorded growth rates are not affected by gonadal growth, or subsequent spawning. While it would be possible to model older foragers, due to their reduced specific growth rates, increased variability in body size and energy budgets associated with reproduction (Figure 4.8; Table 4.6), this increased complexity would best be reserved for future work, concentrating on management outcomes that aim to address issues with the management of adult fish, for example, coarse fishing objectives, re-stocking exercises or predicting the impact of invasive species or parasites of adult fish.

Besides forager variables, the greater size and age of 1+ over 0+ fish, permitted the recording of specific growth rate though scale back-calculation, with this being used in model validation, following a pattern-oriented modelling approach (Grimm & Railsback 2012). Further to this, the use of two-pass depletion electric fishing and stop nets allowed the proportional distribution of the 1+ fish to be described. It was not possible to estimate potential changes in stretch-level distribution patterns, at the individual level i.e. the degree of fidelity to a specific stretch displayed by the tagged fish. The distribution of adult fish between the stretches could only be described in terms of

proportions of the whole population. Proportional distribution of captured roach, between the stretches, was used as part of the model validation process. The datasets used in addition to sampling at the study site also allowed habitat association and growth rates in relation to fish age to be described in all three rivers.

As for growth rates, the outputs of both the growth curves and growth increments between 1 and 2 years, produced in each river were not seen to differ significantly between the rivers, whilst also being similar to growth curves and growth increments in other riverine roach populations (Britton 2007; Mann et al. 2007; Ibanez et al. 2008). Given the fundamental role of growth and body size in the recruitment success and therefore, year class strength of juvenile fish (Bolland et al. 2007; Beardsley & Britton 2012), it was important to ensure the virtual foragers closely matched the real population in response to environmental conditions, including prey item availability bioenergetic factors. As there were no significant differences in growth curves or increments between the three river data sets (Section 4.3.3), this reinforces the idea that the Stour is a typical lowland river and therefore the IBM predictions, in the form of river management recommendations, may be applied across similar lowland riverine systems (Shugart 1992; Letcher et al. 1996).

In terms of recruitment, it was apparent that length at the end of the first year of life was an important factor influencing year class strengths, with years of low flows and higher temperatures contributing to strong year class strengths. It is likely that these factors are all inter-related, with years of high temperatures and low flows enabling the 0+ roach to growth faster through increased food supply and energy assimilation (Nunn et al. 2003, 2007). Moreover, the regression equation of year class strength versus mean length at age revealed a decrease in mean length of 0.5 mm reduced year class strength by a value of 6. As an output of the IBM, the effect of river management on 0+ roach growth can also now be related to an change in their recruitment success, i.e. should the model predict a reduced 0+ roach growth, this will then negatively impact their recruitment success.

Table 4.9 Summary of Chapter 4 outputs for the development and validation of the roach IBM

The outputs of this chapter that will be used in Chapters 5 and 6 are detailed in Table 5.1

Model parameter	Data type	Output
Number of Stretches	Environment	5 stretches
Number of Patches	Environment	34 patches
Mean Water Temperature	Environment	14.2 ^{0}C
Mean Patch Area	Environment	86.7 m
Mean Water Depth	Environment	0.76 m
Mean Macrophyte cover	Environment	25%
Mean flow (Open Channel)	Environment	0.62 ms^{-1}
Mean flow (Bank-side Channel)	Environment	0.23 ms^{-1}
Mean Turbidity	Environment	4.23 FTU
Mean Benthic energy	Invertebrate	2.92 KJ/m^2
Mean 0+ Fork Length	0+ Roach	33.4 mm
Mean 0+ Body Mass	0+ Roach	2.68 g
Mean 0+ SGR	0+ Roach	0.99 % body mass day^{-1}
Mean 1+ Fork Length	1+ Roach	128 mm
Mean 1+ Body Mass	1+ Roach	37.2 g
Mean 1+ SGR	1+ Roach	0.62 % body mass day^{-1}

4.7 References

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5. Predicting growth and distribution of roach in lowland rivers: an individual-based modelling approach

This chapter incorporates the foraging behaviour data from forager experiments (Chapters 2 & 3) and fieldwork data (Chapter 4) in order to describe the construction of an IBM for roach. The final developed model represents the product of the work detailed in the previous chapters and will be applied subsequently to predicting how aspects of river management influence the roach population (Chapter 6).

5.1 Introduction

Freshwater resources provide key ecosystem services, including potable water, sewage treatment and disposal, sport fishing, aquaculture, and protection from natural hazards such as flooding (Acreman & Ferguson 2010; Gozlan & Britton 2013). However, as open and dynamic systems, freshwater resources are under threat through issues including pollution, abstraction, over-exploitation and biological invasions (Dudgeon et al. 2006, Vörösmarty et al. 2010). Consequently, the prioritisation of the human demands on freshwater is required if the major ecosystem services are to be protected and maintained. As the subsequent management actions can have consequences for other aspects of the ecosystem then it is important that the consequences of management actions are understood, for example how flood defence schemes might increase protection for property at the cost of in-channel habitat heterogeneity (Downs & Thorne 2000) To understand the ecological consequences of such management actions, it is advantageous to measure the responses in species that are generalist (as specialist species are most likely to respond negatively to change anyway through their specific requirements, whereas generalist species might have some capacity for adaptation) and ubiquitous, as any negative consequence could then have far-reaching impacts at the population and community level (Holker & Breckling 2001). In European lowland rivers, roach is a successful generalist fish, where it is usually the numerically dominant species in the fish community, especially in riverine habitats that have been heavily modified by management actions such as for flood risk management (Schulze et al. 2006; Beardsley & Britton 2012). For these reasons, the species has been well studied, meaning that their responses to disturbance events, such as their rates of somatic

growth, survival and recruitment, are strong indicators of the extent of the disturbance (Holker & Breckling 2001; Schmutz 2004).

River managers have a range of tools to inform their management decisions, such as habitat association and demographic models (Railsback et al. 2003). However, these are often reliant upon historical data and extensive data gathering. Further, these models are often based on empirical relationships that may change markedly under different environmental conditions (Railsback et al. 2003). This limits their ability to predict how proposed management scenarios will affect aspects of river ecology. For example, the removal of instream macrophytes is a common management practice in lowland rivers that reduces flood risk and maintains the navigability of the channel (Acreman & Ferguson 2010). In removing this macrophyte cover, however, there is also a concomitant increase in flow rate. The consequence of this mass macrophyte removal and increased flow regime on aspects of fish ecology and population demography, such as rates of growth, recruitment and survival, can currently only be assessed post-removal (Garner 1996), discouraging the use of more novel approaches to managing flood risk through macrophyte control (Bass & Collett 1996; Watkins et al. 1997).

The lack of power of these models to predict ecological changes under different environmental conditions does not apply to individual-based models (IBMs), as they are based on individuals within the system and can incorporate their adaptive behaviours in response to individual, population and environmental parameters (Judson 1994; Grimm & Railsback 2005). These individual decisions are based on the principle of fitness maximising behaviour and the behaviours that emerge from these decision processes (Stillman & Goss-Custard 2010). As fitness maximising behaviour is a product of natural selection, it is assumed that animals in an IBM respond to environmental changes in the same manner as animals in the real world (Grimm & Railsback 2005; Stillman & Goss-Custard 2010). This means IBMs rely less upon historical data and, as fitness maximising behaviour should remain unchanged under different biological conditions, predictions can be made for how the population responds to a wide range of scenarios (Stillman 2008). By modelling cumulative interactions at the level of individuals, patterns at the population level may then be described. This has been shown to be successful in producing robust predictions for population dynamics under

scenarios of environmental change in a range of applications, including management of costal birds populations (Stillman & Goss-Custard 2010; Toral et al. 2012), aggregation of sea snails (Stafford et al. 2007), and increasingly in other species (Philips et al. 2003; Railsback et al. 2009; Sibly et al. 2013).

In recent years, a range of IBMs have been developed that build on the successful use of IBMs for managing coastal bird populations in relation to development (Stillman & Goss-Custard 2010; West et al. 2011). The development of IBMs for freshwater fish has the potential to provide a strong tool to advise managers of potential outcomes of their actions through predicting how fish populations respond to proposed river management schemes. This has been demonstrated in both fishes of the Salmonidae (Railsback & Harvey 2002; Railsback et al. 2009) and Cyprinidae families (Holker & Breckling 2002; Holker et al. 2002), and in both riverine and lake systems (McDermot & Rose 2000; Breckling et al. 2005; Li et al. 2010).

The IBM to be developed here will be used to predict how roach populations respond to river management schemes designed to decrease flood risk through macrophyte control. It builds upon, and further develops, previously accepted IBM frameworks, specifically the MORPH IBM framework (Durell et al. 2006; Stillman 2008). To clearly describe and explain the development and replication of the model, this Chapter will use the Overview, Design and Details (ODD) protocol (Grimm et al. 2006, 2010). The developed IBM will be spatially explicit, using bioenergetics and associated potential growth parameters to determine behavioural decisions of movement and time budgets. The results will focus on growth and recruitment of juvenile *R. rutilus* in heavily modified lowland rivers, where such outcomes can effect trophic interactions (Nilsson 2001; Martin et al. 2010), biodiversity patterns (Pinder 1997; Clark et al. 2012) and environmental health assessments (Schiemer et al. 2002; Schmutz 2004). The IBM will be validated using the 'pattern-oriented modelling' approach (Grimm & Railsback 2005) and the results interpreted from a river management perspective.

5.2 Materials and Methods

5.2.1 Virtual environment

The virtual environment modelled in this chapter is designed and parameterised to reflect environmental conditions in the Suffolk Stour River, UK, during the summer of 2011. For a detailed description of the environmental data collected in order to parameterise the virtual environment and the study site itself, see chapter 4.

5.2.2 Model description

Overview

This roach IBM is designed to predict the behaviour of juvenile roach in a lowland river environment. Young-of-the-Year (YOY) and 1+ roach interact with the virtual environment, performing adaptive behaviours related to habitat selection and feeding behaviour. These behavioural decisions are defined by bioenergetic outcomes on forager growth rate and, by extension, survival and recruitment, as these are influenced by body size. This roach foraging IBM is based on the MORPH optimal-foraging individual-based modelling platform (*c.f.* Stillman 2008).

A field study of natural roach distribution and growth patterns in lowland river environments was undertaken (Chapter 4) to provide population and environmental data to parameterise and validate the model. The virtual environment is parameterised to simulate the observed environmental conditions, while the foragers are parameterised and initialised from the population data collected at the start of the field study.

5.2.3 Purpose

The model is designed to produce valid and useful predictions about population level distributions and bioenergetics of the juvenile roach population, described as information on location (or mesohabitat utilisation) and somatic growth rates (hereafter referred to as growth rates) respectively. This model will be applied to understanding how changes in river management influence these life stages of roach, as well as other cyprinid fish, as it is in these age classes when they are most vulnerable to displacement and mortality. The specific management regimes considered are in-stream macrophyte

removal and flow rate regulation as these are commonly applied to lowland rivers across Europe (Garner 1996).

Model validation will be based on comparisons of virtual versus observed patterns of fish behaviour and growth over the summer growth period, the critical period for fish that influences their ability to survive the subsequent winter period (Nunn et al. 2003, 2007). Model predictions will be validated by identifying and comparing several complimentary patterns found in both the virtual, modelled environment and the fieldwork data, as defined by the 'pattern-orientated modelling' (POM) methodology (Grimm & Railsback 2005).

5.2.4 Entities, state variables and scales

The MORPH framework is based on a system of entities whereby global, patch and forager entities are described in decreasing order of scale: (i) global parameters are applied throughout the modelled system, (ii) patch parameters describe patch-specific variables, and (iii) forager parameters describe foraging animals within the system, consuming diets and assimilating components.

5.2.5 Spatial extent of the model

The model global environment represents a 220 m stretch of heavily modified lowland river, with a mean wetted-width of 9.5 m. The virtual environment is further divided into mesohabitats and macrohabitats; the mesohabitats are defined as 'patches' comprising areas of relatively homogeneous environmental characteristics, such as water velocity, macrophyte cover and depth, with a mean area and standard error of 85.1 ± 19.2 m^2. The macrohabitats, or 'stretches' are comprised of a series of these patches, chosen on the basis of more general morphological similarity with 5 stretches in the river, mean area 562.6 ± 113.0 m^2 (see chapter 4 for more detailed information of the study site). As the modelled system is considered closed, modelled foragers are not able to leave the system once they have entered.

5.2.6 Global parameters

Global parameters are those that affect the entire modelled environment. Global variables include the total duration of model simulations which comprises of time steps

within the model, each of one hour in length. Water temperature, discharge and turbidity are also modelled across the virtual environment (Table 5.1a).

5.2.7 Patch parameters

Patch parameters are those that vary spatially within the modelled environment, with each patch having physical variables including area and location. Variables including water depth, flow rate and turbidity are described relative to a global value. Sequentially located patches of similar environmental characteristics are grouped into stretches, with variables of predator density, zooplankton prey density and invertebrate prey density being constant within a stretch (Table 5.1b).

5.2.8 Forager parameters

Each simulated forager has a variable that describes its body mass, as well as a range of variables that relate to its feeding, behaviour and bioenergetics, including reaction distance, swimming speed, handling time, consumption rate, respiration rates and the food items that are available for its consumption. Further parameters are used to describe initial body mass, initial length and arrival stretch (Table 5.1c). Foragers are divided into groups, defined by their age. These *forager types* are listed as 'YOY' for roach of 0+ years and 'OnePlus' for roach of 1+ years.

Global parameters: Table 5.1a   *The global parameters and formulas used to describe the virtual environment of this roach individual-based model (mean ± SE).*

Simulated time period (days)	115	This study P148
Time step length (hour)	(Simulated dates)	This study P142
Day length (hours)	1 (2760 in total)	This study P148
(Approx hours of light)	24	This study P88
Water temperature (°C)	13.3 ± 1.5 Deg C	This study P88
Discharge (m^{-3}/s)	0.49± 0.2	This study P142, 88
Turbidity (FTU)	4.6 ± 0.8 FTU	This study P88

Patch parameters: Table 5.1b   *The patch parameters and formulas used to describe the virtual environment of this roach individual-based model (mean ± SE).*

Stretches number	1-5 (Total 5)	This study P84
Patches number	1-34 (Total 34)	This study P84
Mean patch area (m^2)	86m^2 ± 9.1	This study P84,90
Mean water velocity (ms^{-1})	0.12 ± 0.03	This study P88, 90
Mean water depth (depth, m)	Variable, mean value of 0.99 ± 0.22	This study P88, 90
Mean benthic invertebrate density (individuals/m^2)	2.2 ± 0.45	This study P94
Invertebrate prey energy density (KJ d.w. g-1)	23.002	This study P94
Mean zooplankton density (individuals/m^2)	3468 ± 625	This study P97, 150
Zooplankton prey energy density (KJ d.w. g-1)	12	This study P97, 150
Large predator density (ind/ m^3)	0.01	This study P151
Small predator density (ind/ m^3)	0.02	This study P151

Forager parameters: Table 5.1c   *The forager parameters and formulas used to describe the virtual environment of this roach individual-based model (mean ± SE).*

Total number of individuals	325	This study P152
Number of YOY individuals	200	This study P152
Number of OnePlus individuals	125	This study P152
Mean initial body length of YOY fish (mm)	22.2 ± 0.68	This study P101
Mean initial body length of OnePlus fish (mm)	80.5 ± 2.1	This study P119
Mean initial body mass of YOY fish (mm)	0.5 ± 0.2	This study P101
Mean initial body mass of OnePlus fish (mm)	11.04 ± 2.13	This study P119
Relationship between length and weight	Log10 Mass= -2.559+3.55*(Log10 Length)	Papageorgiou (2006)
ReactionDistance (mm) (RD)	0.179*((BodyMass+2.442)/3.36)^0.3028	This study P62
Maximum swimming Speed (cm s-1)	Log$_{10}$((BodyMass-2.55)/3.55)-0.029125	Mann & Bass (1997); This study P61, 65
HandlingTime (s)	0.5*(RDistance/MaxSpeed)+0.5*(RDistance/Flowrate)*Prey item mass	Hughes et al. (2003); This Study P35
Maximum consumption rate (s individual prey item^{-1})	(0.01825*(BodyMass^0.84)*EXP((0.133*Temperature)/24)/Prey item mass)	Holker & Breckling (2002); This study P145
Maximum respiration Rate (mg O2 h-1)	(0.034*(BodyMass^0.785)*^(0.088*Temperature))	Koch, Wieser & Niederstatter (1992); Holker & Breckling (2002)
Standard respiration Rate (mg O2 h-1)	(0.034*(BodyMass^0.76)*^(0.088*Temperature))	Koch, Wieser & Niederstatter (1992); Holker & Breckling (2002)
Digestion Respiration Rate (mg O2 h-1)	(Rmax-Rstandard)	Koch, Wieser & Niederstatter (1992); Holker & Breckling (2002)
Energetic cost of swimming while feeding (mg O2 h-1)	0.07*((Velocity)^0.64)*(BodyMass^0.60)	Holker et al. (2002);Hammer et al. (1994)
Energetic cost of low intensity swimming (mg O2 h-1)	(0.9)^1.22*(BodyMass^0.89)	Holker et al. (2002);Hammer et al. (1994)
Specific energy density (KJ)	5.08*BodyMass	Schreckenbach, Knoesche & Ebert (2001)

5.2.9 Environmental variables

At the start of each time step, the global parameters are initialised, followed by the patch and forager parameters. Once defined, the environmental parameters remain unchanged for the duration of the time step. Prey resource densities experience depletion when a prey item is removed from the system following consumption by a forager. However, at the start of each time step, the resource density is assigned a value based on estimates from fieldwork data (Peterson 1962; Hildebrand 1974; Dimond 2013), meaning the resource density is associated with real prey item densities, while the influence of forager activity only affects the time step in which it occurs.

5.2.10 Forager processing and scheduling

Forager scheduling is random, reflecting the lack of dominance behaviour in roach (Persson 1987). During the first time step when all foragers enter the model, each forager is randomly assigned an arrival stretch, with an even distribution between the 5 stretches. Each forager is initially able to occupy any patch within their assigned arrival stretch, selected on the basis of their user-defined fitness measure. During subsequent time-steps forager patch assessment is restricted to 15 m for 0+ fish and 30 m for 1+ fish, reflecting the ontogenetic shift in swimming performance of roach (Mann & Bass 1997; Ohlberger et al. 2006). This effectively limits the 0+ foragers to the patch it currently occupies and one patch upstream or downstream, and for 1+ foragers, to two or three patches upstream or downstream, with the patches chosen based on their associated fitness measures.

During a time step, foragers can select one of two behaviours, 'feeding' or 'resting', with these having associated swimming costs. When consuming benthic invertebrates, this cost is a function of swimming speed as well as forager and environmental parameters. When filter feeding, the swimming cost is a function of forager and patch parameters (Holker & Breckling 2002; Ohlberger et al. 2006; Sagnes & Statzner 2009). It is only during this 'feeding' behaviour that prey items are consumed and patch water velocity directly influences swimming costs. During the 'resting' phase, swimming cost is reduced, relative to the feeding phase, and related to forager parameters including body length (Holker et al. 2002; Railsback & Harvey 2002).

Energy from consumed prey items undergoes loss through imperfect energy assimilation and the bioenergetic costs of digestion, swimming costs and metabolism. This energy budget is converted into growth (positive or negative) by dividing net energy intake by the specific energy content for roach. Forager diet consumption rate is regulated by a Type I functional response during filter feeding and a Type II response during predation on benthic invertebrates (Holling 1959; Jeschke et al. 2004; Holker & Haertel 2006; Chapters 2 & 3). A maximum consumption rate is also set by a maximum hourly intake capacity, an allometric function of fish mass based on feeding experiments (Holker & Breckling 2002; *c.f.* Chapters 2 & 3). The body mass and energetic store of each forager is calculated and updated every time step.

Design concept

5.2.11 Basic principles
MORPH is based on the principles of optimal foraging theory (Stillman 2008), whereby foragers select behaviours aimed at achieving a user-defined 'fitness measure'. By incorporating growth, predation risk and habitat preference into the fitness measure, foragers will distribute and grow inside the virtual environment accordingly. The IBM is parameterised using published roach feeding information and bioenergetics equations.

5.2.12 Emergence
The model does not explicitly define i) the distribution patterns of the foragers at the stretch level (with the exception of the first time step, where the stretch population is evenly distributed to represent the lack of distribution information prior to the start of the study period); ii) the patch to be occupied by an individual; and iii) the growth rates of foragers. Distribution patterns emerge during model simulations as a result of individual forager adaptive behaviours that are in relation to the user-defined fitness measures. The initial distribution is defined at the macrohabitat (stretch) level, but which patch the forager occupies within the stretch in not restricted, with this being true of all simulations. After the first time step, there are no restrictions on movement between patches or stretches, so as foragers move within the virtual environment, distribution patterns emerge at the macrohabitat (stretch) and mesohabitat (patch) scale.

Growth rates are derived from bioenergetic inputs, generated by forager adaptive behaviours, traits and environmental variables.

5.2.13 Adaptation and fitness

Forager adaptive behaviours are i) the ability to move between patches and stretches, selecting patches based on returns of the fitness measure; and ii) the choice between spending the time-step feeding or resting, based on functional response rates of foraging for prey items and the associated bioenergetic costs.

5.2.14 Objectives

The principal concern of the foragers is to increase their energy stores, leading to growth in body mass and length. Roach experience a primary growth period in lowland rivers during the warmer summer months when rivers tend to be more productive, prior to cooler and cold conditions where little growth is expected; in mature individuals, warmer periods early in the summer are also associated with spawning behaviour (Mills 1981; Koch et al. 1992). The amount of body growth produced is a function of net energy intake and is influenced by both environmental conditions (patch resource density, temperature, flow rate, turbidity) and forager parameters (body mass, reaction distance, diet consumption rate, swimming speed). Depending on the user-defined fitness measure, a forager may consider the risk of predation, or benefit of macrophyte cover, in the patches that it could occupy, if it is possible to achieve a maximum prey item consumption rate in several potential locations.

5.2.15 Learning

This model does not explicitly contain any mechanisms for forager learning, foragers are provided with complete awareness of parameters and variables from the start of the simulation.

5.2.16 Prediction

Predictive behaviour is only displayed by the foragers at the start of each new time step, when they select the behaviour that will result in the highest fitness values. No predictions are made regarding future fitness, conditions or growth, beyond the current time step.

5.2.17 Sensing

Foragers have complete knowledge of the state variable of the patches within their patch location distance, which is restricted to their current patch plus 15 m upstream or downstream for 0+ fish and 30 m upstream or downstream for 1+ fish, reflecting the difference in swimming performance between the forager types.

5.2.18 Interaction

Foragers interact indirectly as consumption of prey items removes them from the prey item resource density, resulting in a reduced number of available prey items. However, given the density of prey items and maximum consumption rate, this interaction is not likely to result in altered adaptive decisions. More direct interactions occur when assessing the predation risk of a patch, this being a function of predator density and the number of similarly vulnerable foragers within a patch. There is no interaction through competition for space, territory or dominance, reflecting a lack of dominance behaviour in roach (Persson 1987).

5.2.19 Stochasticity

At model initialisation, the initial body length and mass of each forager is assigned, drawn from a normal distribution with the mean and standard deviation values based on recorded observations and controlling for age. A stochastic process is also used when deciding the order with which the foragers of the same forager type are handled by the model. Finally, under circumstances when several available patches all return the same fitness values, the forager will select a patch randomly.

5.2.20 Collectives

A forager in the model represents a single individual forager.

5.2.21 Observation

Morph saves output data at user-defined time steps; output comprises all global, forager and patch parameters, as well as diet parameters, as per Stillman (2008). For subsequent analysis and validation, the time steps chosen correspond to the dates on which fieldwork took place. MORPH also produces a colour-coded graphical output,

displaying the location of each forager, patch and stretch, allowing observation of potential patterns and behaviour as the simulation progresses.

Details

5.2.22 Initialisation

The virtual environment is initialised at the start of each simulation, using external files detailing the environmental parameters that are read-in (Table 5.1a & 5.1b). A total of 325 foragers are initialised, comprising 200 0+ (YOY) and 125 1+ (OnePlus) fish. Each forager has an initial body mass and length drawn from a normal distribution, specific for its age class (Table 1c). Similarly, during initialisation, each forager is randomly assigned an arrival stretch, with an even distribution between the 5 stretches, the forager then decides which patch it first enters, based on the user-defined fitness measure.

5.2.23 Input data

Environmental variables can be dynamic during a simulation, but do not differ between simulations unless they are further altered prior to simulation, for example as part of scenario testing. The parameters are read into the model from external files detailing the value of a specific variable for each time step, with the same external files used for every simulation, unless they are modified by the user for comparative study or testing. The environmental parameters are not influenced by forager activity; after model initialisation, all changes to forager parameters result from interactions between the foragers themselves or between foragers and the environment.

Submodels

5.2.24 Environment

An entire simulation run represents 115 days, each divided into 24 hours (i.e. 24 time steps); of this, 41 simulated days is used during model validation in order to correspond to fieldwork data on fish growth and distribution. Water temperature for each time step was measured in the field and averaged to give mean daily temperatures, with these values calibrated for each patch using field survey data. Other environmental variables comprise flow rate, turbidity, depth, patch area and macrophyte cover, with these being read from files based on recorded data for each patch (Chapter 4). Flow rate and

turbidity values are provided for each time step, while depth is averaged to give a daily mean. Finally, patch area and macrophyte cover are constant throughout the simulation, unless modified as part of scenario testing.

5.2.25 Resource (Benthic invertebrate) density

Invertebrate drift nets were used to characterise the population size structure and abundance of macro-invertebrate drift in each stretch (Chapter 4). Known biases in sampling drift densities, arising from net clogging and complex flow issues (Faulkner & Copp 2001) were addressed by attempting to estimate proportional differences in drift abundance and size ranges of invertebrates between each stretch. It is assumed that whilst sampling bias may affect the estimates of total drift density, this should be constant when estimating size distributions and proportional differences between stretches.

Given the relationship between benthic invertebrate density and invertebrate drift of aquatic origin (Hemsworth & Brookers 1979; Brittain & Eikeland 1988), it is possible to make estimates of benthic invertebrate energy availability by recording drift invertebrate density and energetic content, while controlling for the effects of invertebrate size and density dependence on drifting potential (Peterson 1962; Hildebrand 1974; Dimond 2013). By defining a relationship of 23.5% of recorded drift invertebrate densities being available as benthic invertebrate prey (Diamond 1967; Herpher 1998; Haertel & Eckmann 2002; Holker et al. 2002), it is possible to estimate the number of benthic invertebrates in each stretch based on drift sampling and patch area. Drift sampling was performed in each stretch, three times a day (at dawn, midday and dusk), with these time periods used as temporal reference points with a linear interpolation between the points in order to fit the invertebrate densities at time steps between the sampling reference points. Similarly, a linear relationship is also used to estimate resource densities between sampling dates; this approach makes the least assumptions about potential changes in resource densities during the intervening period.

For each invertebrate captured of aquatic origin, their average dry mass (mg), energy density (KJ g^{-1}) and energy content (J) was calculated using published length-mass, mass-energy relationships (Cummins & Wuycheck 1971; Ganihar 1997; Benke et al.

1999; Sabo et al. 2002). This enabled conversion of drift densities into energy, relative to the area searched. This allowed the amount of energy available in each stretch to be calculated, from which the amount of energy available as benthic invertebrates could be estimated. No drift feeding behaviour was modelled this only occurs in roach under conditions of relatively high visibility that allow drifting invertebrates to be visible (Diel 1988; Fladung et al. 2003; Nurminen et al. 2010; Chapter 3). As such, drift feeding was not expected to occur at all during night-time light levels, or under conditions of high turbidity.

5.2.26 Resource (filter-feeding prey) density

Known intake and evacuation rates of roach (mg dry mass hour^{-1}), collated from literature (Karjalainen et al. 1997; Haertel & Eckmann 2002; Specziar 2002), were used to estimate the amount of filter feeding prey items that would be consumed by the foragers, based on their body size and water temperature. By combining this information with data on the mass and energetic content of various potential prey items (Persson 1983; Karjalainen et al. 1997; Viroux 1997; Garcia-Berthou 1999; Mehner 2000), the amount of energy available to the filter feeding roach could be estimated. Given the generalist foraging and feeding behaviour of roach (Stenberg & Persson 2006), the filter-feeding prey items comprised zooplankton, plant matter, algae and detritus. It has been shown that in the presence of piscivorous predators, such as pike (*Esox lucius*) and perch (*Perca fluviatilis),* roach will move from a mainly zooplanktivorous diet to consuming a greater proportion of plant matter and detritus, producing an overall, approximately even distribution between the main filter-feeding components (Holker et al. 2002). This pattern is also repeated during the hours of darkness. The mean value of energy per individual item (J mg^{-1}) and mean mass per item (mg) were combined across the filter-feeding prey items to create an estimated value for the energy resource density available for filter feeding roach across the system, with no variation between the stretches.

Diet shifts associated with ontogenetic changes are handled by the model using a forager parameter of available diet, whereby foragers are restricted to filter feeding during their earlier developmental stages before switching to predating upon

invertebrates as they develop, with this controlled by total body length (Van Den Berg et al. 1994; Hjelm et al. 2003).

5.2.27 Predator densities

The study site is representative of lowland riverine systems (Chapter 5). As such, the main aquatic predators of roach were pike and perch (Schulze et al. 2006). Data on the abundance and distribution of pike and perch at the stretch level were collected during fieldwork along with the collection of data on roach, (Chapter 4). Pike and perch were divided into two classifications, separating them into 'small' and 'large' predators according to their gape size as this determines the maximum size of fish they can capture, handle and consume, resulting in prey size selectivity (Nilsson & Bronmark 2000; Dorner & Wager 2003). Effectively, the small pike, large pike and small perch groups are modelled to act as the predators of the smaller roach in the model population (YOY), while the large pike and large perch groups act as the predators of the larger roach in the model population (1+). For pike, this classification threshold was below 350 mm total length for the smaller pike category and above 350 mm total length for the larger pike category (Nilsson & Bronmark 2000), with this reflective of the pike population structure of the study site (see Chapter 4) as well as the gape-size limitation (Nilsson & Bronmark 2000). For perch, the classification threshold used in the model dictated that perch of total body length between 9.6 mm and 31.1 mm would be able to predate 0+ roach, while the larger predator classification was restricted to perch between 103.7 mm and 345.4 mm total body length. These classifications were based on maximum and minimum prey size ratios, limited by gape-size, detection probability and energetic cost/benefits (Dorner & Wager 2003). In the model, this equates to all 0+ and 1+ roach below a total body length of 170 mm being vulnerable to both large and small pike and small perch, while roach above this threshold are only vulnerable to large pike and large perch.

Pike and perch predator densities, after being classified and combined into large and small roach predators, are modelled as environmental parameters at the stretch level (number of predators m^3), with each patch within a stretch having equal densities.

5.2.28 Forager types

Each forager is defined by their forager type, based on their age class with 'YOY' forager type being 0+ roach and 'OnePlus' forager type being 1+ roach. These forager types allow for a more accurate representation of the observed juvenile population structure, with the forager types differing in their distribution functions related to initial mass and length. Both forager types are not required for the model to run and further, while the number of foragers of each forager type is representative of field observations, they may be easily modified by the user for future work, including scenario testing and application to alternative river systems.

5.2.29 Population characteristics

The total number of individuals, of both forager types, is derived from actual population estimates, based on field observations, of the initial electric fishing survey. Population age structure is calculated from scale samples (Horppila, & Nyberg 1999; Ibáñez et al. 2008), with length-weight relationships and population characteristics recorded. Initial forager body mass and length are drawn from a normal distribution of these variables, for each forager type (Chapter 2).

5.2.30 Forager bioenergetics

Research has already been completed on roach bioenergetics (Karjalainen et al. 1997; Holker & Haertel 2004; Holker 2006), including their application to individual-based models (Holker & Breckling 2001, 2002) and comparison to wild populations (Koch et al. 1992; Holker 2003, 2006). The equations detailed in Holker (2003; 2006) and Holker & Breckling (2005) that provide units in calories day $^{-1}$ were converted into KJ hour^{-1} (1 calorie = 4.1868 KJ). Equations dealing with respiration and oxygen consumption rates (Holker & Breckling 2005) also provide information in units of mg O_2h^{-1}, with this being converted using an Oxycolorific Coefficient (Qox) from Brafield & Lewellyn 1982 (from SanzRus et al. 2000) to generate a value of 13.78 KJ gO_2^{-1}. These equations and roach-specific energetic parameters allow the costs of metabolism, swimming and respiration to be estimated, relative to the type of activity being performed (Table 5.1c). These energetic costs are then subtracted from any energy input from digestion of prey items in order to produce the net energy change and associated growth (positive or negative) in each forager, with this calculation occurring at every time step.

5.2.31 Diet consumption rate

During foraging, the rate at which the foragers can consumer prey items is defined by a functional response curve. This is a Type I functional response when filter feeding and a Type II when predating on benthic invertebrates (Holling 1959; Jeschke et al. 2004; Holker & Haertel 2006; *c.f.* Chapter 2 & 3). The parameters used to describe functional response are handled as forager parameters, specifically handling time, reaction distance and swimming speed (used to calculate the attack rate) (Chapter 2 & 3). These parameters are related to values of prey item size and forager size respectively (Mann & Bass 1997; Hughes et al. 2003; Chapters 2 & 3).

A maximum consumption rate, for both potential diets is modelled using 'CMax' following the approach used by Holker & Breckling (2001) and Hayes et al. (2002) (Equation 5.1). This parameter is related to the available diet, forager size and environmental temperature (Table 5.1c).

$$\text{CMax} \left(0.01825 * \left(\text{BodyMass}^{0.84} \right) *^{(0.133*\text{Temperature}))/24)/\text{Prey item mass}} \right) \quad (\textbf{Eqn 5.1})$$

During modelling, CMax sets a maximum rate of prey item consumption for each time step. This limitation to consumption rate may influence forager distribution through the user-defined fitness measure, as if a forager is able to reach a rate of diet consumption equal to CMax in several available patches, then further fitness considerations may be taken into account, for example predator avoidance or energetic costs associated with water flow rate.

5.2.32 Diet assimilation efficiency

Potential dietary energy lost as a result of inefficient diet assimilation was calculated, along with constant proportions of energy loss for egestion and excretion, based on roach feeding experiments (Holker & Breckling 2001; Holker & Haertel 2004). This value of 0.68 relative to dietary and forager energy density (Table 5.1c) was constant across forager types and time steps.

5.2.33 Respiration and swimming costs

The total energy represented by respiration processes consists of three components: RMax, RStandard and RDigestion, where Rstandard is respiration by standard metabolic processes, excluding digestion costs (Equation 5.2), RMax is the same standard energetic costs as well as those associated with digestion, and RDigestion is equal to the value of RStandard, subtracted from RMax (Equation 5.3). These values were based on roach bioenergetic feeding experiments, controlling for forager body mass and environmental temperature (Koch et al. 1992; Holker & Breckling 2001, 2002; Holker 2003; Holker & Haertel 2004; Ohlberger et al. 2006; Table 5.1c).

$$\text{RMax} \quad \left(0.034 * \left(\text{BodyMass}^{0.785}\right) *^{(0.88*\text{Temperature})}\right) \textbf{ (Eqn 5.2)}$$

$$\text{RStandard} \quad \left(0.034 * \left(\text{BodyMass}^{0.76}\right) *^{(0.88*\text{Temperature})}\right) \textbf{ (Eqn 5.3)}$$

These respiration rates were modelled as major components of the different metabolic costs associated with forager activities, with the addition of any swimming costs incurred as a result of the forager activities. Such swimming costs were based on roach swimming metabolism experiments (Holker & Breckling 2001), with swimming costs estimated for both low and high cost swimming patterns, estimated using an experimentally determined relationship between oxygen consumption, fish body mass and average swimming speeds (Hammer et al. 1994). The estimated low and high swimming patterns were modelled as the swimming cost when resting and feeding respectively, as higher energy swimming patterns were only modelled when actively feeding (Railsback & Harvey 2002; Holker et al. 2002) (Equations 5.4, 5.5).

$$\text{Swimming cost Feeding} \quad 0.07\left(\left(\text{Velocity}^{0.64}\right) * \left(\text{Bodymass}^{0.62)}\right)\right) \textbf{ (Eqn 5.4)}$$

$$\text{Swimming cost Resting} \quad (0.9)^{1.22} * \left(\text{Bodymass}^{0.89)}\right) \quad \textbf{ (Eqn 5.5)}$$

Finally, the metabolic costs when moving between patches is modelled as a user-defined cost, based on the body mass of a forager, such that movement through the virtual environment is more energetically costly for smaller fish (Mann & Bass 1997).

5.2.34 Fitness measure

Patch choice decisions follow the fitness-maximising principle that emphasises growth rates and survival of the forager (Stillman 2008). Three alternate fitness measures were modelled, effectively producing three distinct versions of the model, with the subsequent processes of validation and model analysis selecting the most accurate or useful fitness measure.

The three fitness measures state:

i) 'Select behaviour and patch that maximises consumption rate.' This is the '***No Predation***' fitness measure, whereby the foragers simply seek to maximise their consumption rate in KJ, taking into account the available diet and energetic costs associated with forager activities.

ii) 'If rate of consumption does achieve Cmax; select behaviour and patch that minimises predation risk.' Otherwise 'Select behaviour and patch that maximises consumption rate.' This is the '***Predation***' fitness measure, whereby the foragers seek to maximise their consumption rate, however if their consumption rate can reach CMax in several patches, the forager will select the patch with the lowest risk of predation.

iii) 'If rate of consumption does achieve Cmax; select behaviour and patch that maximises the amount of macrophyte cover.' Otherwise 'Select behaviour and patch that maximises consumption rate.' This is the '***Safety***' fitness measure, whereby the foragers seek to maximise their consumption rate, however if their consumption rate will reach CMax in several patches, the forager will select the patch with the highest amount of in-stream macrophyte cover.

Predation risk is calculated at the patch level as a function of predator density and the number of similarly vulnerable foragers, as defined by their body size. Habitat selection preferences of roach favouring in-stream macrophytes are associated with reduced predation risk and water flow rate (Chick & McIvor 1997; Jacobsen & Berg 1998; Grenouillet & Pont 2001).

Model analysis

5.2.35 Specific growth rates (SGR)

Forager growth rates were calculated as specific growth rates, or the percentage change in body mass per day (% body mass day^{-1}) (Equation 5.6).

$$SGR = \frac{\ln(W_{tn}) - \ln(W_{t0})}{t_n - t_0} * 100 \qquad \textbf{(Eqn 5.6)}$$

Where SGR is the specific growth rate, W_{t0} is the initial mass of a forager at survey time (t_0) and W_{tn} is the subsequent mass of a forager at survey time (t_n), finally t_n-t_0 is the number of days between surveys.

Forager population distribution at the macrohabitat (stretch) level

The stretch level forager distribution is a measure of the distribution of the forager in the virtual environment expressed as the number of foragers in a stretch, as a proportion of the whole population (Equation 5.7).

$$\text{Proportion}_{Strech(i)} = \frac{number \quad individuals \quad in \quad stretch_i}{total \quad number \quad individuals \quad in \quad stretch_{all}} \textbf{(Eqn 5.7)}$$

Where *i* is the stretch being analysed and *all* is all the stretches in the virtual environment.

5.2.36 Measuring model variation

In order to assess the effect of intrinsic model variation on the predicted pattern outcomes, 50 replicate model simulations were run on the same parameter set, with the variation between specific growth rates assessed for 1+ roach in the 'no predation', 'predation' and 'safety' models. Confidence intervals (95 %) of estimated specific growth rates were calculated, initially using two model outputs that were randomly selected. This process was repeated using an increasing number of models outputs, in increments of 1 extra model from 2 to 50, where these were randomly selected, with no

model output used more than once in each calculation. This allowed the relationship between the number of model runs and the confidence in the model predictions to be described. The number of model replicates to be used in future analysis was determined by the asymptotic, plateau phase, where further increasing the replicate number did not produce significantly reduced confidence intervals.

5.2.37 Comparing predicted and observed patterns

In all three models, the specific growth rates of foragers (i.e. 0+ and 1+ roach) were modelled during a summer growth season. These specific growth rate values were compared against tagged and recaptured roach sampled during field surveys as well as in changes in population mean body mass based on field surveys and back-calculation of body length, based on scale samples for 1+ roach, with literature values of specific growth rate being used for 0+ roach. Macrohabitat distribution was also compared in 1+ roach, based on electric fishing field surveys. These patterns of growth rate and distribution were not used for model calibration, but emerged from the interactions between individuals and their environment (Grimm & Railsback 2005).

5.2.38 Sensitivity analysis

Sensitivity analysis was performed for each parameter not measured in the field through modification of its value by ± 25%, with model simulations run independently for each parameter and replicated ten times (Stillman et al. 2000). Model sensitivity was measured by comparing specific growth rate and a sensitivity index, expressed as the ratio of change in specific growth rate between observed and predicted values relative to the change in parameter value (Gusset et al. 2009), with this being performed for all three models and both forager types.

5.3 Results

5.3.1 The effect of increasing the number of model simulations on confidence intervals of forager growth rates

Through repeated simulation runs of the same parameter set, it was possible to describe the variation in forager specific growth rates (SGR, % body mass day-1), indicating that an increase in the number of replicate simulations produced a more accurate prediction

of mean model outputs (Figure 5.1), with this being seen in the SGR of 1+ roach foragers in all three models (Figure 5.1a - 5.1c). The number of replicates used in model analysis was subsequently set at 10 replicates as a trade-off between parameter estimate confidence intervals and computing time. The 95% confidence interval in predicted SGR for 1+ roach after ten model replicates was calculated to be below 0.005% body mass day^{-1} (Figure 5.1).
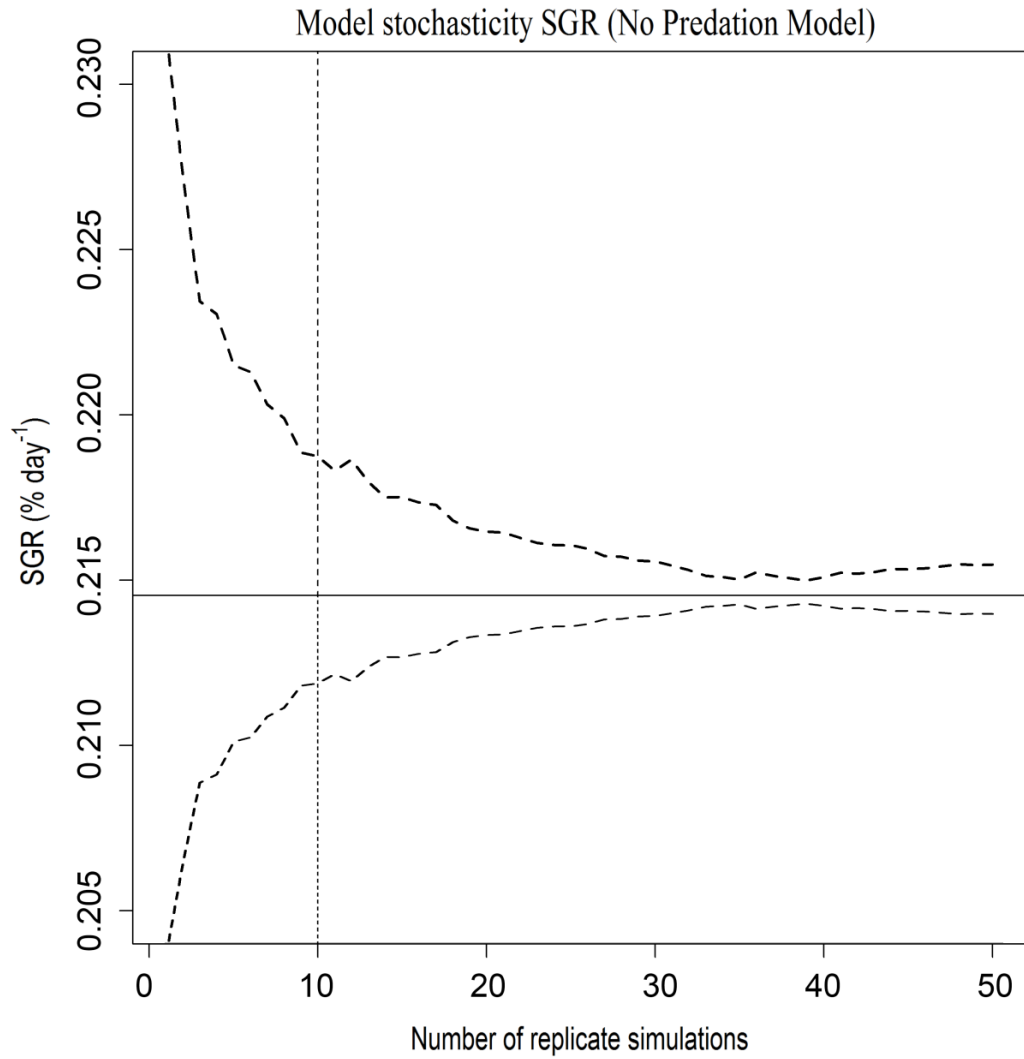
Figure 5.1a The relationship between the number of model replicates and the confidence in estimating the mean population specific growth rate in 1+ roach, in the 'no predation model'. The solid line represents the mean specific growth rate from all 50 replicates, dashed lines indicate 95% confidence intervals of mean specific growth rate and the vertical dotted line indicates the position of ten model replicates.
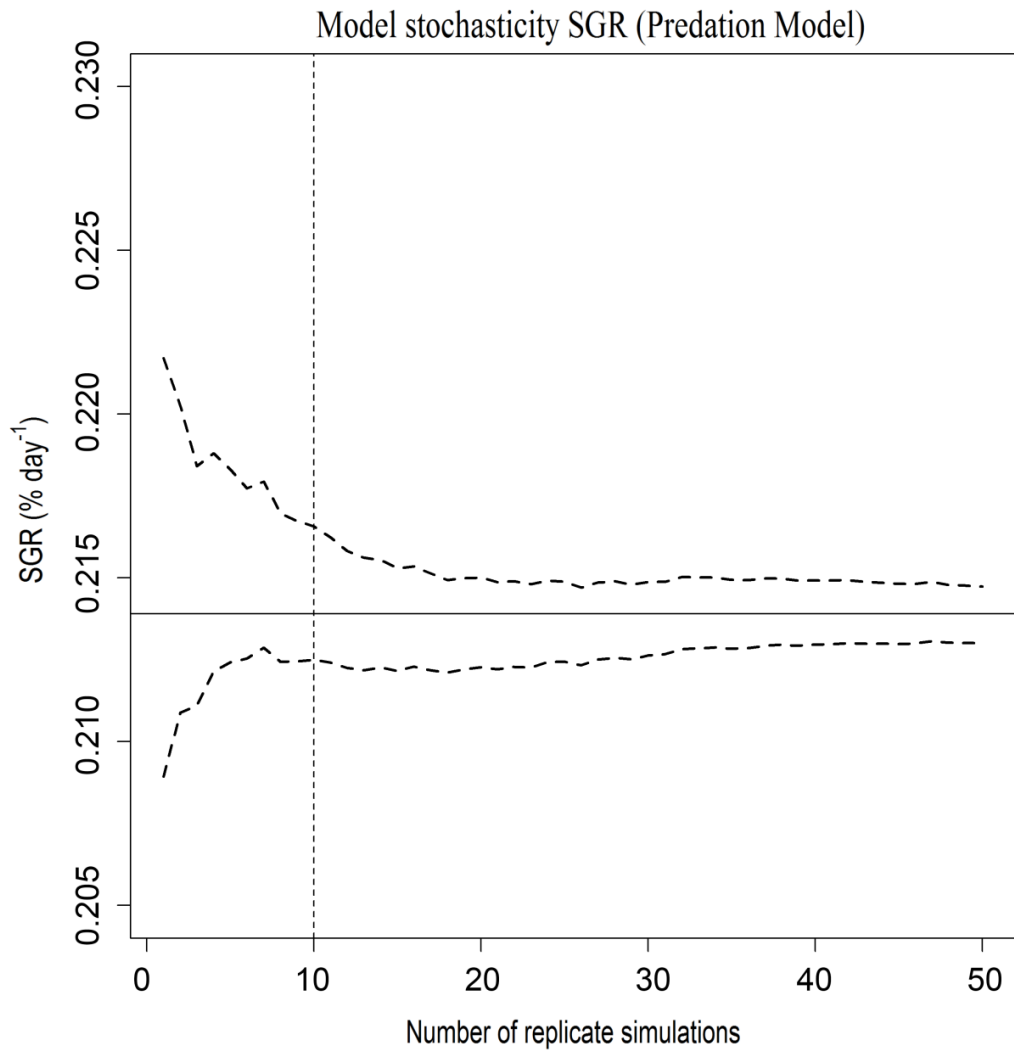
Figure 5.1b The relationship between the number of model replicates and the confidence in estimating the mean population specific growth rate in 1+ roach, in the 'predation model'. The solid line represents the mean specific growth rate from all 50 replicates, dashed lines indicate 95% confidence intervals of mean specific growth rate and the vertical dotted line indicates the position of ten model replicates.
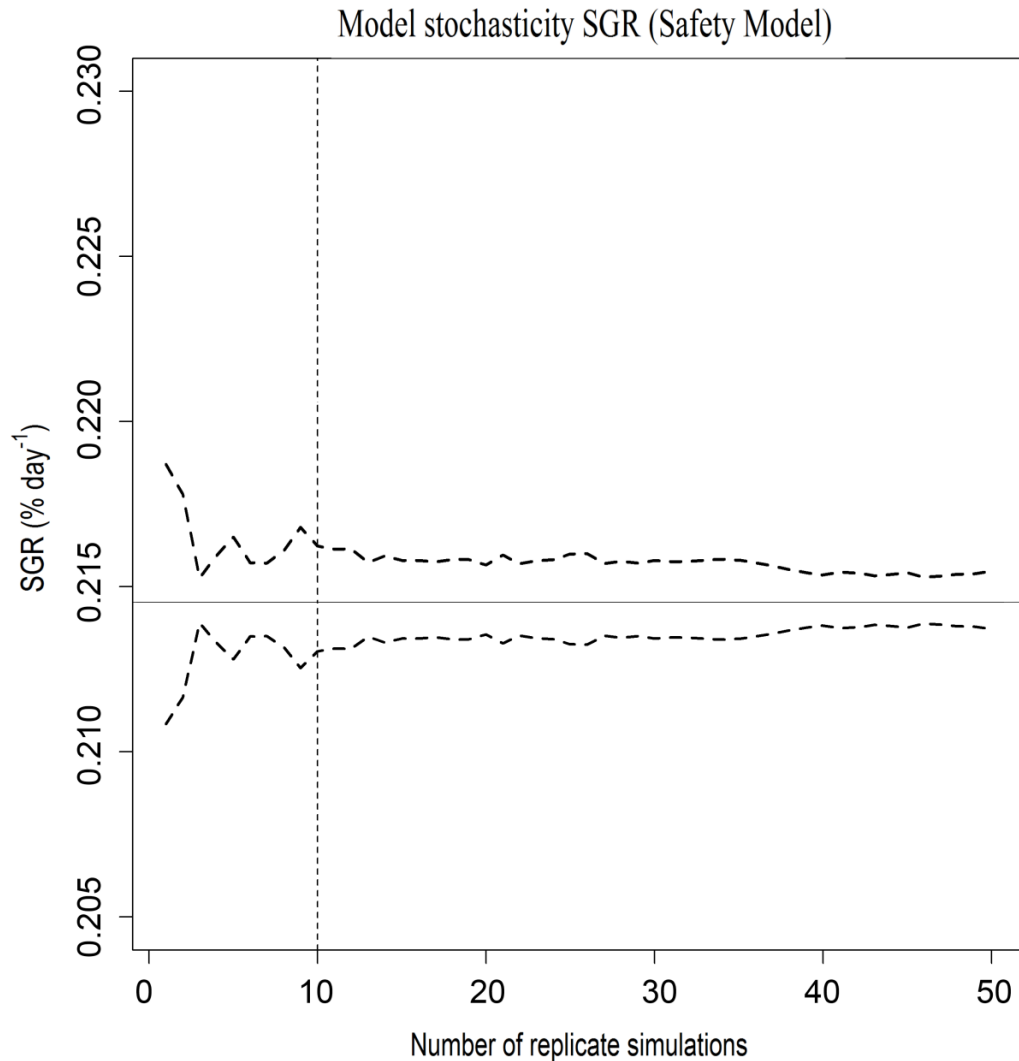
Figure 5.1c The relationship between the number of model replicates and the confidence in estimating the mean population specific growth rate in 1+ roach, in the 'safety model'. The solid line represents the mean specific growth rate from all 50 replicates, dashed lines indicate 95% confidence intervals of mean specific growth rate and the vertical dotted line indicates the position of ten model replicates.

5.3.2 Predicted vs observed specific growth rates (SGR)

Comparison of observed versus predicted SGR revealed a strong relationship (Figure 5.2d - 5.2f), where observed SGR was derived from back-calculated growth rates and population means over the corresponding growth season (Chapter 4). A similarly strong relationship was seen between predicted SGR for 0+ fish and literature values under similar environmental conditions (Figure 5.2a - 5.2c). Mean predicted SGRs tended to be underestimated when compared to observed SGR's in 1+ fish, with slight

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overestimation being observed in 0+ fish. However, the predicted SGRs were not significantly different from observed rates for both forager types and across all three models (t-test, $P > 0.05$) (Figure 5.2a - 2f).
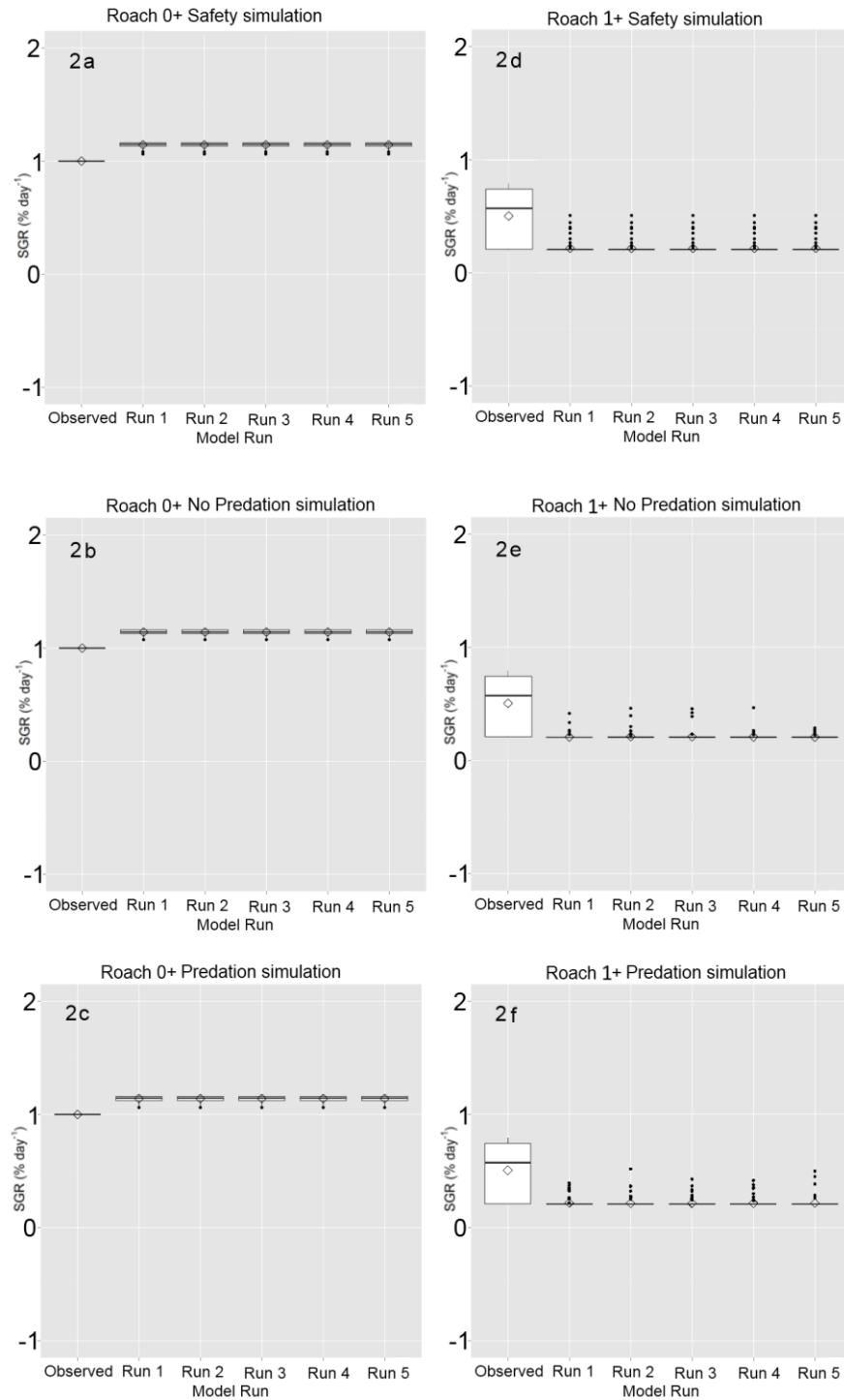
Figure 5.2 Observed and predicted population specific growth rates of 0+ and 1+ roach, left and right columns respectively. Observed growth rates were collected at a lowland river field site or based on data from published literature, predicted growth rates are from the roach individual-based model. The virtual environment reflects the conditions at the study site. The diamond indicates mean SGR for each distribution. While ten model runs were performed for each analysis for the sake of parsimony, only the first five are displayed here.

5.3.3 Distribution at the stretch level

The patterns of relative distribution of foragers at the macrohabitat (stretch) level revealed some agreement with the observed patterns recorded during fieldwork and those predicted by the models (Figure 5.3a - 5.3c). However, the model predictions tended to overestimate the relative abundance of foragers in Stretch 3, whilst underestimating the relative abundance of foragers in Stretch 5, with this more pronounced in the 'Safety' (5. 3a) and 'No predation' model (Figure 5.3c).
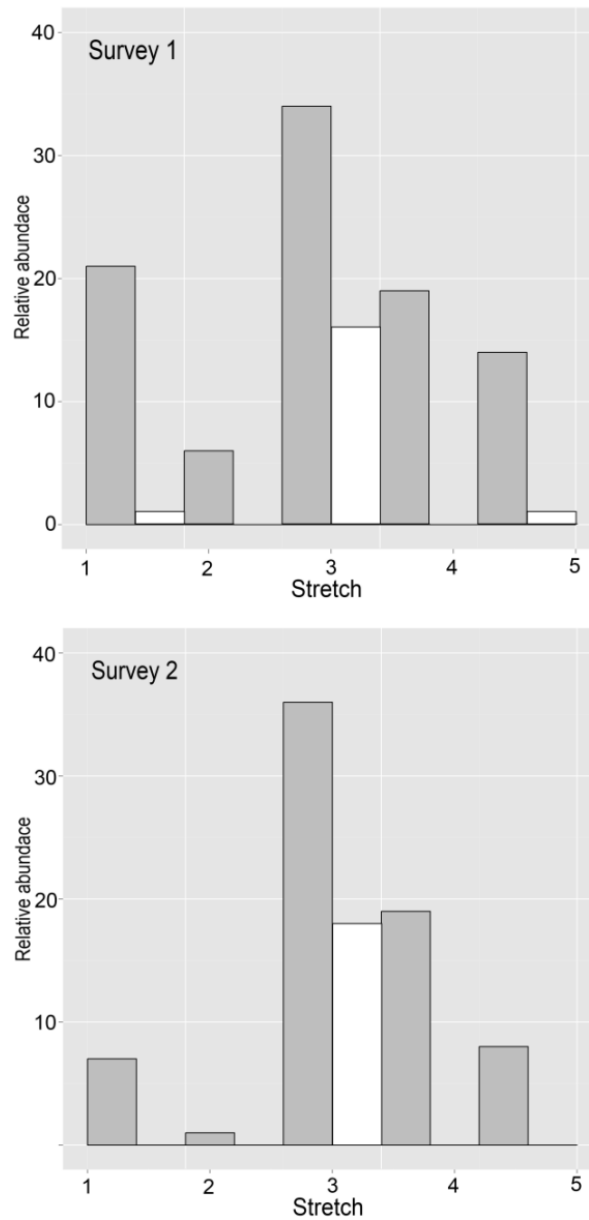
Figure 5.3a Comparing observed and predicted distributions of 1+ roach as relative proportions (% of total population) across the five stretches or macrohabitats. Observed distributions are shown in grey, as recorded by two-pass depletion electric fishing. Predicted distributions are shown in white, based on the 'Safety' model where macrophyte cover is the secondary component of the user-defined forager fitness measure, after diet consumption. The model distribution output was compared to the observed distribution at time steps corresponding to field survey dates.
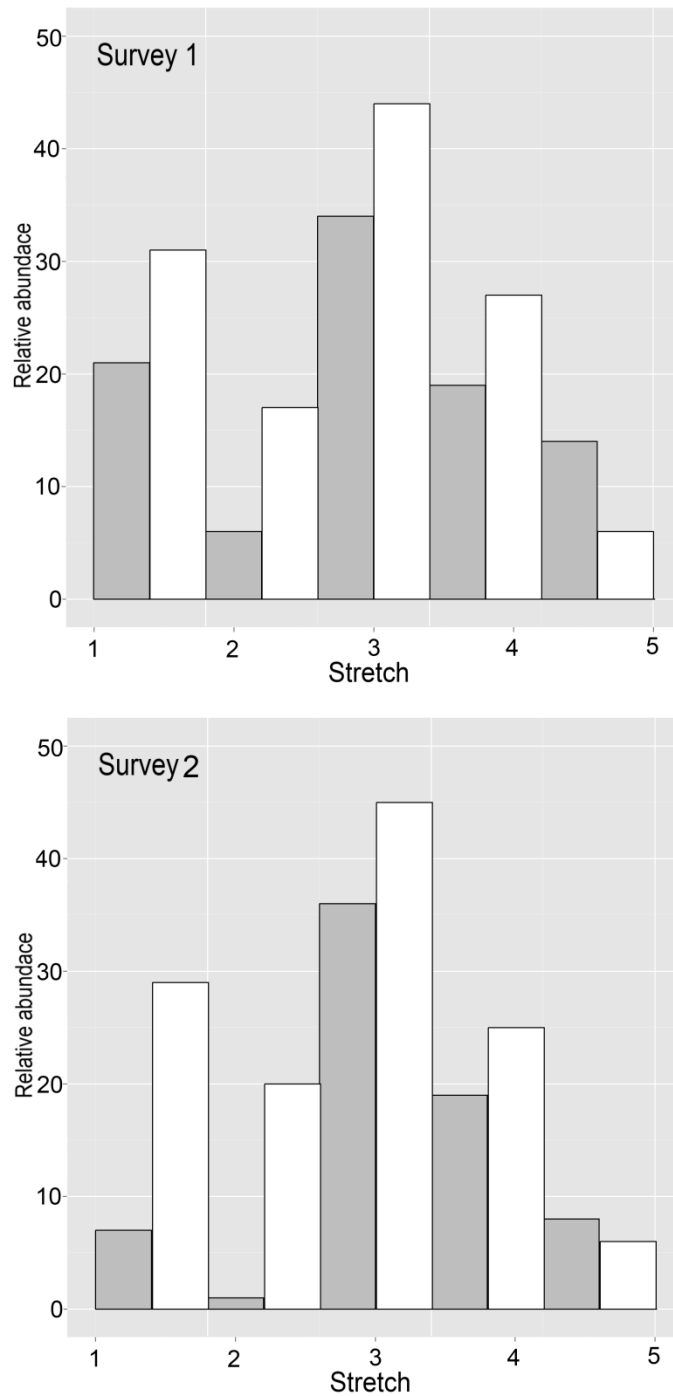
Figure 5.3b Comparing observed and predicted distributions of 1+ roach as relative proportions (% of total population) across the five stretches or macrohabitats. Observed distributions are shown in grey, as recorded by two-pass depletion electric fishing. Predicted distributions are shown in white, based on the 'Predation' model where predation risk is the secondary component of the user-defined forager fitness measure, after diet consumption. The model distribution output was compared to the observed distribution at time steps corresponding to field survey dates.
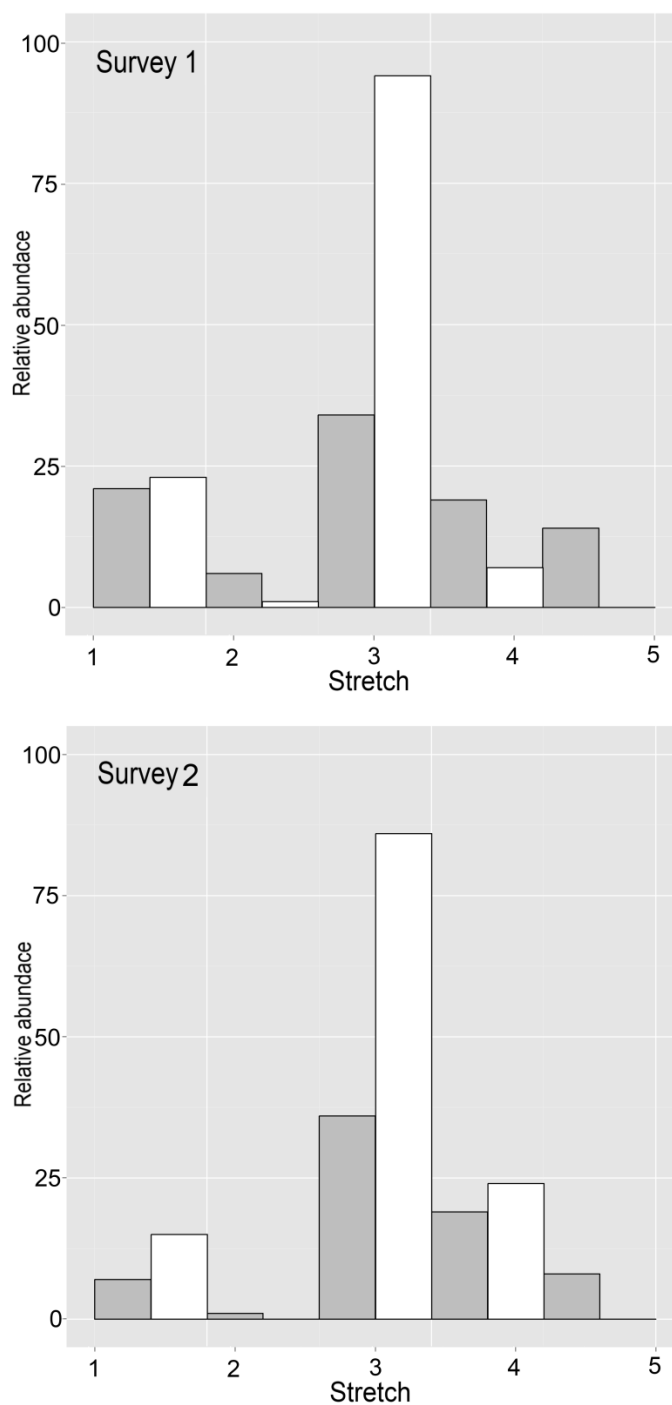
Figure 5.3c Comparing observed and predicted distributions of 1+ roach as relative proportions (% of total population) across the five stretches or macrohabitats. Observed distributions are shown in grey, as recorded by two-pass depletion electric fishing. Predicted distributions are shown in white, based on the 'No Predation' model where the rate of energy intake is the sole component of the user-defined forager fitness measure. The model distribution output was compared to the observed distribution at time steps corresponding to field survey dates.

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Figures 5.4a to 5.4c compared observed versus predicted forager distributions. Testing a linear relationship between observed and predicted densities against a 1:1 relationship, revealed varying predictive power across the three models. The 'Safety' model had the closest match, defined through this 1:1 comparison and associated t-test, followed by the 'No predation' model; with both of these models not significantly differing from the 1:1 relationship (linear regression intercept compared to (0,0), t-test, $P > 0.05$; linear regression gradient compared to (1), t-test, $P > 0.05$). However the 'Predation' model did vary from the 1:1 relationship, with the intercept significantly different to (0,0), (t-test, $P < 0.05$), although this was not apparent in the gradient of the regression compared to (1) (t-test, $P > 0.05$).
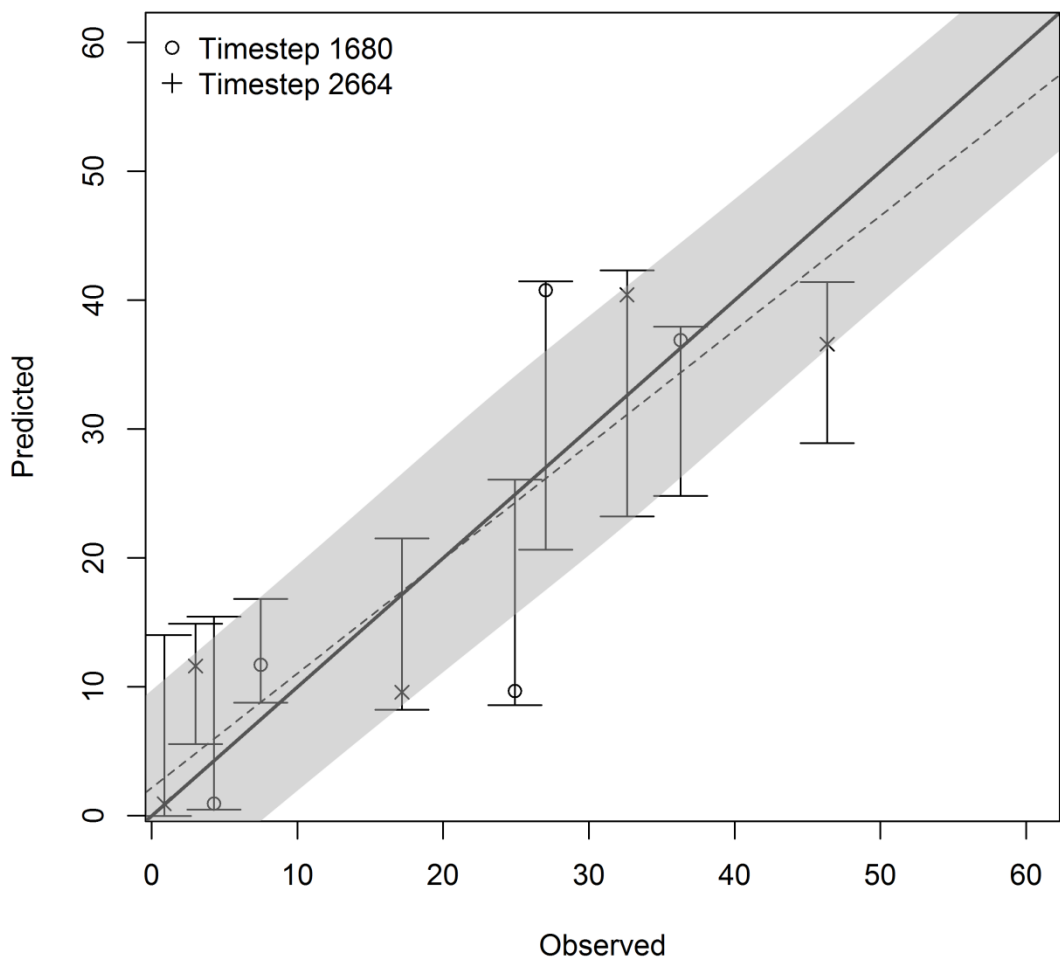
Figure 5.4a The ability of the 'Safety' model to predict the macrohabitat, stretch level distribution of 1+ roach. Observed and predicted distributions are plotted against each other. The dashed line is a linear regression of the relationship compared to an ideal 1:1 ratio, shown as the solid line. The error bars represent the 95% confidence intervals of 5 model replicates. While the shaded area shows the 95% confidence interval for the linear regression. The time steps displayed correspond to the same survey dates.
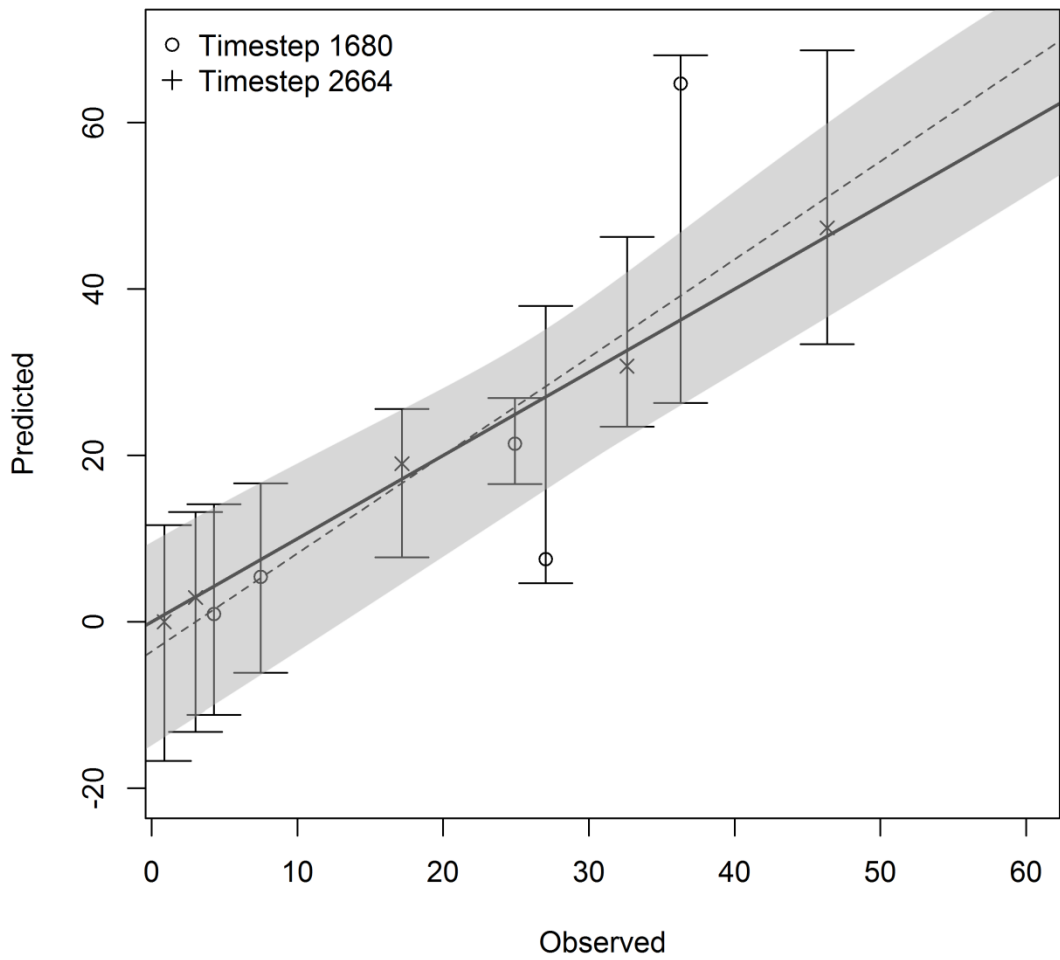
Figure 5.4b The ability of the 'No predation' model to predict the macrohabitat, stretch level distribution of 1+ roach. Observed and predicted distributions are plotted against each other. The dashed line is a linear regression of the relationship compared to an ideal 1:1 ratio, shown as the solid line. The error bars represent the 95% confidence intervals of 5 model replicates. While the shaded area shows the 95% confidence interval for the linear regression. The time steps displayed correspond to the same survey dates.
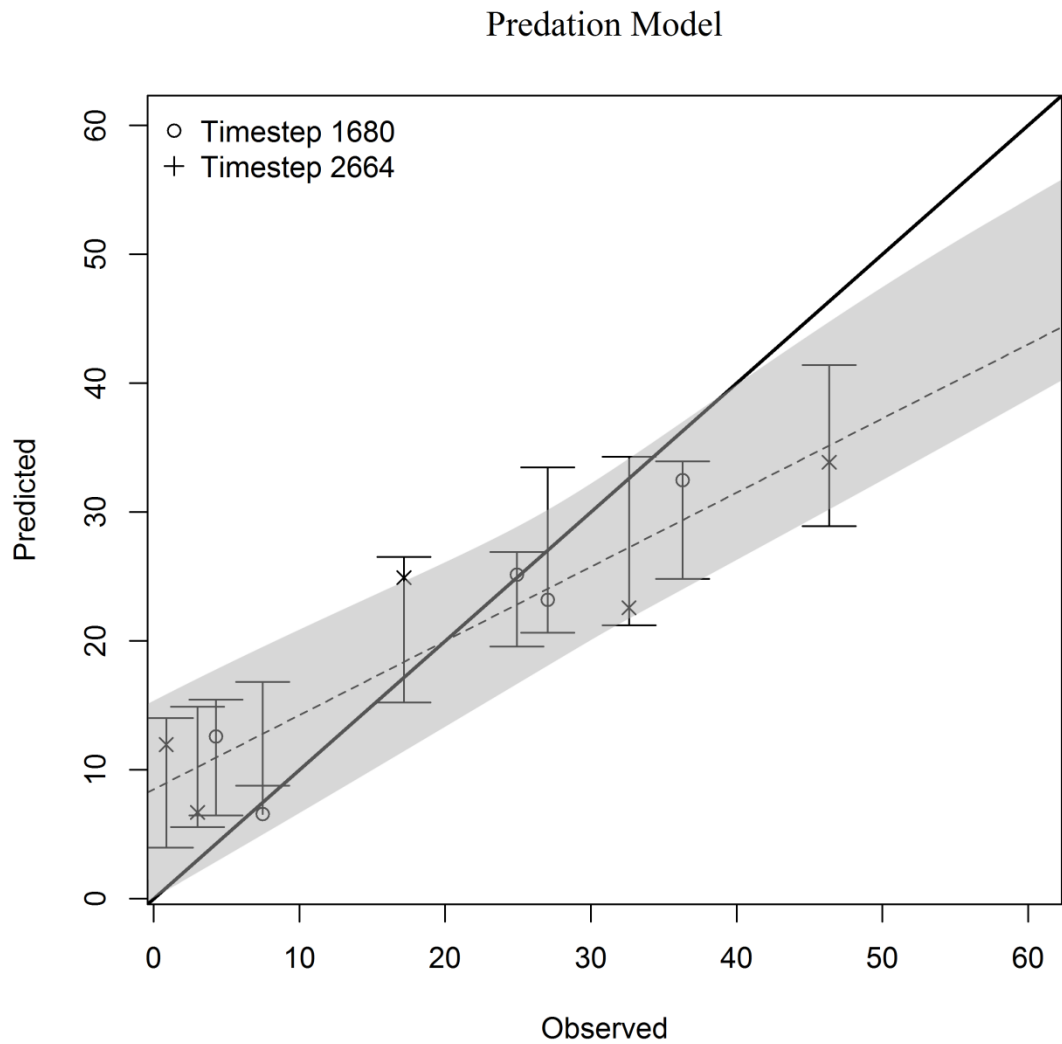
Predation Model

Figure 5.4c The ability of the 'Predation' model to predict the macrohabitat, stretch level distribution of 1+ roach. Observed and predicted distributions are plotted against each other. The dashed line is a linear regression of the relationship compared to an ideal 1:1 ratio, shown as the solid line. The error bars represent the 95% confidence intervals of 5 model replicates. While the shaded area shows the 95% confidence interval for the linear regression. The time steps displayed correspond to the same survey dates.

5.3.4 Sensitivity analysis

Sensitivity analysis for each parameter that was not measured in the field revealed a high variance in their impact on the specific growth rates in the model outcomes (Figure 5.5a,b). Parameters relating to feeding behaviour or energetic costs associated with

swimming or metabolism had little effect on the predicted SGR (Figure 5.5a,b). Parameters relating to bioenergetics, specifically energy input from dietary components, had the greatest effect, with forager SGR being most sensitive to Resource component density, Diet assimilation efficiency and Zooplankton energy density. The ranking of sensitive parameters showed little variation between the three models, besides any parameters only found in once version of the model, associated with model-specific fitness measures. Similarly, the ranking of sensitive parameters showed little variation between 1+ (Figure 5.5a) and 0+ roach (Figure 5.5b), despite their body size and differences in diet composition.
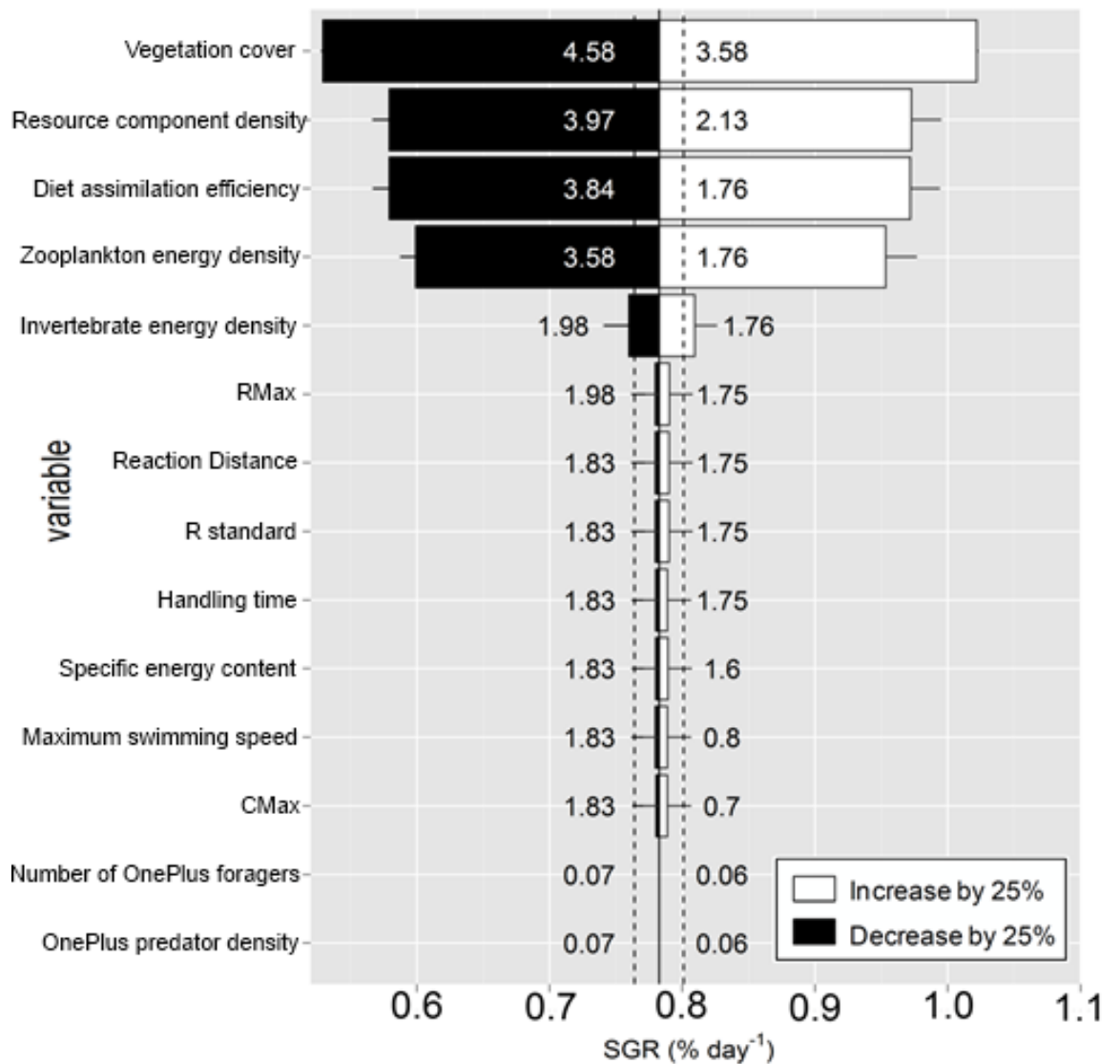
Figure 5.5a A sensitivity analysis of the 'Safety' model parameters and their effect on the predicted specific growth rates (SGR, % body massday⁻¹) of **1+** roach with parameters set to 75%, 100% and 125% of the of the best estimates from published literature sources or experimental data. Parameters are ranked on level of impact, error bars are standard deviations from ten replicate simulations. The dashed lines are standard deviations and the solid line the mean SGR from the unaltered model predictions. The sensitivity index (the ratio of change in specific growth rate between observed and predicted values relative to the change in parameter value) is displayed for each parameter increase and decrease.
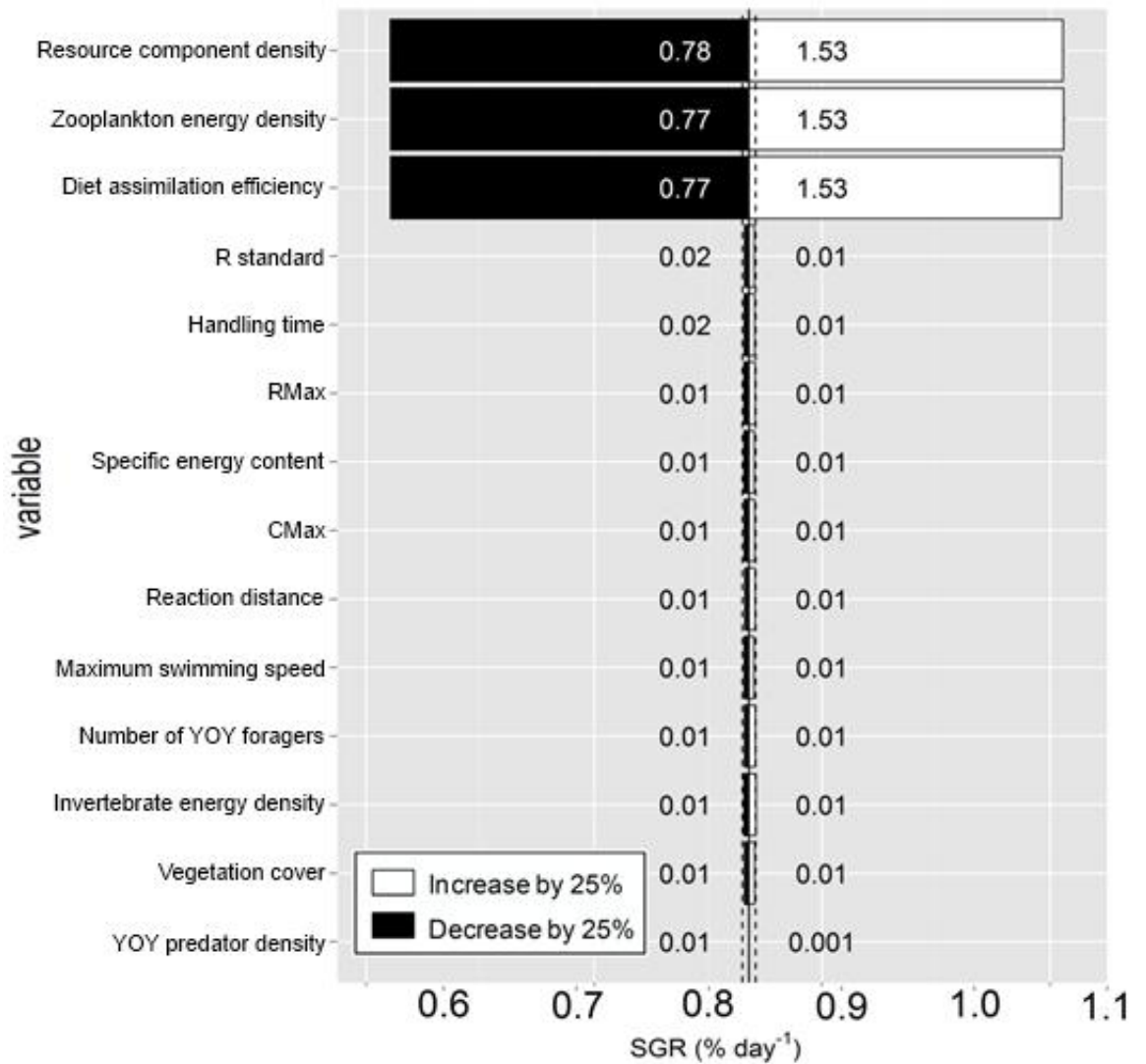
Figure 5.5b A sensitivity analysis of the 'Safety' model parameters and their effect on the predicted specific growth rates (SGR, % body massday⁻¹) of **0+** roach with parameters set to 75%, 100% and 125% of the of the best estimates from published literature sources or experimental data. Parameters are ranked on level of impact, error bars are standard deviations from ten replicate simulations. The dashed lines are standard deviations and the solid line the mean SGR from the unaltered model predictions. The sensitivity index (the ratio of change in specific growth rate between observed and predicted values relative to the change in parameter value) is displayed for each parameter increase and decrease.

5.5 Discussion

Population level patterns of foragers in the virtual environment of the model closely resembled the patterns of roach under similar environmental conditions in the real system. The simulated foragers grew and distributed themselves throughout the system in a similar fashion as the real fish, suggesting that the virtual roach were behaving as per live roach. This can be interpreted as a validation of the assumptions and internal structure of the model, parameterised without using calibration processes, providing a successful example of an individual-based modelling approach used to make quantitative ecological model predictions of freshwater cyprinid fish growth and habitat selection.

Individual-based models differ from traditional ecological models in that their underlying philosophy is based on interactions at the level of individuals, with this scaling up to determine the patterns produced at the population level (Grimm & Railsback 2005). While this principle has long been established, it is only with relatively recent advances in computing power and data collection technology that modelling such numerous interactions are now practicable (Evans et al. 2012). Virtual individuals within this model system are designed and parameterised to be subject to identical bioenergetic (e.g. metabolic and respiration processes), physiological (e.g. body mass and swimming costs) and behavioural conditions (e.g. habitat selection and prey selection) as roach (Wieser & Niederstatter 1992; Hammer et al. 1994; Mann & Bass 1997; Holker & Breckling 2001; Schreckenbach et al. 2001; Holker et al. 2002; Hughes et al. 2003; Koch, Holker 2003; Holker 2006; Papageorgiou 2006; Chapter 2, 3). The level of agreement between observed and predicted patterns in forager growth and distribution validates the assumptions about how these parameters interact to determine model outputs. If the assumptions were incorrect then the patterns would not be such a close match between the virtual and real foragers (Grimm & Railsback 2005). This demonstrates the utility of IBMs in linking behavioural studies at the level of individuals with predictions at the level of populations with the eventual aim of informing conservation practices and water resource management (Caro 2007).

Whilst predictions of population patterns were generally seen to match observed patterns across all three models, the 'Safety' model and 'No predation' model were better able to predict observed patterns than the 'Predation' model. All three models predicted specific growth rates that did not significantly differ from observed, indicating a high model predictive power for this pattern. However, when comparing observed versus predicted patterns of stretch-level distribution, only the 'Safety' model and the 'No predation' model were seen to not be significantly different from the 1:1 relationship. Specifically, linear regression analysis of the 'Predation' model predictions against observed patterns and in relation to an intercept of zero, was significantly different, although the gradient of the linear relationship was not. The importance of 'weak' patterns are still useful when validating model predictions (Grimm & Railsback 2005), with the 'Predation' model still predicting the specific growth rate and most densely populated river macrohabitats as observed at the study site.

Across all three models, there were slight discrepancies between predicted and observed growth rates, as well as macrohabitat distribution in 1+ roach. These might be explained by limitations in the modelled forager feeding behaviour. More specifically, the available diet of both forager types was limited by forager size, simulating the role of forager gape size and gill raker spacing in diet availability (Mann et al. 1997; Hjelm et al. 2003). However, model foragers are limited to exploiting a single dietary resource within a time step, so whereas a real roach may be able to exploit different resources based on a complex trade-off between energetic costs of feeding, prey energetic resource density and environmental condition (Mikheev et al. 2002; Nurminen et al. 2010), virtual foragers simply exploited the single resource they were most well suited to exploit, as based on their body size. The inclusion of a more complex available diet within the MORPH framework would require several new diet resources to be made, based on the physiological characteristics of the forager (van den Berg et al. 1994; Nurminen et al. 2010). Each diet would represent a specific stage of allometric diet shift as the forager changed size (Wanzenbock 1992; Wanzenbock et al. 1996; Hjelm & Persson 2001). Similarly, roach are known to consume macroinvertebrates both as benthic and drift resources, and whilst drift feeding is unlikely in the relatively high turbidity conditions of the field site, such behaviour could occur under clearer conditions (Copp 1992; Zamor & Grossman 2007). Given the increased input of

terrestrial invertebrates and fast-flowing, clearer habitats selected for when drift feeding, the forager energetics associated with drift feeding is expected to differ from that of benthic feeding and this difference could result in altered predictions for forager SGR and macrohabitat distribution. While drift feeding is not expected to occur at the current study site, this behaviour could be incorporated into the model when describing other systems, which feature faster flowing, clearer habitats. This would require information on river turbidity at the time step scale, based either on field data, for example using turbidity data-loggers, or estimated as a function of river discharge (Goransson et al. 2013). A complex 'available diet' rule could be used to compare the energetic costs, benefits and potential environmental conditions between benthic and drift feeding. A simpler approach would be to assess the likelihood of drift feeding behaviour, based on the characteristics of the study site, this likelihood ratio could then be incorporated into a combined available diet, with associated prey energetic resource density and foraging energetic costs.

While the stretch-level, macrohabitat distribution patterns were similar between virtual and real foragers, the analyses did show some significant differences, specifically in the 'Predation' model. However, it is also worthwhile considering the potential biases in the observed patterns, based on the assumption that fieldwork observations are an accurate representation of study site conditions (Quinn & Dunham 1983; Johnson & Omland 2004). Incomplete observational data may result from increased difficulties in catching all the fish present in deep and or fast flowing patches (Chapter 4). These issues will be common to many aspects of ecological fieldwork and may be mitigated through techniques such as two-pass depletion electric fishing or catch per unit effort (Harley et al. 2001). This line of reasoning is an argument against using statistical tests when validating IBMs, and is encapsulated in the 'pattern-orientated modelling' approach encouraged by Grimm & Railsback (2005). Another issue in assuming fieldwork data is a true representation of the study site is that of the stop nets used when dividing the river into the stretches to be fished (Chapter 4). Placing the stop nets along each stretch boundary, prior to fishing, was designed to limit each population estimate to a single stretch. However, the boundaries between the stretches may fall across the natural habitat ranges of the captured fish. Whilst this may not be a large source of error when considering the roach and perch (Persson & Eklov

1995), the use of more territorial pike, usually an ambush predator (Schulze et al. 2006; Cucherousset et al. 2010), in the 'Predation' model may explain the relatively weaker level of agreement between predicted and observed distribution patterns. Lastly, all of the models tended to underestimate the proportion of foragers in Stretch number 5 (Chapter 4), the furthest downstream stretch. While the model represents the system as closed (i.e. no foragers or predators were able to leave or enter the system, short of the initialisation phase or through mortality effects), in reality, the study site was limited on one side by a weir, but the other 'boundary' being open. When surveying, a stop net was used to prevent both foragers and predators leaving the system, however the act of placing the stop net may have potentially disturbed the fish, causing them to move out of the system. As home range and swimming ability tend to increase with fish body size (Hodder et al. 2007) this may introduce bias as larger, older and fitter fish are more able to leave the system as a result of disturbance, or more likely to have a natural habitat range that falls across a stretch boundary.

In order to increase the level of agreement between predicted and observed patterns, estimated parameters could be calibrated so as to best match one set of patterns (Wiegand et al. 2004; Grimm & Railsback 2005; Kramer-Schadt et al. 2007). For example, suitable parameters would include the swimming costs associated with different activities, given their impact across the model and the importance of bioenergetics in determining forager specific growth rate. However, while better able to predict a specific set of observed patterns, the model would be calibrated for a specific scenario, at the cost of more general applicability when applied to other systems or conditions. For this reason, model calibration was not performed and this did not affect the ability of the model to predict forager specific growth rates and their macrohabitat distributions.

For the sake of simplicity, the model intentionally omitted some aspects of the real system. Firstly, drift feeding behaviour in roach; while rarely described, it is associated with altered energetic costs and benefits when compared to predating on benthic invertebrates. It is also limited to fast flowing, less turbid rivers, as well as larger roach (Lobon-Cervia & Rincon 1994; Davies et al. 2004). For this latter reason, drift feeding behaviour was excluded from the model, but if it was applied elsewhere, such as to a

chalk stream system, or was applied here under altered characteristics, incorporation of drift feeding might have to be considered. Secondly a diel cycle was not included in the model. While roach foraging behaviour does differ diurnally (Jamet 1994), given the modelling of predominantly filter feeding and benthic foraging, as well as the simulation period representing the summer growth period of juvenile fish and high water turbidity, a day-night cycle was assumed to be unlikely to significantly impact the model outcomes.

Predicted specific growth rates displayed less variation than observed growth rates across all three models and both forager types. The variation in observed growth rates may be a result of more complex habitat heterogeneity and residual sampling error in the mean SGR of captured fish that arise through individual trait differences. Within the model, foragers only differed through their initial body mass and length as well as their initial stretch location (Railsback 2001a,b).

As MORPH is based on optimal-foraging theory, simulating discrete individuals, it is possible to incorporate the effects of density dependence on simulated populations (Toral et al. 2012). However, in this case, density-dependent process that may impact population characteristics are neither modelled, nor seen as emergent qualities of the model. This is due to the lack of interference behaviour or direct or indirect competition between juvenile roach (Cryer et al. 1986; Hjelm & Persson 2001), other than for food resources. Given the juvenile life-stages of the modelled foragers and the open nature of the real-world system, it can be assumed that food item resources were limited. In the model, food items were removed from the system upon consumption by a forager and not replenished during that time step, although this did not significantly reduce the food item density in even the most crowded patch. Indirect competition for food resources and/or space could be considered when modelling higher population densities, larger fish that would more predominantly favour benthic foraging, or predation risk (Persson & Eklov 1995; Bartosiewicz & Gliwicz 2011).

A validated individual-based model allows the user to modify parameters at the level of the virtual environment - population and individual - providing scope for variations of the model to be created in order to investigate impacts or changes at these

scales. One such area of interest, from the perspective of water management, would involve assessing the impact of in-stream macrophyte removal and flow rate regulation, with the outcomes focusing on growth and recruitment of larval and juvenile cyprinid fish (Garner et al. 1996; Copp 1997; Mann et al. 1997; Pinder 1997; Chapter 7). The implicit objective behind the construction of this model is providing a tool for determining the potential impacts of such scenarios on fish recruitment, along with cyprinid population ecology and fish-based ecological status assessments (Pont et al. 2007; Bond et al. 2010; Zarkami et al. 2012; Chapter 7).

A validated roach individual-based model, along with its flexible framework is a valuable tool for fresh water managers to add to their repertoire when making management decisions by providing predictive results and using reality-based management scenarios. The individual based, bottom up approach can work along-side current models and techniques (Grimm & Railsback 2005) and thus be viewed as complementary approaches. The roach individual-based model framework presented is capable of using site-specific environmental and forager data, to produce output tailored to further management needs and would apply initially to any heavily modified, lowland river system. The generic juvenile roach MORPH framework, while still highly simplified and in a relatively early stage of development, is capable of predicting observed patterns as evidence of its predictive ability and overall utility, and such, is an example of the value of individual based models in conservation generally and fisheries management specifically.

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6. Assessing the impact of aquatic macrophyte management and flow rate regime on growth and recruitment using a roach individual-based model

The aim of this chapter is to use the roach IBM developed and validated in Chapter 5 to make predictions about the potential impact of river management strategies on juvenile roach growth, survival and recruitment.

6.1 Introduction

Degradation and destruction of freshwater riverine habitats is a major threat to the abundance of fish populations and the diversity of their communities (Degerman et al. 2007). Heterogeneous river habitats are required to support the varied lifecycle requirements of freshwater fishes, with this heterogeneity heavily influenced by river management practices (Acreman & Ferguson 2010). In lowland rivers in the UK, aquatic macrophyte cover is an important part of the riverine habitat; it influences local hydrology, physical habitat, primary productivity and provides nursery areas and refugia for many fish species (Gregg & Rose 1985; Stromberg 2001; Tolonen et al. 2003). In the study site, aquatic macrophytes that were growing in abundance in some patches - and are typical of those encountered in macrophytes communities in similar lowland rivers - included Common lily (*Nuphar lutea*), Arrowhead (*Sagittaria sagittifolia*), Hornwort (*Ceratophyllum demersum*) Burreed (*Sparganium erectum*), Common reed (*Phragmites australis*) and Bulrush (*Schoenoplectus lacustris*). However, these submerged and semi-submerged aquatic macrophytes have the capability to grow sufficiently dense so as to increase the risk of flooding and hinder channel navigability without proper management (Dawson 1979; Johnstone 1986). This is because their volume restricts the passage of water through them, slowing down the flow rate, and they can occupy substantial proportions of the river channel, reducing its volume (Johnstone 1986). Consequently, flood risk management schemes often incorporate the removal of much of these in-stream macrophytes (Acreman & Ferguson 2010). In doing so, however, they are likely to be removing important nursery habitats and areas of refugia for the fish community, as well as for other aspects of the aquatic communities including macro-invertebrates and zooplankton (Garner 1996). Thus, if river management schemes are to take a holistic perspective of the impacts of activities on all

aspects of the river environment, including its biota, then it is important to understand how such weed cutting and removal practises affect the fish community (Garner 1996). In particular, focus on the consequences for juvenile fish, especially those in their first year of life, is critical given the value of strong recruitment in ensuring strong cohorts of adult fish are subsequently present in their populations (Nunn et al. 2002, 2007).

In-stream macrophytes affect river flow by increasing hydrological drag, reducing flow rates and either trapping or allowing suspended sediments to settle (Madsen et al. 2001). This produces reduced flow rates and increased sedimentation immediately downstream from in-stream macrophytes (Merrit et al. 2010). In addition to reducing flow rate and increasing deposition of upstream materials, in-stream macrophytes provide both vital habitat and food resources for riverine fish, especially juvenile fish, which is the life-stage most vulnerable to the deleterious effects of issues including high flows (leading to displacement), predation and starvation (Garner 1996; Copp 1997a). As well as fish species, phytoplankton, zooplankton and aquatic invertebrates also benefit from the protection provided by in-stream macrophytes against high flow or abrupt changes in flow (Garner 1996). Consequently, areas of in-stream macrophyte cover provide substantial proportions of the food resources for juvenile cyprinid fishes whose varied diet includes macro-invertebrates, zoo- and phyto-plankton, as well as detritus and plant material (Garcia Berthou 1999). This macrophyte cover also provides egg-laying sites for many cyprinid species, including roach, where the eggs receive some protection from high flows, with the emerging and developing larvae then using these areas as nursery habitat until they reach body sizes capable of withstanding higher flow rates (Mills 1981). Finally, the refugia provided by this macrophyte cover for small fishes from piscivorous animals, including fish like perch and pike (Martin et al. 2010; Jacobsen & Berg 1998; Chapters 4, 5) and fish-eating birds such as grey heron *Ardea cinerea* (Allouche & Caudin 2001). Notwithstanding, these areas of macrophytecover also provide the piscivorous fish with areas of refuge as they tend to be ambush predators (Nyqvist *et al.*, 2012).

Whilst cutting and removal of instream macrophytes from lowland rivers is often viewed as an important river management technique to maintain channel navigability and reduce flood risk, the consequences for the fish community and the important

processes within their population dynamics requires consideration. This is increasingly important given how fish-based assessments of both habitat quality (Schmutz 2004; Pont, et al. 2007; Schmutz et al. 2007) and ecological status are now used within monitoring programmes that feed into assessment schemes within the Water Framework Directive (Noble et al. 2007). Indeed, where there is deviation away from the type-specific species and their predicted abundances in relation to their habitat then ecological status is likely to fail and require remediation (Pont et al. 2007).

Besides removal of instream macrophytes, river management schemes may also seek to regulate flow rate, in the case of the study site (Chapter 4) using automatic sluice gates and pumping stations with the aim of reducing flood risk and maintaining flows in adjoining river systems during periods of drought. Flow rate regulation may also occur as a result of small-scale hydropower schemes and damming (Cowx et al. 2012). In riverine systems, flow is a major determining factor of physical habitat, influencing the abundance and distribution of aquatic communities as well as potential water system connectivity (Bunn & Arthington 2002), which is known to play an important part in creating and connecting nursery areas for juvenile fish (Gregg & Rose 1985; Stromberg 2001). Flow rate can affect fish directly though increased bioenergetic costs associated with swimming or keeping station during periods of increased flow rate (Ohlberger et al. 2006; Liao 2007). There is also the potential risk of displacement under conditions of exceptionally high flow, with juvenile fish being more vulnerable than adults (Mann & Bass 1997). Increased river discharge is also associated with increased turbidity (Goransson et al. 2013) which may affect foraging behaviour (Diehl 2010). Therefore, river managers should consider the potential impacts of flow rate regulation, either as a product of direct control over river discharge, or as a result of in-stream macrophyte removal (Garner 1996).

The aim of this chapter is to thus apply the developed individual-based model for roach (Chapter 5) to test how river management practises affect roach growth and recruitment. The practises used are macrophyte removal using a range of cutting strategies (e.g. indiscriminate removal of between 50 and 95 % of all macrophytes, and removal from one side of the river channel only) and flow management techniques.

6.2 Materials and Methods

6.2.1 Model overview and purpose

The roach IBM that was developed in the preceding chapter was designed to predict the behaviour of 0+ and 1+ year group roach as they interact with the virtual environment, performing adaptive behaviours related to habitat selection and feeding behaviour. These behavioural decisions are defined by bioenergetic outcomes on forager growth rate and by extension survival and recruitment. This roach foraging IBM is based on the MORPH optimal-foraging individual-based modelling platform (Stillman 2008).

The model is designed to produce valid distribution and bioenergetic predictive outcomes for the roach age classes, providing information on their location or mesohabitat utilisation, growth rates and final lengths. The intended application is to aid river management through understanding the effect of in-stream macrophyte removal and flow rate regulation on the growth, recruitment and survival of juvenile roach.

6.2.2 Virtual environment

The virtual environment modelled in this chapter is designed and parameterised to reflect environmental conditions in the Suffolk Stour River, Eastern England, during the summer of 2011, with emphasis on environmental parameters and roach population responses to river flow and macrophyte cover. For a detailed description of the environmental data collected in order to parameterise the virtual environment and the study site itself, see Chapter 4. For a full description of the construction and validation of the individual-based model, see Chapter 5.

6.2.3 Spatial extent of the virtual environment

The virtual environment consists of the same section or river, with the same divisions into macro and mesohabitat as was described and used in Chapter 5, with the river again being modelled as a closed system.

6.2.4 Global parameters

Global variables such as water temperature, flow rate and turbidity are modelled across the virtual environment, based on environmental recordings from the Suffolk Stour in 2011. These global variables are unchanged from Chapter 5, except during scenario testing when user-defined alterations are made. The bioenergetic aspects of the model, such as assimilation rate, energetic content of prey item and respiration energetics are unchanged (Chapter 5).

6.2.5 *Stretch resource densities*

Benthic invertebrate density was estimated from drift sampling of macroinvertebrate population abundance and size structure, performed in 2011. Linear regression was used to estimate densities between sampling across different times of day and between sampling dates. By assessing invertebrate origin (aquatic or terrestrial), energy (based on length, dry mass and energy density) energetic content was calculated, using published length-mass, mass-energy relationships (Cummins & Wuycheck 1971; Ganihar 1997; Benke et al. 1999; Sabo et al. 2002). By including information of patch area and water depth, this provided a means to convert drift densities into the amount of energy available as benthic invertebrates (Diamond 1967; Herpher 1998; Haertel & Eckmann 2002; Holker et al. 2002; Chapter 5).

As for filter feeding resources, literature values of intake and evacuation rates (Karjalainenet al. 1997; Haertel & Eckmann 2002; Specziar 2002) were used to estimate the amount of filter feeding prey items that would be consumed by the foragers, with this principally influenced by forager size and environmental temperature. This information was used in conjunction with data on the mass and energetic content of various potential prey items (Persson 1983; Karjalainen et al. 1997; Viroux 1997; Garcia-Berthou 1999; Mehner 2000), providing an estimate of the amount of energy available to filter feeding roach.

Diet shifts associated with ontogenetic changes are described in the model by a forager parameter of available diet, with smaller, usually younger, foragers restricted to filter feeding before switching to predating upon invertebrates as they grow, with this controlled by total body length (Van Den Berg et al. 1994; Hjelm et al. 2003).

6.2.6 Patch flow rate

Flow rate is based on recorded data for each patch, with the value being read from a user-defined file for each time step (Chapters 4 & 5). A normal flow rate scenario, based on field work data, is unchanged from the variable used in the original model (Chapter 5). A file providing higher flow rate values may also be used for scenario testing, based on flow variability data from the Suffolk Stour, recorded in 2009 by the Environment Agency. Lastly, patch flow rate information for a flow regime under which the normal flow rate is punctuated by short periods of increased flow rate may be simulated. This normal flow with peaks of greatly increased flow rate is based on Q1 and Q5 values (mean flow rates that are only exceeded 1% and 5% of the time respectively), based on recorded data from the Environment Agency and Hannaford & Buys (2012).

6.2.7 Forager types

Each forager is defined by their forager type, based on their age class with 'YOY' forager type being 0+ roach and 'OnePlus' forager type being 1+ roach. These forager types provide a more accurate representation of the juvenile population structure observed at the study site, with the forager types differing in size and allometric related functions such as swimming speed and available diet. The forager types, as well as their forager parameters, remain unchanged from the original model (Chapter 5).

6.2.8 Fitness measure

Patch choice decisions follow the fitness-maximising principle (Stillman 2008) that emphasises growth rates and survival of the forager. The fitness measure used incorporates both diet consumption rate and macrophyte cover, and was shown to produce the most accurate model outcomes when validated against observed patterns, compared to the alternate fitness measures discussed in Chapter 5.

The fitness measure states that:
'If rate of consumption does achieve Cmax; select behaviour and patch that maximises the amount of macrophyte cover.' Otherwise, 'Select behaviour and patch that maximises consumption rate.'

This is the 'Safety' fitness measure, whereby the foragers seek to maximise their consumption rate. However, if their consumption rate will reach CMax in several patches, the forager will select the patch with the highest amount of in-stream macrophytes. While predation risk is not calculated in this model, habitat selection preferences of roach favouring in-stream macrophytes is associated with reduced predation risk and water flow rate (Chick & McIvor 1997; Jacobsen & Berg 1998; Grenouillet & Pont 2001).

Model analysis

6.2.9 Specific growth rates (SGR)

Forager growth rates are calculated as specific growth rates, or the percentage change in body mass per day (%body mass day^{-1}). This calculation is expressed as:

$$SGR = \frac{\ln(W_{tn}) - \ln(W_{t0})}{t_n - t_0} * 100 \qquad \textbf{(Eqn 6.1)}$$

Where SGR is the specific growth rate, w_{t0} is the initial mass of a forager at survey time (t_0) and w_{tn} is the subsequent mass of a forager at survey time (t_n), finally t_n-t_0 is the number of days between surveys.

6.2.10 Forager total length

The total length of the foragers at the end of the simulation is estimated based on their total body mass. This is calculated as:

$$BodyLength = (47.25 * BodyMass)^{0.5303} \qquad \textbf{(Eqn 6.2)}$$

Where BodyLength is the total length of a forager (mm), and BodyMass is the final mass of a forager at the end of the simulation run (g). This is based on similar equations used by Holker and Breckling (2002) to describe roach, calibrated to describe the length/ weight relationship specific to juvenile roach in the Suffolk Stour, based on fieldwork data, data provided by the Environment Agency and Cryer et al. (1986).

6.2.11 Validation

The original model was validated by comparing the predicted mesohabitat distribution of modelled foragers against that of the observed fish recorded at the study site. Predicted distribution proportions were plotted against observed proportions and the estimated linear regression for that relationship statistically tested against an equal 1:1 relationship, with a slope of 1 and an intercept of (0,0). The t-value of the difference in gradient and intercept was used to calculate the probability of difference in a two-tailed evaluation. The original model was also validated through comparison of observed and predicted specific growth rates.

This validated original model now serves as a basis of comparison, indicating the impact of various scenarios on the model output, compared to both the observed patterns and those of a validated model.

6.2.12 Scenario testing

Two types of scenario are tested, relating to flow rate and macrophyte cover (Table 6.1; Section 6.1). Specifically, scenarios of increased flow rate and removal of macrophyte cover, as well as their combined, antagonistic effects, were tested. The flow rate levels are described in the patch flow rate section (Table 4.3; Section 4.3), based on flow rate data from the Suffolk Stour. There are two such altered flow rate regimes, reflecting an increased flow rate, sustained over several weeks, as well as very high, acute increases in flow rate, sustained over a matter of hours before returning to more normal flow rate levels. These two altered flow rate regimes are referred to as 'High Flow' and 'Normal Flow with peaks', the original, unaltered flow regime is referred to as 'Normal Flow' (Table 6.1).

Along with flow rate, the amount and location of macrophyte cover is altered, simulating macrophyte removal as an integral part of the management practises on the river. There are six such macrophyte scenarios, whereby the macrophyte cover patch parameter is reduced, either selectively, in some patches but not others, or across all patches to the same degree (Table 6.1). Macrophyte Scenario '1' and '2' model the removal of all macrophytes on the right hand bank (RHB) and left hand bank (LHB) of the river respectively, as recommended by Garner, Bass & Collet (1996). Scenario 3

simulates the removal of 50% of all macrophyte cover, but across all patches equally. Scenarios 4, 5 and 6 represents the selective removal of macrophyte cover from the majority of the patches, leaving only a few patches untouched, with such patches selected for the presence of heavy or prominent macrophyte vegetation at the study site (Dawson & Haslam 1983; Johnstone 1986). Scenarios 4, 5 and 6 differ in the proportion of unaltered patches that remain, from 25%, 15% and 5% respectively. These 6 Macrophyte Scenarios will be tested in conjunction with the altered flow rate scenarios, in order to describe both the relationship between in-stream macrophytes and flow rate as well as any potential antagonistic effects on foragers of both an altered flow rate and altered macrophyte habitat availability.

Table 6.1 The various simulated management interventions, applied as part of the scenario testing (6.2.12). Initially each scenario was tested individually, after which the macrophyte scenarios were tested in combination with the flow rate regimes.

Scenario Number:	Macrophytes Management:	Flow Rate Regime:
1	LHB (50%) of total remains	Normal Flow
2	RHB (50%) of total remains	Normal Flow
3	Both Banks (50%) of total remains	Normal Flow
4	Selective (25%) of total remains	Normal Flow
5	Selective (15%) of total remains	Normal Flow
6	Selective (5%) of total remains	Normal Flow
7	NA	High Flow
8	NA	Normal Flow with peaks

6.3 Results

6.3.1 Impact of scenarios on 0+ SGR

Under the unaltered flow regime, the specific growth rate of 0+ roach, as predicted by the IBM, was seen to significantly vary from the original model output only under the macrophyte removal scenarios of 25%, 15% and 5% selective, i.e. when simulations represented the removal of 75%, 85% and 95% of all in-stream macrophytes in the modelled river system (Figure 6.1, Welch's T-test $p < 0.05$) The remaining macrophyte removal scenarios of LHB, RHB and 50%, as well as both High and High with peaks flow regimes, with no alterations made to macrophyte cover, revealed that SGR did not vary significantly from the original model output (Figure 6.1, Welch's T-test $p > 0.05$).
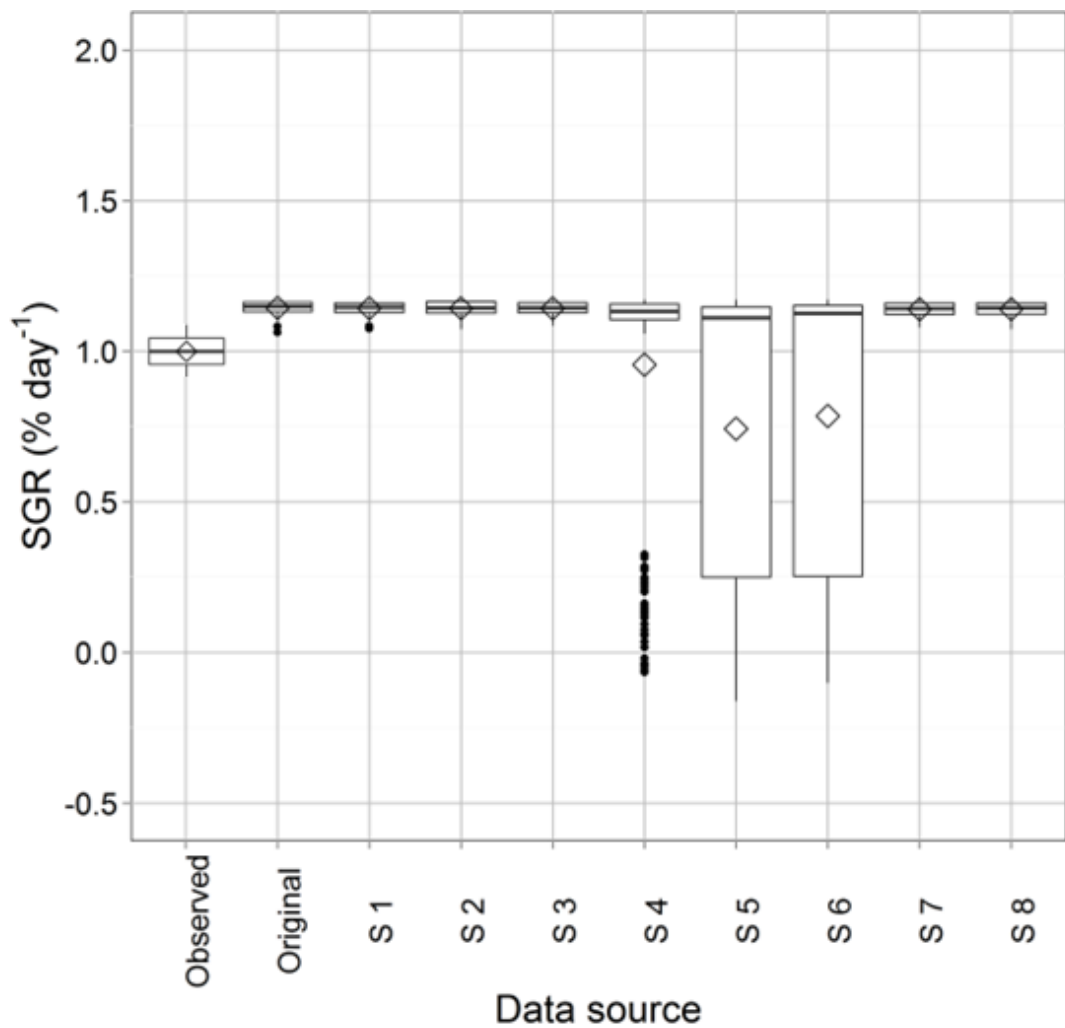
Figure 6.1 Observed and predicted population specific growth rates of 0+ roach. Observed growth rates ('Observed') are based on data from published literature, predicted growth rates are from the roach individual-based model and are listed left to right as the areas of the river where macrophytes remain; The Original model ('Original'), All LHB ('S1'), All RHB ('S2'), All 50% ('S3'), Selective 25% ('S4'), Selective 15% ('S5') and Selective 5% ('S6'). The diamond indicates mean SGR for each distribution. The final two columns display the predicted specific growth rate under unchanged macrophyte scenarios, but altered flow rate scenarios labelled as High Flow ('S7') and Normal Flow with peaks ('S8').

Similarly, the influence of the macrophyte removal scenarios on the SGR of 0+ roach as predicted by the IBM, were also tested under the altered flow rate regimes, with High

flow (Figure 6.2b) and Normal flow with peaks of very high flow (Figure 6.2c) being tested. For comparison, Normal Flow rate scenarios are also displayed (Figure 6.2a). In all cases, only the macrophyte removal scenarios where 25%, 15% and 5% of macrophytes remained in the river were seen to significantly differ from the original model output (Figure 6.2a – 6.2c, Welch's T-test $p < 0.05$). Under the remaining macrophyte scenarios, where more macrophyte cover remains in the system, no significant difference was seen under all three flow regimes (Figure 6.1, Welch's T-test $p > 0.05$).
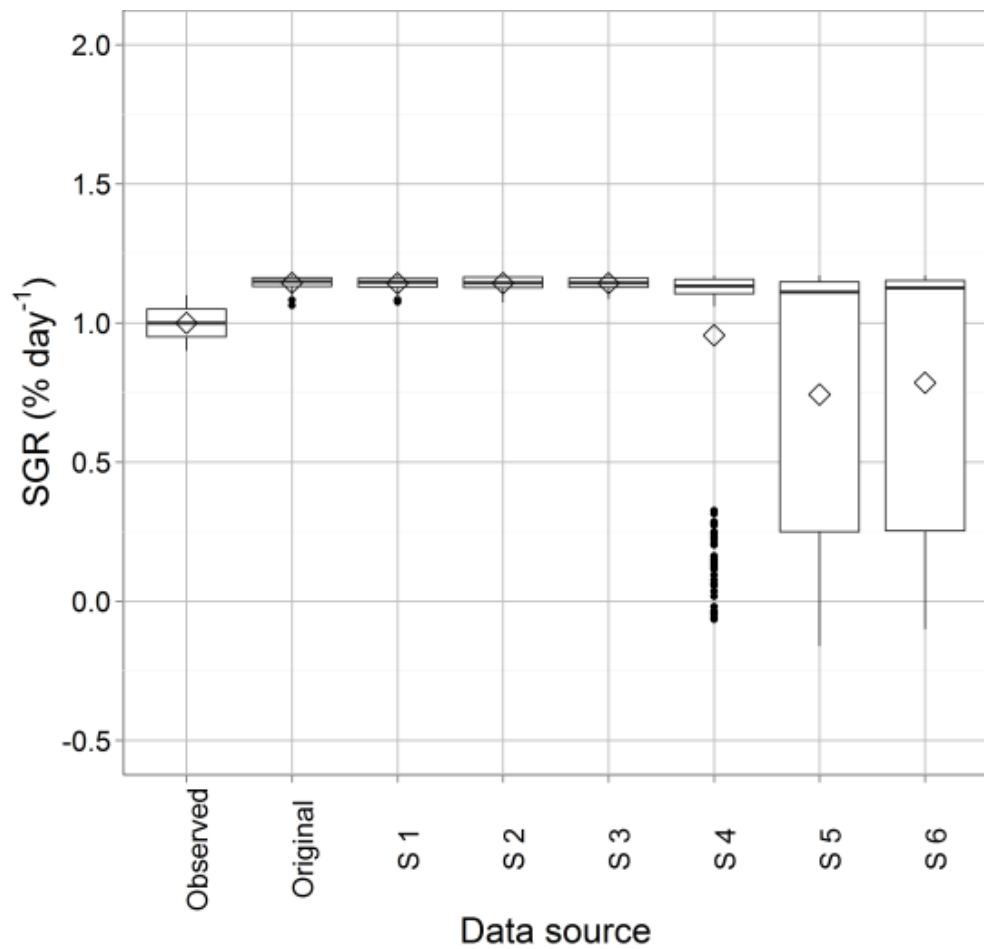
Figure 6.2a Observed and predicted population specific growth rates of 0+ roach. Observed growth rates ('Observed') are based on data from published literature, predicted growth rates are from the roach individual-based model and are listed left to right as the areas of the river where macrophytes remain, **all under normal flow conditions;** The Original model ('Original'), All LHB ('S1'), All RHB ('S2'), All 50% ('S3'), Selective 25% ('S4'), Selective 15% ('S5') and Selective 5% ('S6'). The diamond indicates mean SGR for each distribution.
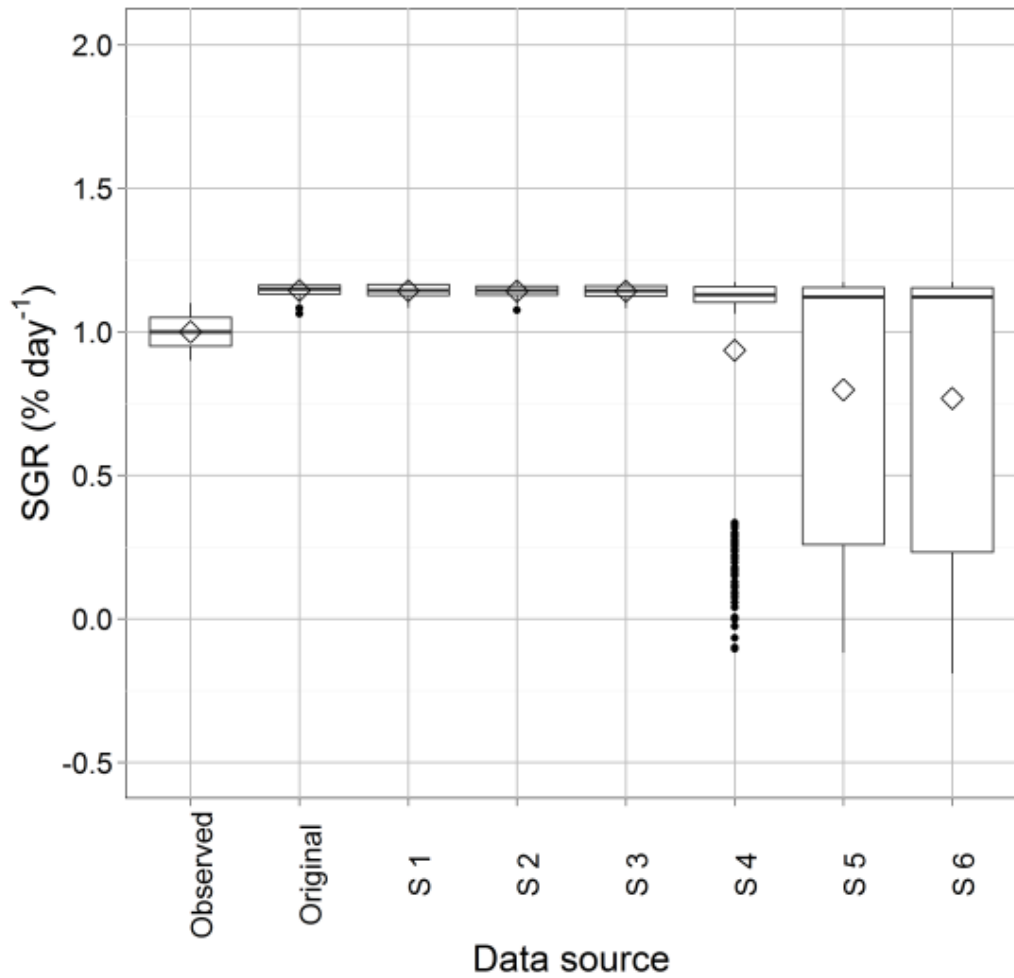
Figure 6.2b Observed and predicted population specific growth rates of 0+ roach. Observed growth rates ('Observed') are based on data from published literature, predicted growth rates are from the roach individual-based model and are listed left to right as the areas of the river where macrophytes remain, **all under high flow conditions**; The Original model ('Original'), All LHB ('S1'), All RHB ('S2'), All 50% ('S3'), Selective 25% ('S4'), Selective 15% ('S5') and Selective 5% ('S6'). The diamond indicates mean SGR for each distribution.
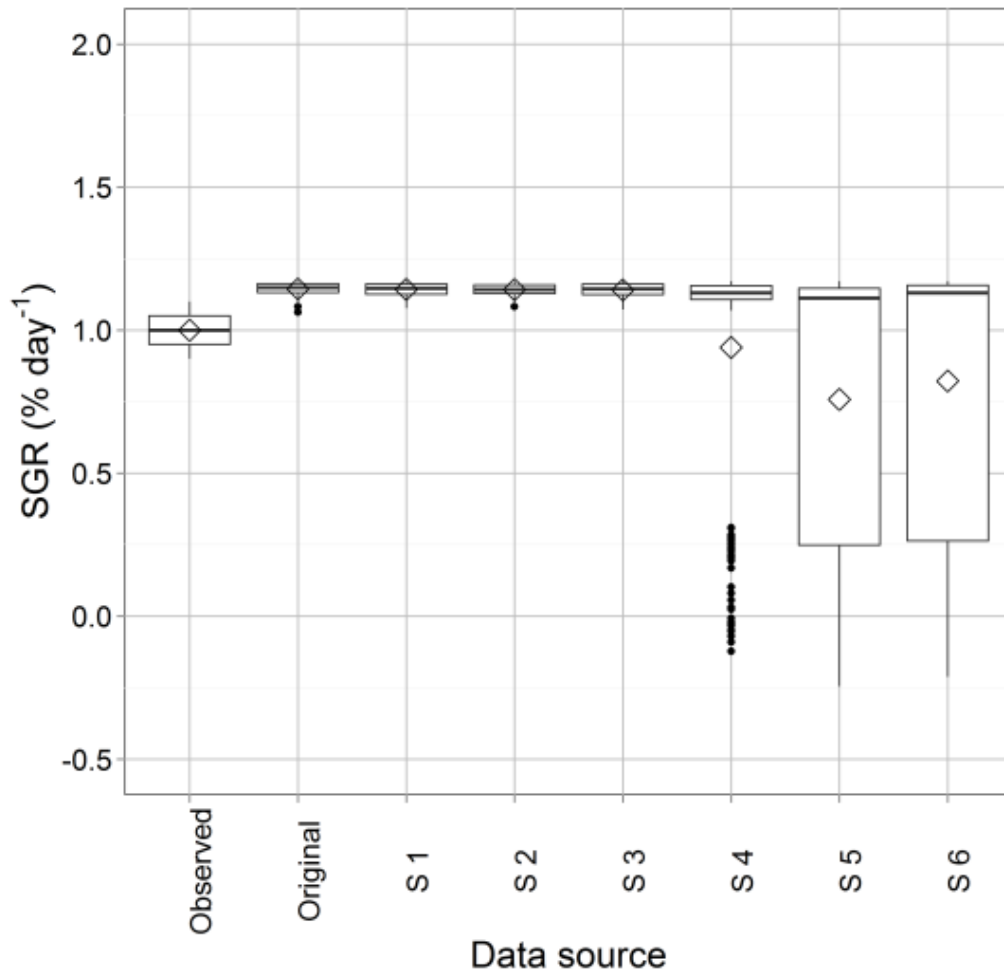
Figure 6.2c Observed and predicted population specific growth rates of 0+ roach. Observed growth rates ('Observed') are based on data from published literature, predicted growth rates are from the roach individual-based model and are listed left to right as the areas of the river where macrophytes remain, **all under normal flow conditions with peaks of very high flow**; The Original model ('Original'), All LHB ('S1'), All RHB ('S2'), All 50% ('S3'), Selective 25% ('S4'), Selective 15% ('S5') and Selective 5% ('S6'). The diamond indicates mean SGR for each distribution.

The same scenarios of flow rate and macrophyte removal, along with their effects on 0+ SGR are displayed as a proportion of the original, unaltered predicted SGR. While little change in SGR was evident in the scenarios where 50% of the in-stream macrophytes were removed, a marked decrease in SGR was predicted once more macrophytes were removed, with this effect being compounded by simultaneous increases in flow rate (Figure 6.3a – 6.3c).
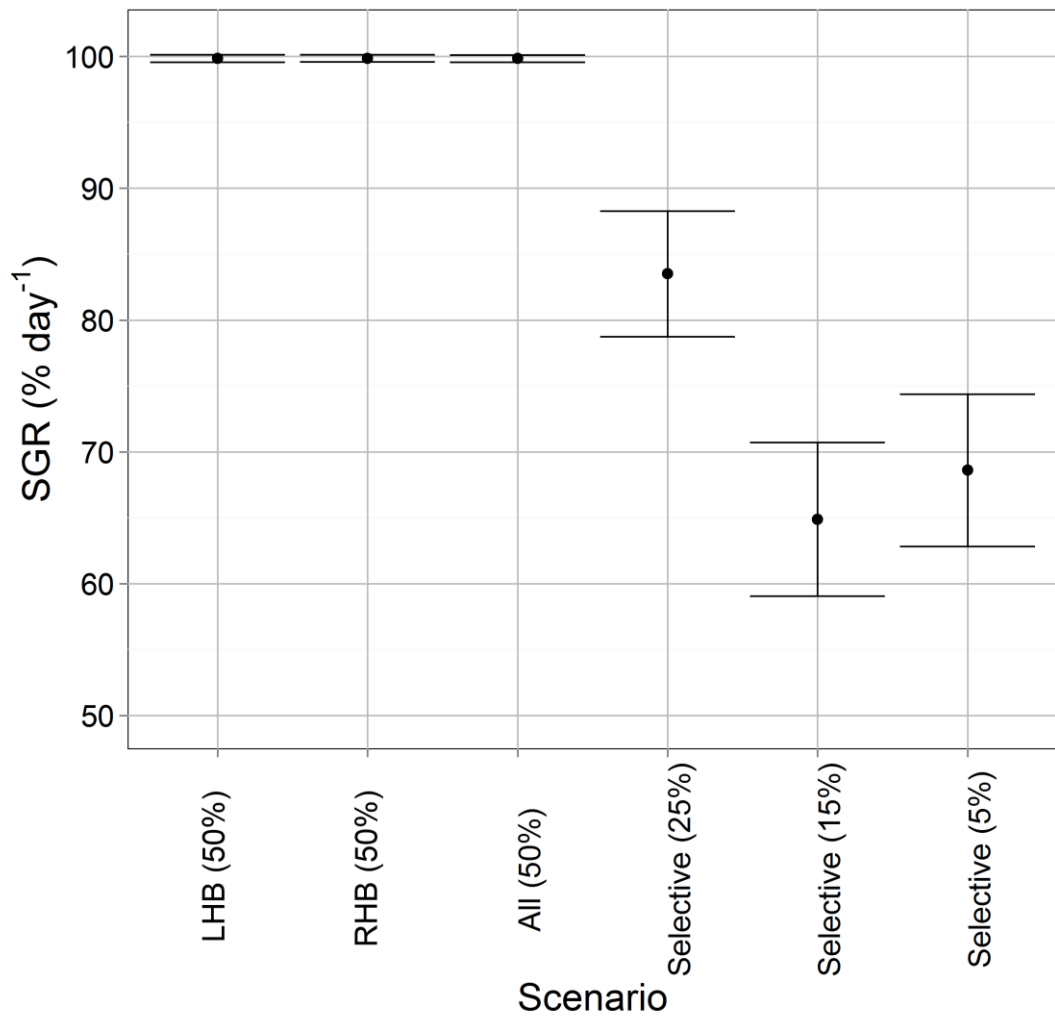
Figure 6.3a The variation in predicted specific growth rate of 0+ roach as a proportion of the original, unaltered model against macrophyte removal scenarios listed left to right in relative proportion of in-stream macrophytes removed, **under normal flow rate conditions**. Filled circles represent predicted population mean specific growth rates with associated 95% confidence intervals.
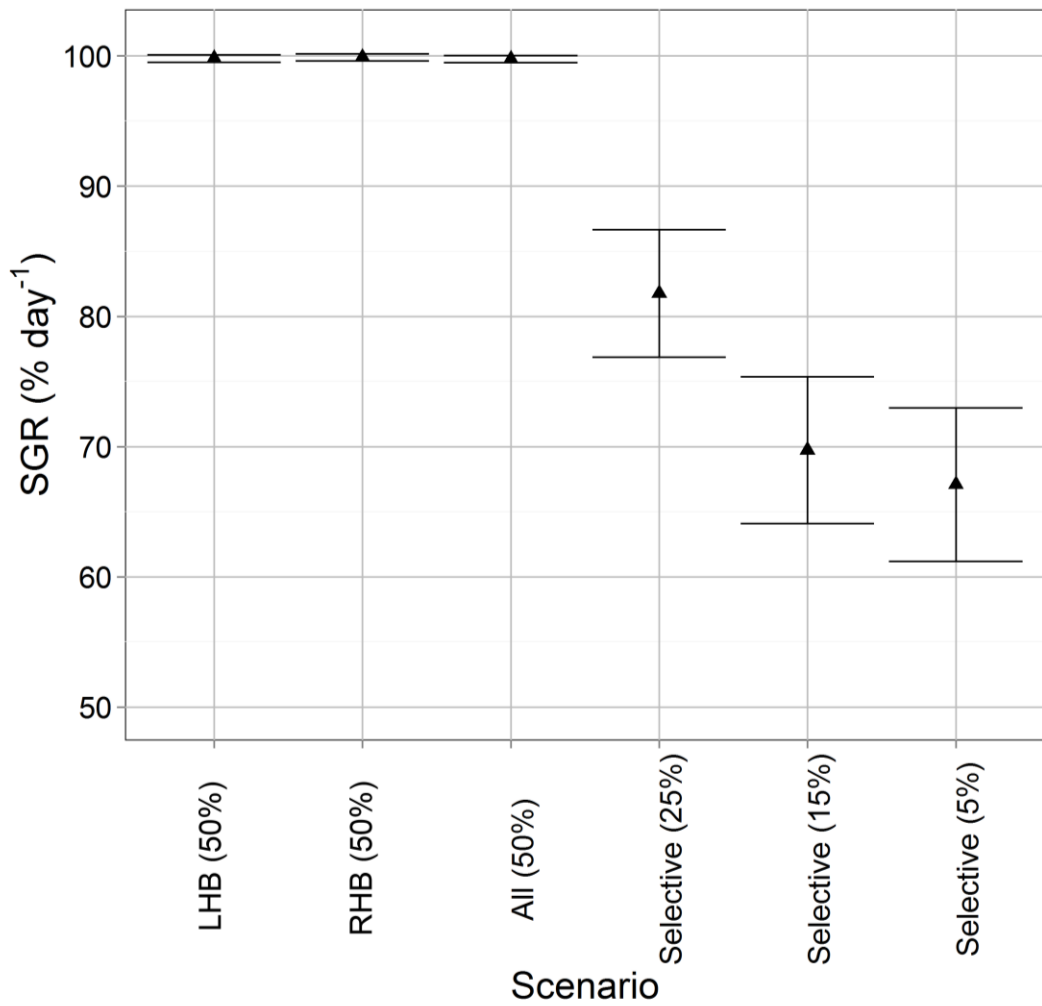
Figure 6.3b The variation in predicted specific growth rate of 0+ roach as a proportion of the original, unaltered model against macrophyte removal scenarios listed left to right in relative proportion of in-stream macrophytes removed, **under high flow rate conditions**. Filled triangles represent predicted population mean specific growth rates with associated 95% confidence intervals.
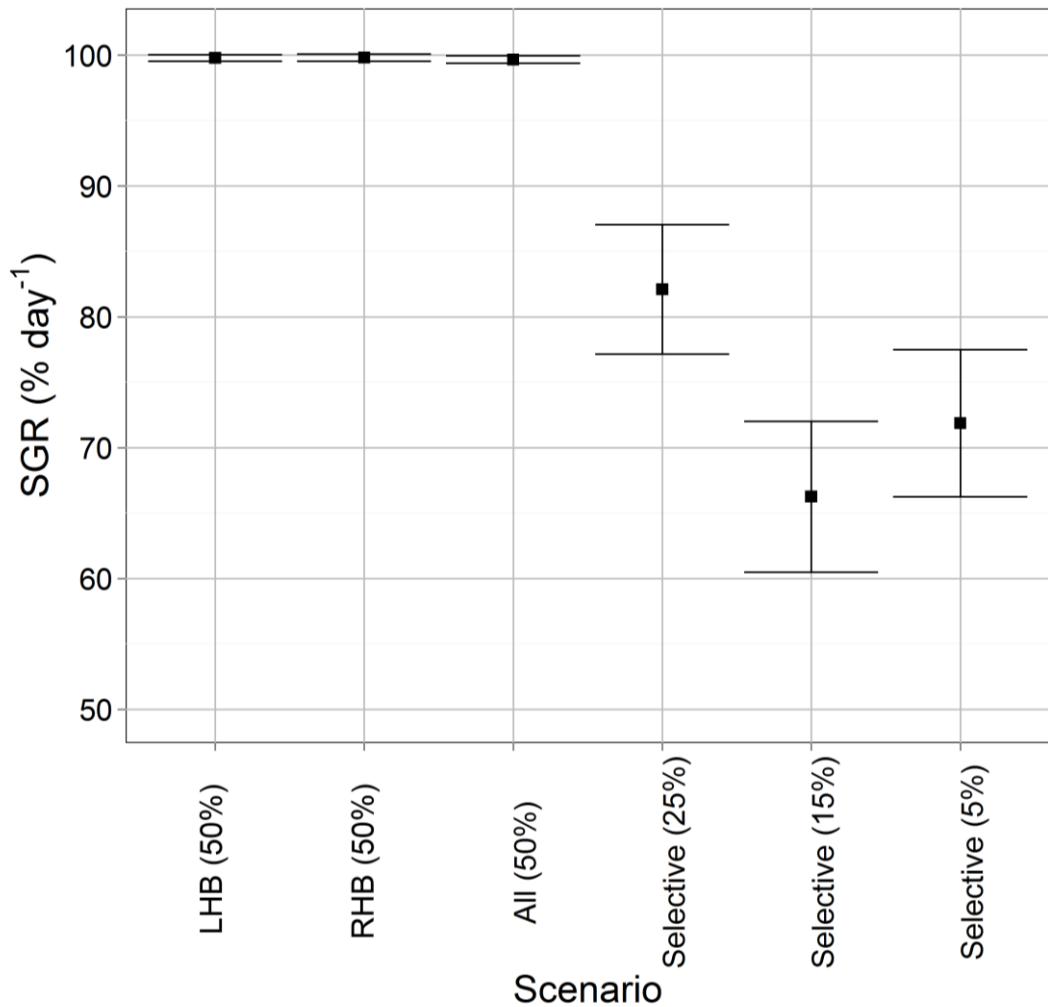
Figure 6.3c The variation in predicted specific growth rate of 0+ roach as a proportion of the original, unaltered model against macrophyte removal scenarios listed left to right in relative proportion of in-stream macrophytes removed, **under normal flow rate conditions with peaks of very high flow**. Filled squares represent predicted population mean specific growth rates with associated 95% confidence intervals.

The final consequence of these scenarios on the 0+ roach was a reduction in their body length, with this consistent with their reduced SGR and is displayed as a proportion of the original, unaltered mean predicted final body length Fig 6.4a – 6.4c). This consequence was, again, marked in the scenarios of reduced macrophyte cover, above 50%, and further influenced by increased flow rate or increased variability in flow rate (Figure 6.4a – 6.4c). Given the relationship between length and year-class strength (YCS) (Nunn et al. 2003, 2007; Britton et al. 2004; Chapter 4) whereby a 0.5 mm decrease in mean population length at the end of the first growth year was seen to

reduce the YCS value by 6; the predicted reduction in mean population length of approximately 4.5 mm, under the selective 25 and 15% scenarios, represents a very large decrease in YCS. This decrease of 63 (with 100 representing a strong YCS) would produce a weak year-class, significantly reducing the number of adult fish able to spawn and thus future recruitment rates.
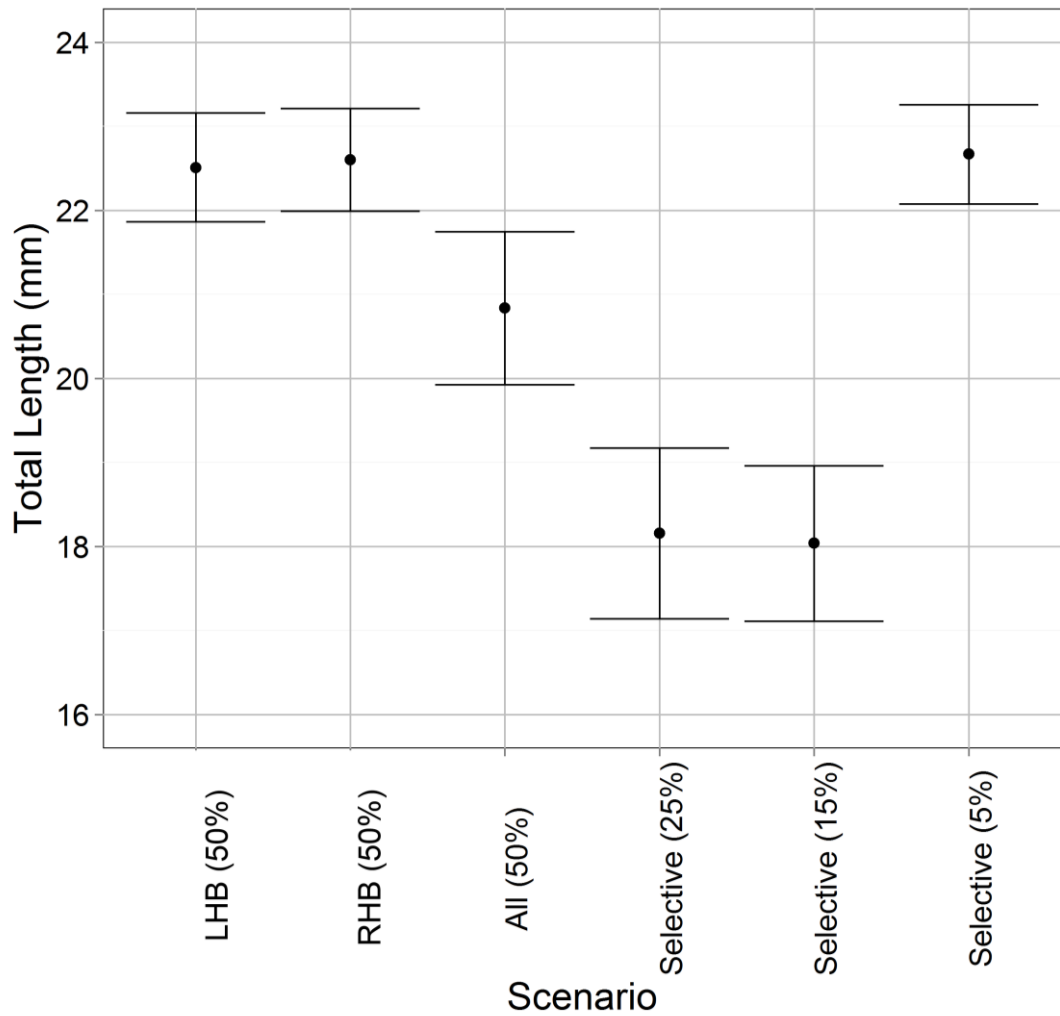
Figure 6.4a The variation in predicted final length of 0+ roach as a proportion of the original, unaltered model against macrophyte removal scenarios listed left to right in relative proportion of in-stream macrophytes removed, **under normal flow rate conditions**. Filled circles represent predicted population mean final total body length at the end of the simulation run, simulating the end of the summer growth season in roach.

Figure 6.4b The variation in predicted final length of 0+ roach as a proportion of the original, unaltered model against macrophyte removal scenarios listed left to right in relative proportion of in-stream macrophytes removed, **under high flow rate conditions**. Filled triangles represent predicted population mean final total body length at the end of the simulation run, simulating the end of the summer growth season in roach.

Figure 6.4c The variation in predicted final length of 0+ roach as a proportion of the original, unaltered model against macrophyte removal scenarios listed left to right in relative proportion of in-stream macrophytes removed, **under normal flow rate conditions with peaks of very high flow**. Filled squares represent predicted population mean final total body length at the end of the simulation run, simulating the end of the summer growth season in roach.

6.3.2 Impact of scenarios on 1+ SGR

Comparison of the predicted influence on SGR of macrophyte removal scenarios and the flow rate regime scenarios, compared to the original, unaltered model, did not show significant variation from the original model output under any specific scenario (Figure 6.5, Welch's T-test $p > 0.05$) for the larger, 1+ roach.
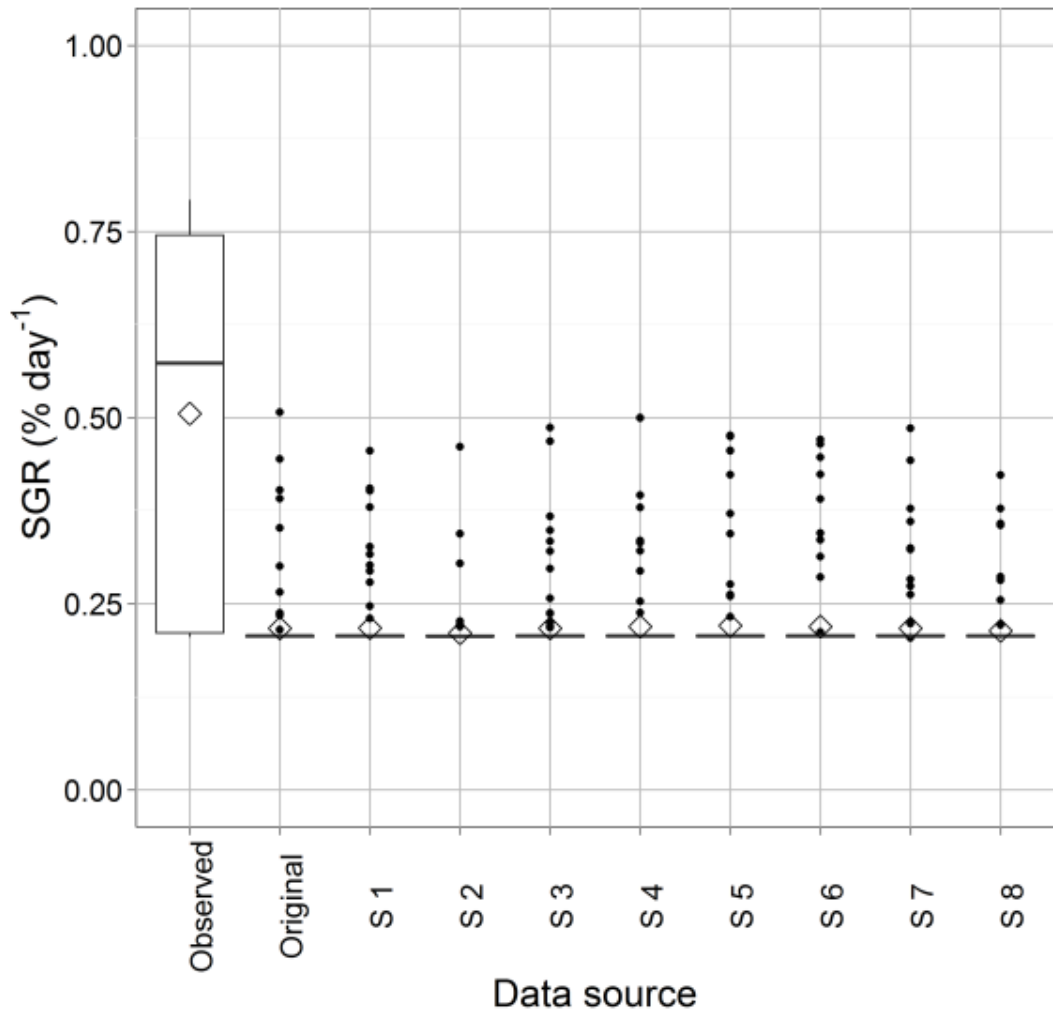
Figure 6.5 Observed and predicted population specific growth rates of 1+ roach. Observed growth rates ('Observed') were collected at a lowland river field site, predicted growth rates are from the roach individual-based model and are listed left to right as the areas of the river where macrophytes remain; The Original model ('Original'), All LHB ('S1'), All RHB ('S2'), All 50% ('S3'), Selective 25% ('S4'), Selective 15% ('S5') and Selective 5% ('S6'). The diamond indicates mean SGR for each distribution. The final two columns display the predicted specific growth rate under unchanged macrophyte scenarios, but altered flow rate scenarios labelled as High Flow ('S7') and Normal Flow with peaks ('S8').

Similarly, the macrophyte removal scenarios, tested under the altered flow rate regimes, showed no significant difference between original and altered model output in terms of population mean SGR under all three flow regimes and all 6 macrophyte removal scenarios (Figure 6.6a – 6.6c, Welch's T-test $p > 0.05$) for 1+ roach.
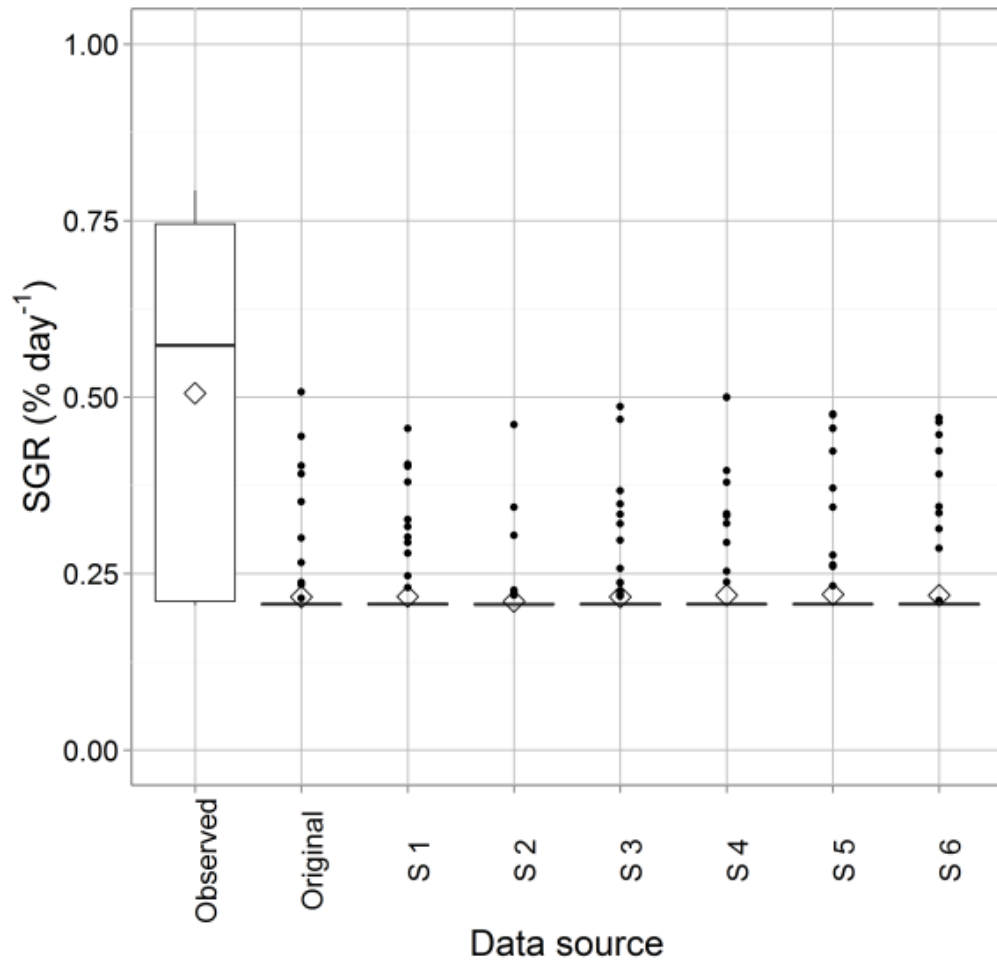
Figure 6.6a Observed and predicted population specific growth rates of 1+ roach. Observed growth rates ('Observed') were collected at a lowland river field site, predicted growth rates are from the roach individual-based model and are listed left to right as the areas of the river where macrophytes remain, **all under normal flow conditions;** The Original model ('Original'), All LHB ('S1'), All RHB ('S2'), All 50% ('S3'), Selective 25% ('S4'), Selective 15% ('S5') and Selective 5% ('S6'). The diamond indicates mean SGR for each distribution.
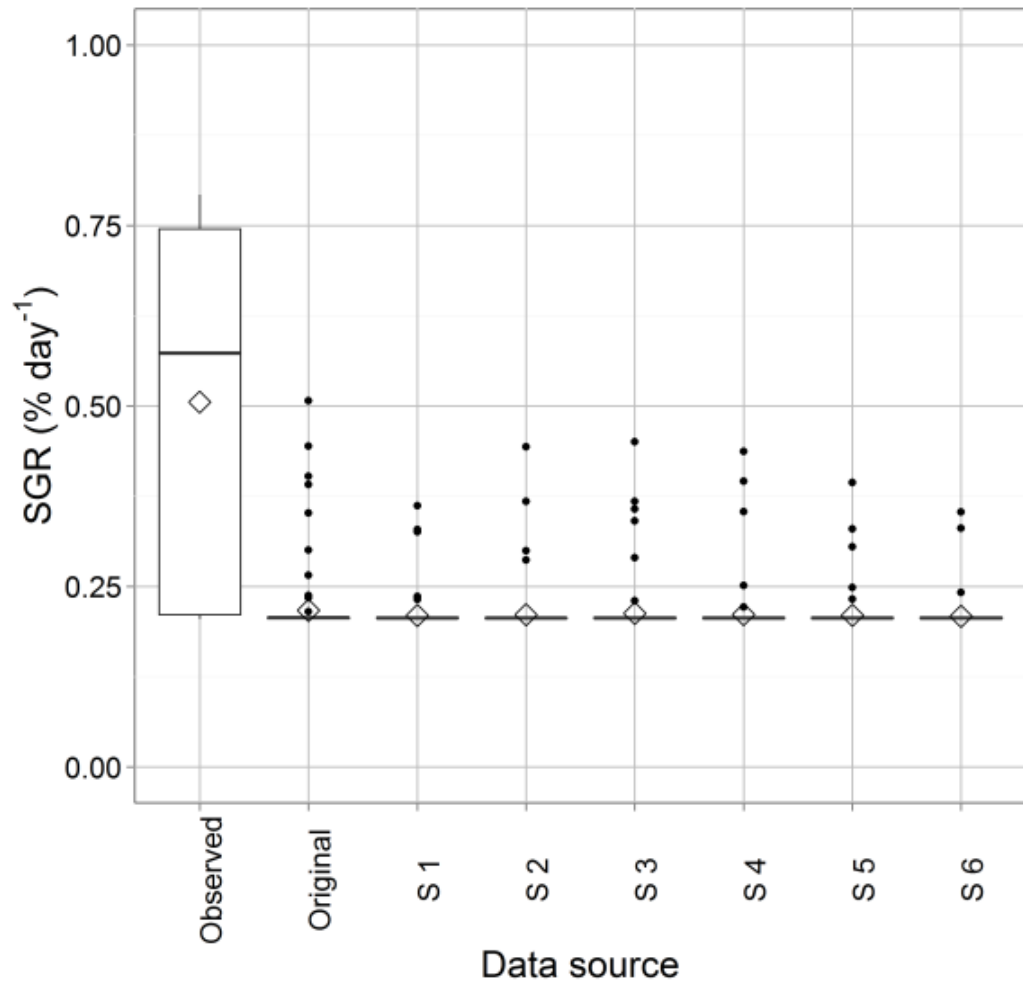
Figure 6.6b Observed and predicted population specific growth rates of 1+ roach. Observed growth rates ('Observed') were collected at a lowland river field site, predicted growth rates are from the roach individual-based model and are listed left to right as the areas of the river where macrophytes remain, **all under high flow conditions**; The Original model ('Original'), All LHB ('S1'), All RHB ('S2'), All 50% ('S3'), Selective 25% ('S4'), Selective 15% ('S5') and Selective 5% ('S6'). The diamond indicates mean SGR for each distribution.
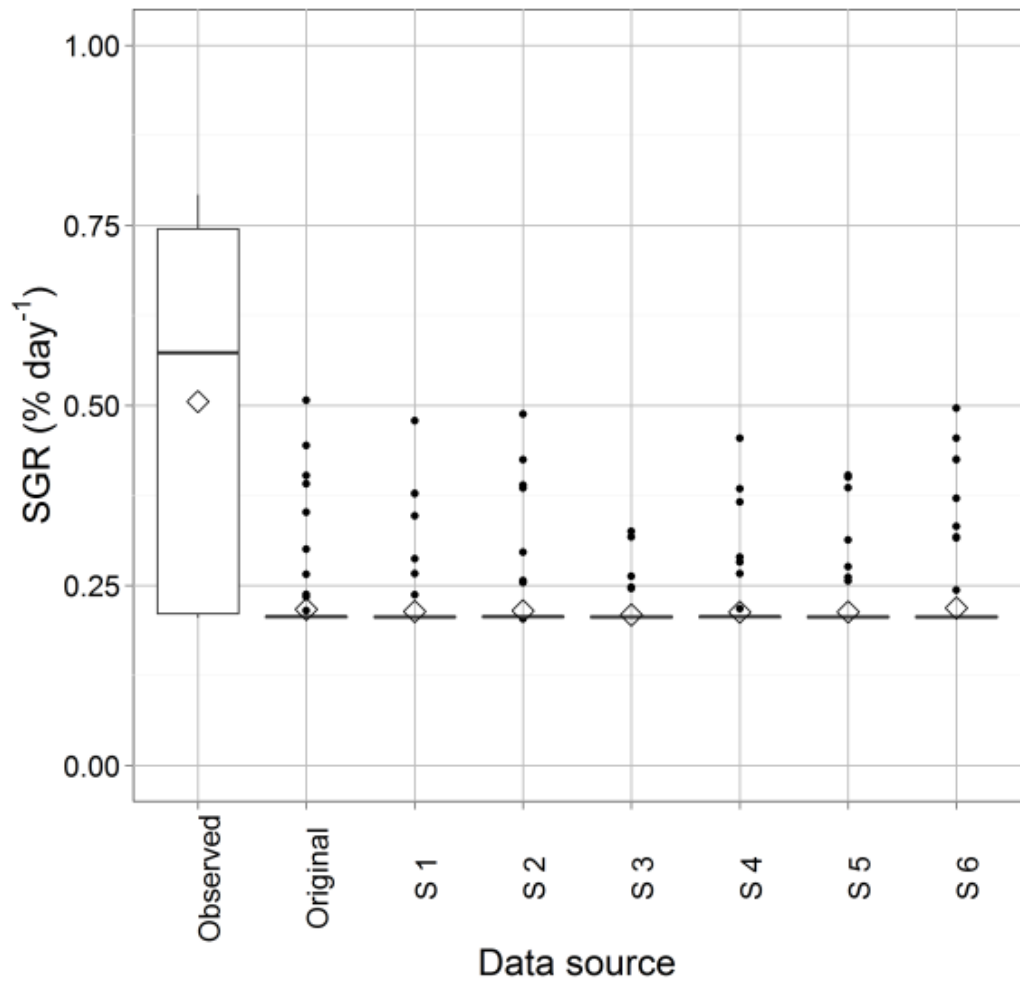
Figure 6.6c Observed and predicted population specific growth rates of 1+ roach. Observed growth rates ('Observed') were collected at a lowland river field site, predicted growth rates are from the roach individual-based model and are listed left to right as the areas of the river where macrophytes remain, **all under normal flow conditions with peaks of very high flow**; The Original model ('Original'), All LHB ('S1'), All RHB ('S2'), All 50% ('S3'), Selective 25% ('S4'), Selective 15% ('S5') and Selective 5% ('S6'). The diamond indicates mean SGR for each distribution.

The same scenarios of flow rate and macrophyte removal, along with their impact on 1+ specific growth rate, are displayed as a proportion of the original, unaltered predicted SGR. These also revealed minimal change in SGR across all the scenarios (Figure 6.7a,b,c).
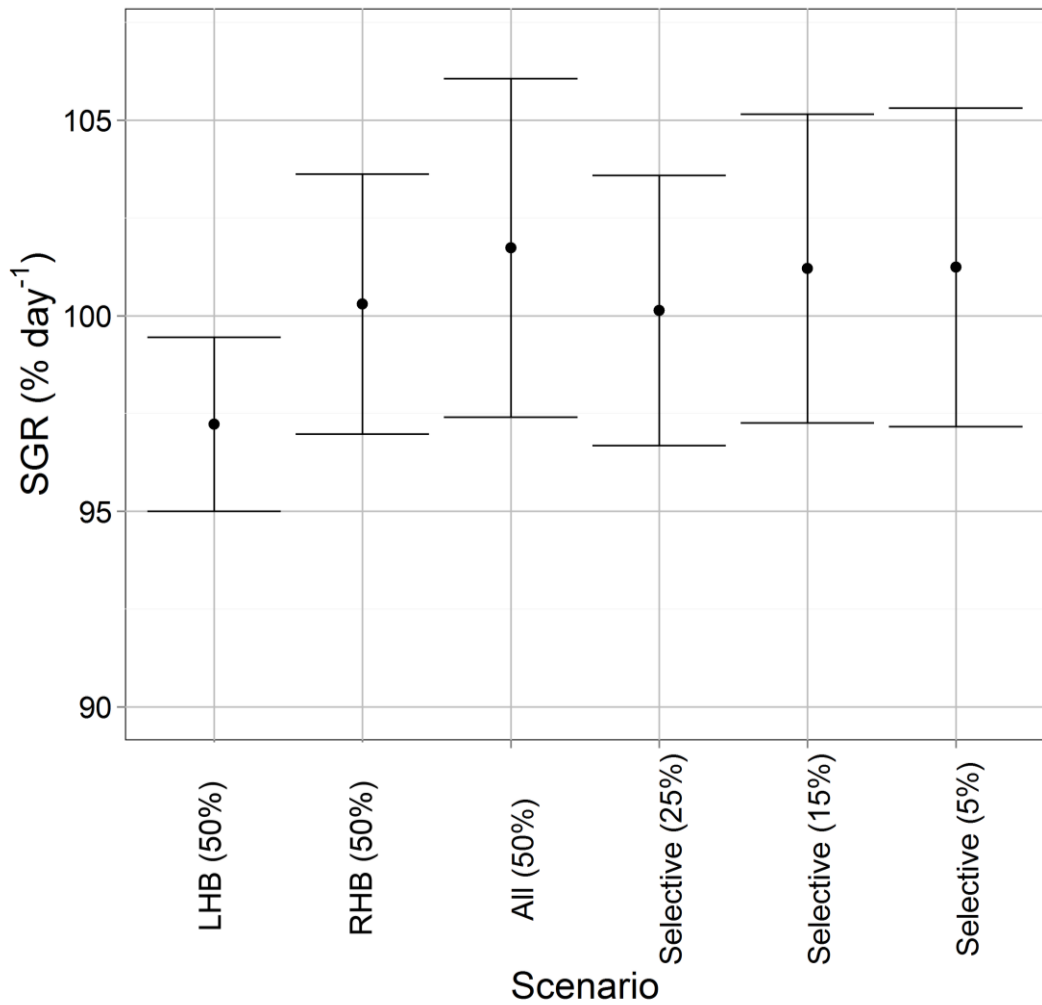
Figure 6.7a The variation in predicted specific growth rate of 1+ roach as a proportion of the original, unaltered model against macrophyte removal scenarios listed left to right in relative proportion of in-stream macrophytes removed, **under normal flow rate conditions**. Filled circles represent predicted population mean specific growth rates with associated 95% confidence intervals.
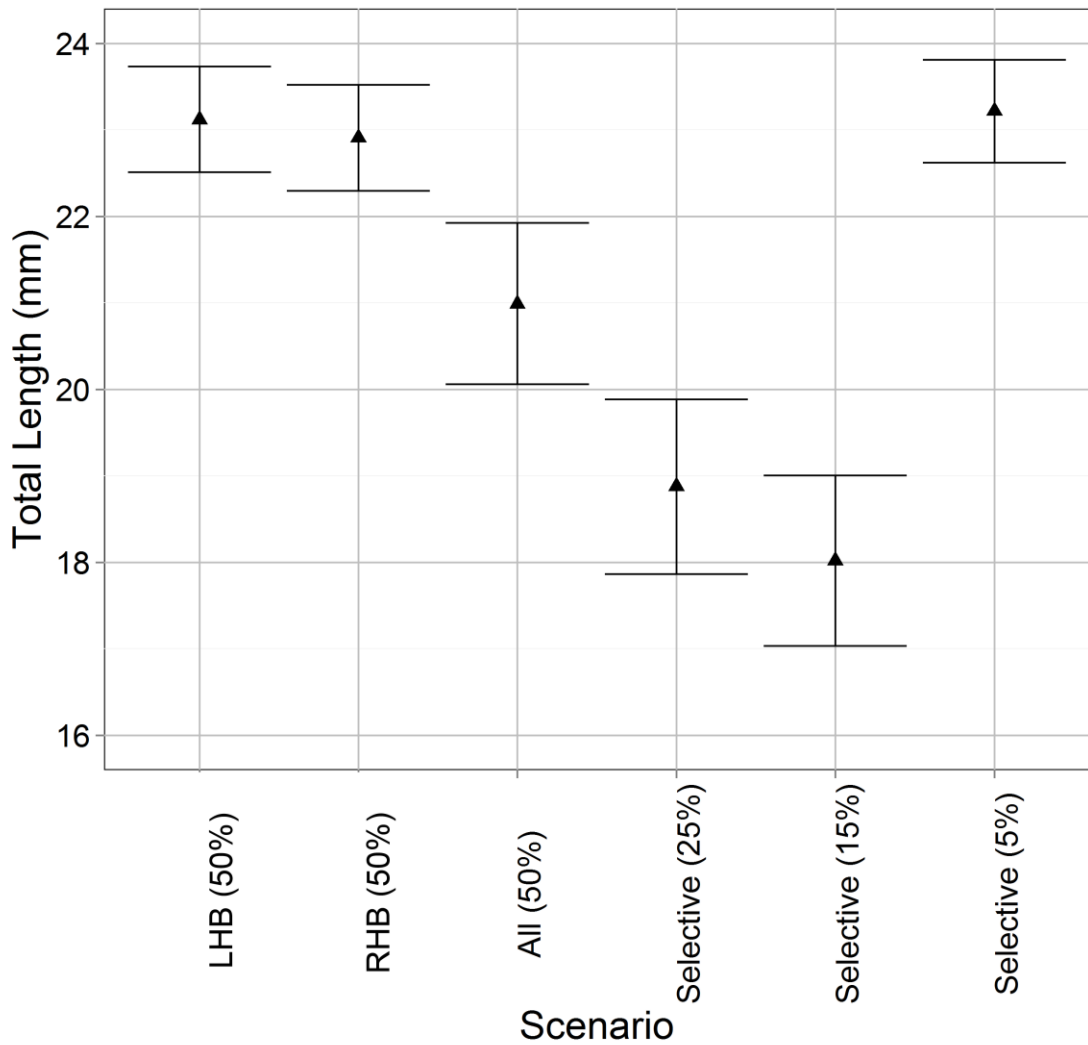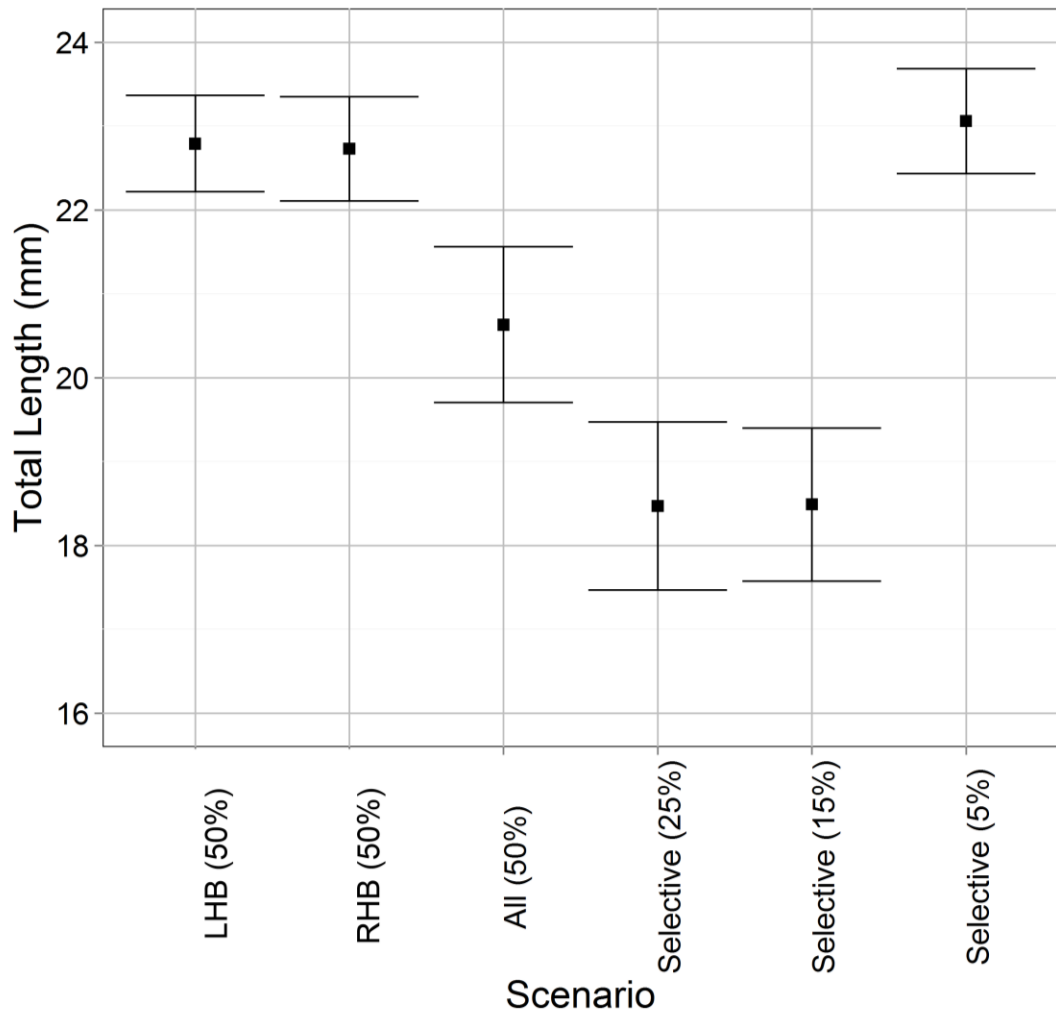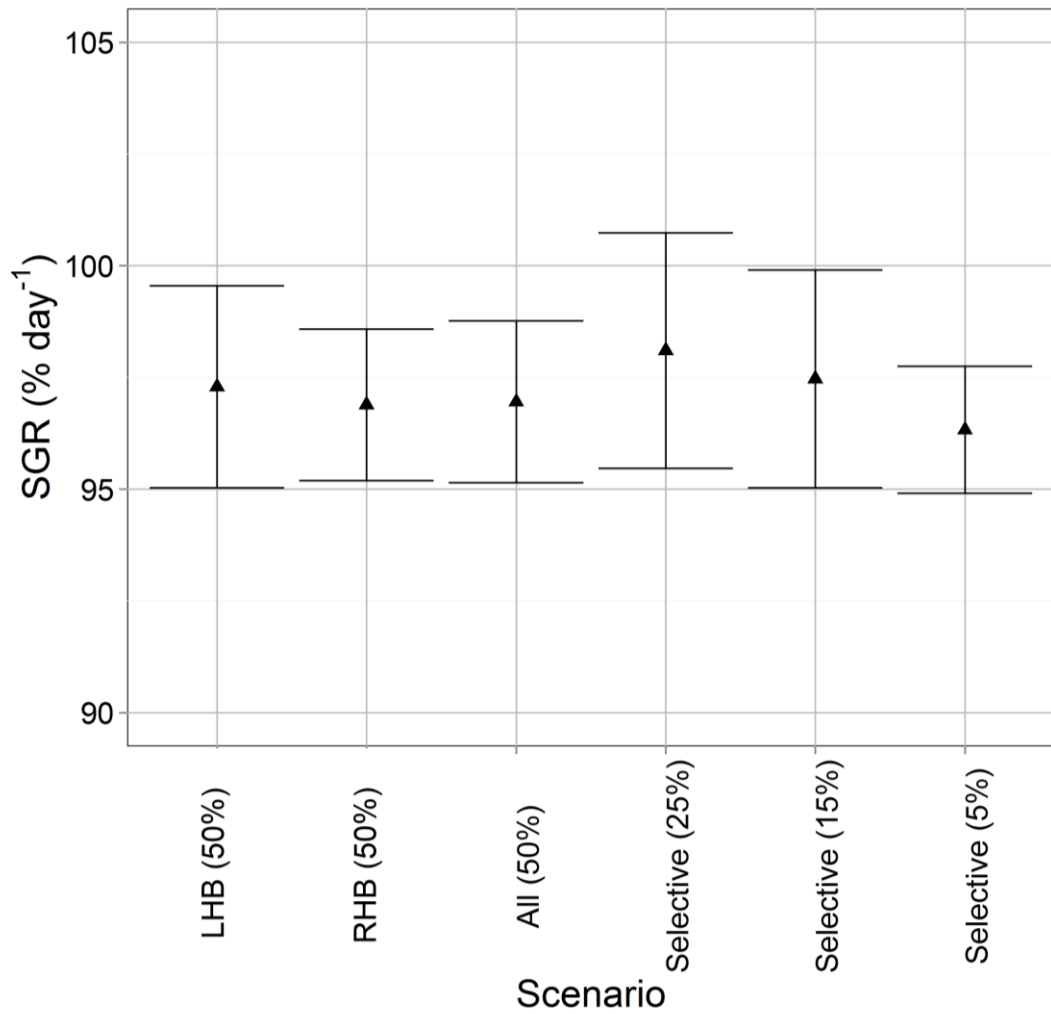
Figure 6.7b The variation in predicted specific growth rate of 1+ roach as a proportion of the original, unaltered model against macrophyte removal scenarios listed left to right in relative proportion of in-stream macrophytes removed, **under high flow rate conditions**. Filled triangles represent predicted population mean specific growth rates with associated 95% confidence intervals.
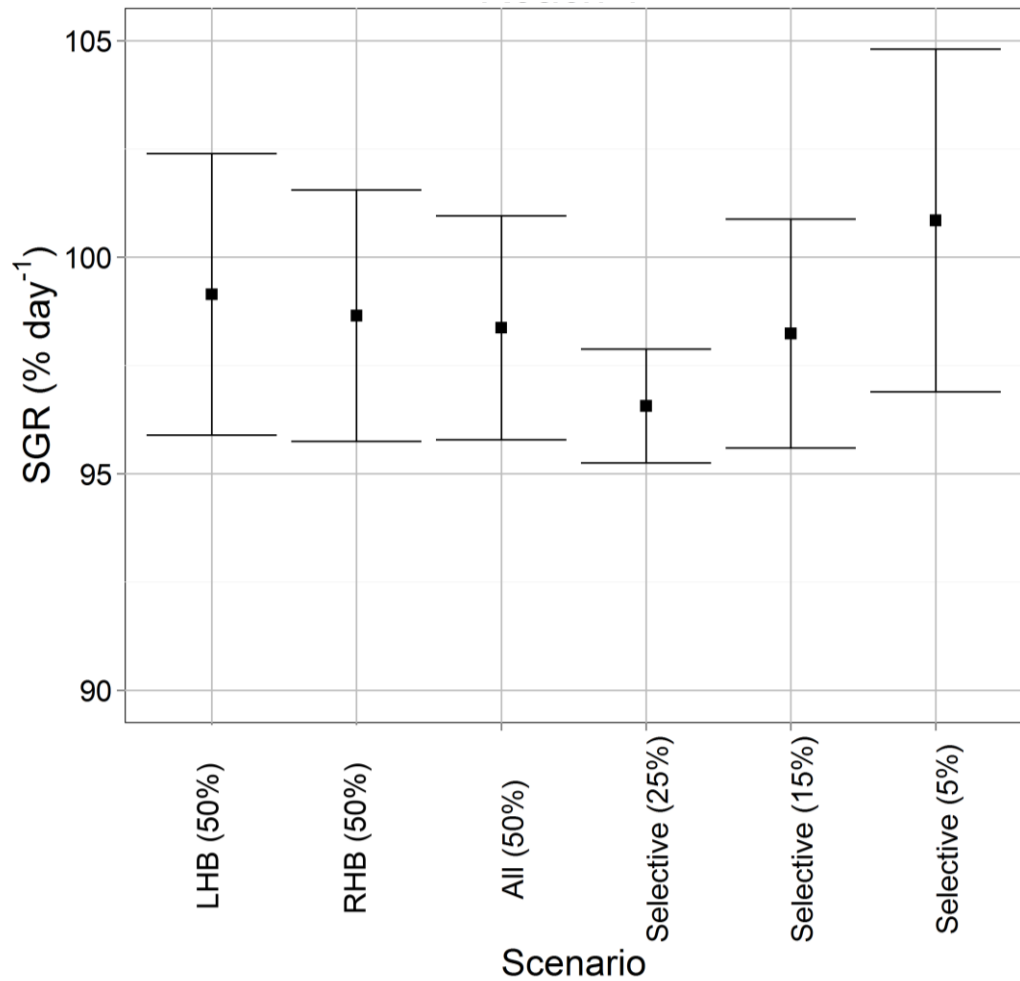
Figure 6.7c The variation in predicted specific growth rate of 1+ roach as a proportion of the original, unaltered model against macrophyte removal scenarios listed left to right in relative proportion of in-stream macrophytes removed, **under normal flow rate conditions with peaks of very high flow**. Filled squares represent predicted population mean specific growth rates with associated 95% confidence intervals.

The consequence of these scenarios on final length of the 1+ roach was also not significant (Figure 6.8a,b,c).
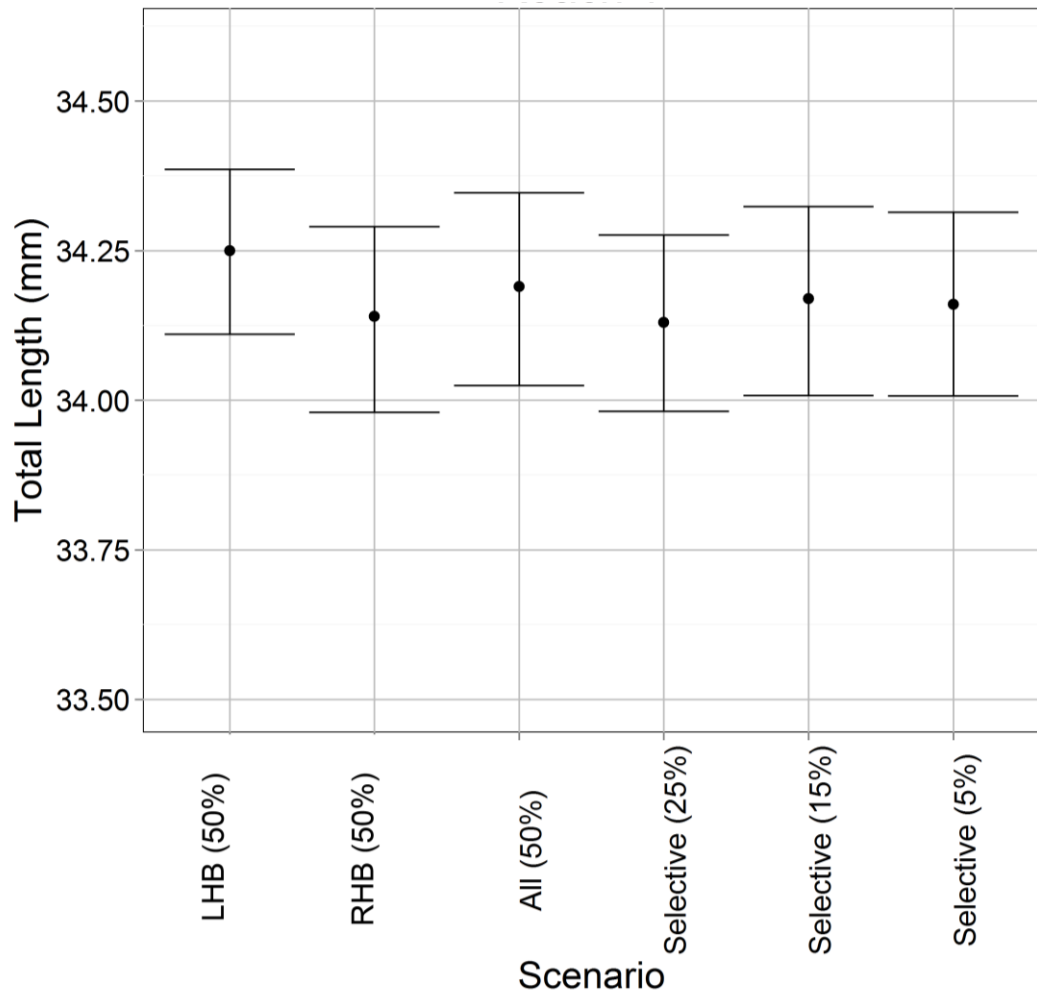
Figure 6.8a The variation in predicted final length of 1+ roach as a proportion of the original, unaltered model against macrophyte removal scenarios listed left to right in relative proportion of in-stream macrophytes removed, **under normal flow rate conditions**. Filled circles represent predicted population mean final total body length at the end of the simulation run, simulating the end of the summer growth season in roach.
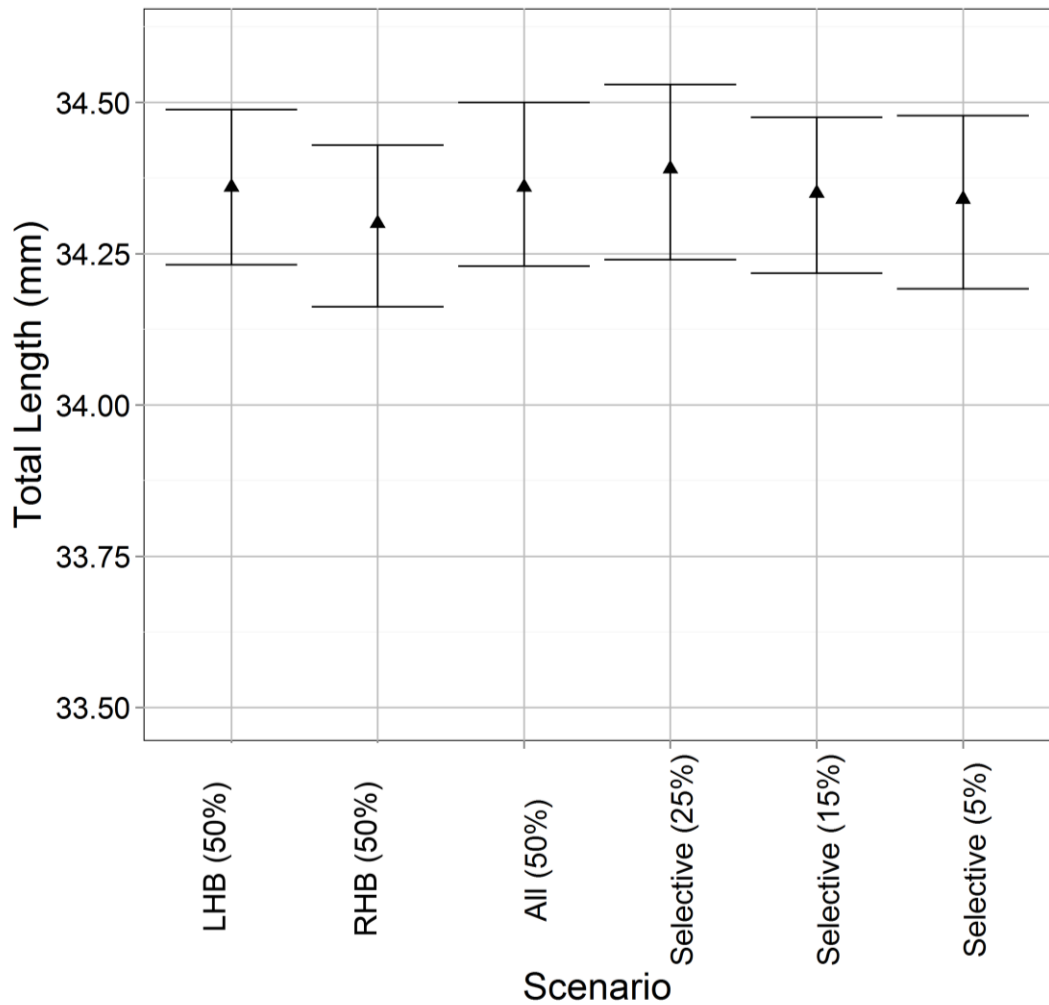
Figure 6.8b The variation in predicted final length of 1+ roach as a proportion of the original, unaltered model against macrophyte removal scenarios listed left to right in relative proportion of in-stream macrophytes removed, **under high flow rate conditions**. Filled triangles represent predicted population mean final total body length at the end of the simulation run, simulating the end of the summer growth season in roach.
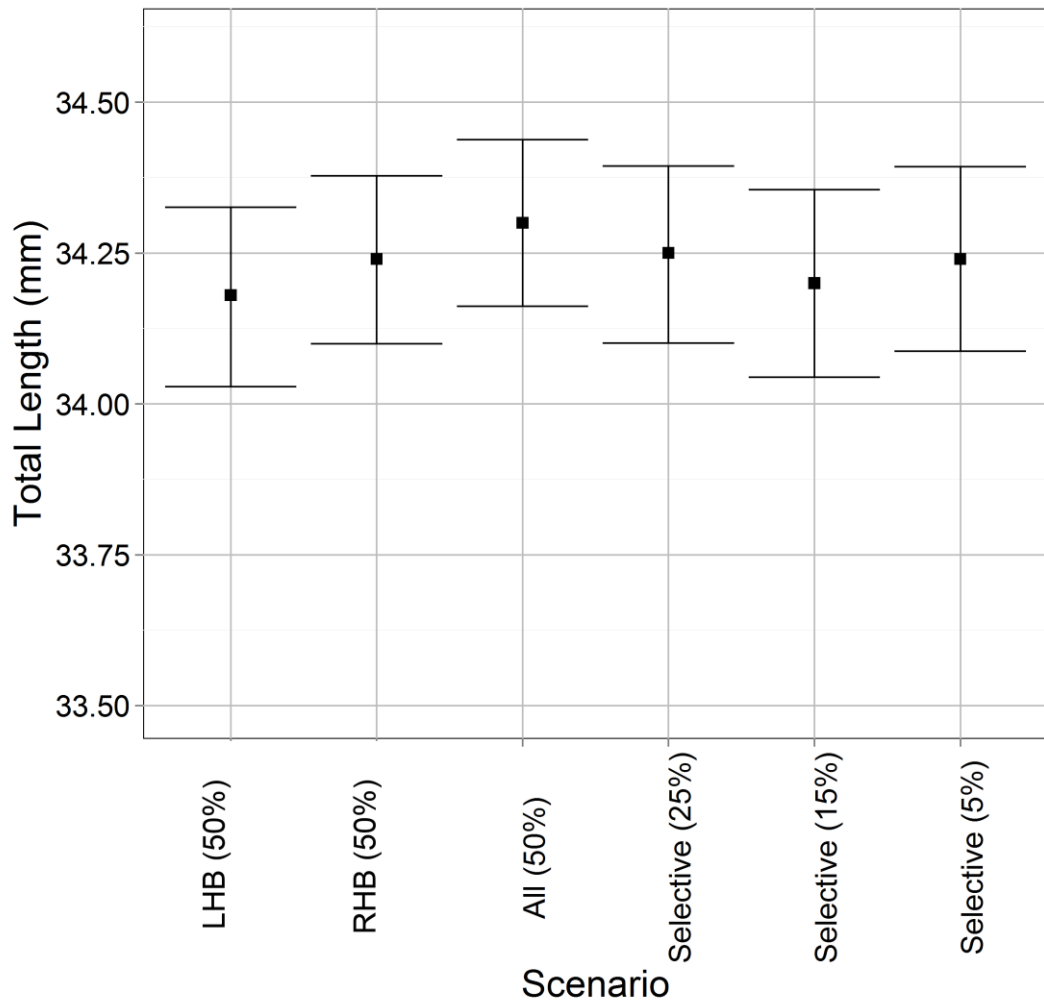
Figure 6.8c The variation in predicted final length of 1+ roach as a proportion of the original, unaltered model against macrophyte removal scenarios listed left to right in relative proportion of in-stream macrophytes removed, **under normal flow rate conditions with peaks of very high flow**. Filled squares represent predicted population mean final total body length at the end of the simulation run, simulating the end of the summer growth season in roach.

6.4 Discussion

The model predicted that loss of in-stream macrophyte cover, as would be caused by macrophyte removal as part of the river management practises, were associated with reduced growth and final lengths of the 0+ roach but not the 1+ fish. The importance of this reduced length of the 0+ roach is that the mean length of these fish at the end of their first growth year was significantly correlated with their subsequent recruitment

strength (as measured by year class strength), with an increase of 0.5 mm in body length increasing the year class strength value by 6. Whilst YCS represents a relative number of recruits into the mature population and so cannot be quantified in terms of fish numbers (Cowx & Frear 2004), this strongly suggests that the weed removal scenarios of 75 and 85% removal that reduced the mean body length of the 0+ roach by approximately 4.5 mm would have had substantial adverse consequences for the recruitment of that cohort.

In riverine roach generally, their populations tend to be dominated numerically by one or two very strong year classes that develop as a consequence of favourable environmental conditions (such as warm temperatures and low flows) in their first summer of life (Mills & Mann1985; Nunn et al. 2003, 2007; Britton et al. 2004). The importance of these year classes is that they subsequently provide high numbers of both mature fish for reproduction and for anglers to exploit by catch-and-release angling when they reach sizes above 120 mm. These year classes can also persist in the population for over 10 years (Beardsley & Britton 2012b). That scenarios of weed removal could reduce the year class strength of a roach cohort by a relative value of 63, where Cowx and Frear (2004) discuss that a strong year class has a value of 100, strongly suggests that the removal could have the consequence of substantially reducing the recruitment rates of roach over time. In a summer that would otherwise produce a strong year class through its warm temperatures and low flows, it could reduce the recruitment strength of the cohort from a 'strong' to an 'average' year class; in a summer that would be predicted to produce a weak class (e.g. cool temperatures, high rainfall and higher river flows; Nunn et al. 2007) this could result in the virtual elimination of that year class. Moreover, these reductions in year class strengths represent a strong deleterious effect on roach population abundance that could have consequences for assessments of ecological status in the Water Framework Directive (Pont et al. 2007).

The original model was constructed without calibrating any parameters and despite this, it was able to produce similar results across the roach growth and distribution patterns as the observed study site from a pattern-orientated modelling approach (Railsback 2001a; Railsback 2001b; Railsback & Harvey 2002). However, the original

model underestimated growth rate in 1+ roach and overestimated growth in 0+ fish, albeit the differences were not significant (Chapter 5). These slight discrepancies have been improved upon with a marginal increase in growth rate of 1+ foragers and a similar decrease in 0+ fish under some macrophyte and flow rate scenarios (Figure 6.1 & 6.2a,b,c). This indicates a potential improvement in the ability of the model to accurately predict growth rate as a result of increased variability in flow rate and available refugia in contrast to the original model where linear relationships were used to estimate environmental variables between survey dates. Scenario testing using the modelled system under three flow regimes ('Normal Flow', 'High Flow' and 'Normal Flow with peaks') and six macrophyte removal regimes ('All LHB', 'All RHB', 'All 50%', 'Selective 25%', 'Selective 15%' and 'Selective 5%') indicated that increased flow rate and decreased in-stream macrophyte cover depressed roach growth rates and by extension, final length at the end of the growth season and subsequent recruitment (Nunn et al. 2010; Beardsley & Britton 2012a). Testing combined scenarios of altered flow rate and macrophyte cover suggested that these scenarios have an antagonistic effect in 0+ roach, producing a threshold of flow rate and macrophyte cover above which few or no negative consequences were seen in terms of growth rate, but below which, they became very apparent (Persson & Eklov 1995; Garner et al. 1996; Watkins et al. 1996; Copp 1997b; Figure 6.3a,b,c & 6.4a,b,c). This matches the current understanding of the role of flow rate and macrophyte management in juvenile fish recruitment and suggests that under circumstances when macrophyte removal is necessary, partial removal may have little impact (Dawson & Haslam 1983; Stanford et al. 1996; Pinder 1997; Kaenel et al. 1998; Bond et al. 2010).

This suggests that it is advisable that consideration is given to a compromise between river management needs and the habitat requirements for strong recruitment rates in the fish community, with the outputs of the model for the 0+ roach providing the evidence basis for this. The model output described a step change in the impact of management practices on 0+ roach, principally as a result of macrophyte removal, with little difference in specific growth rate between the original, unaltered model and removal of up to 50% of in-stream macrophytes, whether the removed macrophytes are on only one side of the river, or taken equally from all patches. This management practice was recommended by Garner, Bass & Collet (1996) as a potential method to reduce the

negative consequences of river management practices on young and juvenile cyprinid fish. However, the modelled absence of negative consequences for foragers at up to 50% macrophyte removal was more likely a result of the simplified model system rather than the absolute efficacy of the proposed management scenario. This is because the negative consequences of energetic costs associated with movement between patches, or mesohabitats, which would be relatively high for smaller fish (Ohlberger et al. 2006) but cannot simulated in the model. Similarly, forager mortality as a result of predation is not directly modelled, so any potential increase in predation risk as a result of reduced macrophyte cover (Chick & McIvor 1997) will not manifest itself as changes in forager population levels. Real life river management scenarios, such as mechanical macrophyte removal or river dredging tend to be unselective, imprecise methods. The simulated scenarios that require removal of a proportion of in-stream macrophytes from many patches may be difficult to achieve (Johnstone 1986). However leaving a few selected areas unaltered, or removing all the macrophytes from only one side of a river is much more feasible. Similarly, leaving a few small areas of a river, or even a few larger, individual plants, when working by hand, would be achievable (Dawson & Haslam 1983). By leaving a few heavily vegetated areas unaltered, especially off-channel, refuges against flow rate changes and predation may be created (Copp 1992). Indeed, it is this kind of management practice that could be used to replicate the results of the 'Selective 25%', 'Selective 15%' and 'Selective 5%' scenarios. Given the predicted negative consequences of the selective scenarios, removing all the macrophytes from only one side of a river seems to be the best approach, from the perspective of cyprinid growth and recruitment, whilst still meeting management needs of flood risk mitigation and channel navigability.

A further limitation in the model that may be addressed during future work is the role of riparian vegetation, specifically in terms of the overhead cover it may provide against aerial predators, such as grey heron (*Ardea cinerea*) and common kingfishers (*Alcedo atthis*) (Allouche & Gaudin 2001). Previous work has shown the potentially important role of overhead cover during habitat selection of foraging fish generally (Pickering 1987) and roach specifically (Brosse & Lek 2000; Hemelrijk & Kunz 2004). This effect could be included in future iterations of the model, given the level of information recorded about the study site. As with the original model construction a further patch

parameter of overhead cover could be included, parameterised, and its impact on the accuracy of model outcomes assessed.

River managers should consider several important factors when planning flow rate and/ or macrophyte removal regimes, these include the timing, magnitude and necessity of the works (Dawson 1979; Dawson & Haslam 1983; Stanford et al. 1996). As for timings, if it were possible to avoid changes or increases in flow rate as well as removal of macrophyte cover during the earliest life stages of cyprinid fish, especially during the start of the summer growth season, then the potential deleterious consequences for the 0+ cohort could be reduced. This could then maximise the number of recruits into the population and so the size of the mature stock (Dawson & Haslam 1983, Copp 1997a,b; Pinder 1997). The IBM itself could be used to predict the effect the timing of management scenarios could have on roach in order to identify a possible compromise time period that would fulfil both management needs, for example flood risk management, whilst minimising impact on juvenile roach (Schiemer et al. 2003; Nunn et a 2010; Beardsley and Britton 2012a). Where macrophyte removal is necessary, then selective retention of certain areas of macrophyte cover based on their location within the river or size may result in adequate management outcomes, such as reduced flood risk or increased channel navigability, whilst maintaining the necessary habitat required for juvenile fish growth and survival (Dawson & Haslam 1983; Copp 1992; Copp 1997a). The potential impacts on cyprinid growth, length at the end of the growth season and potential recruitment success could then be predicted through the use of a model similar to the one described here. Similarly, if necessary to increase or vary flow rate, then consideration of the critical velocities of roach (Mann & Bass 1997), in conjunction with suitable flow rate refuges and the potential energetic impacts of altered flow rate, would assist mitigation of the negative impacts on the juvenile fish (Garneret al. 1996; Holker 2003) . While the effect of flow was not significant on the roach in the study river, in other river systems where flow rates tend to be higher and more extreme between Q5 and Q95, this might be a more important factor to consider (Holker & Haertel 2004; Holker 2006; Sagnes & Statzner 2009).

In addition to dredging and large scale macrophyte removal, river managers may also wish to consider the role of plant growth rates in their management plans, as these will

vary according to levels of, for example, direct sunlight, shade and riverbank height. Such factors can directly affect macrophyte cover in riverine systems, providing an alternative system to directly controlling macrophyte abundance (Dawson 1979; Dawson 1989). While this was not described in this study, it should be possible to build upon the framework described here to make predictions about the natural variation in macrophyte abundance, as well as their impact on both cyprinids and river management outcomes.

In summary, this chapter revealed the crucial role macrophyte cover has on 0+ roach growth and final body length and recruitment, and how macrophyte removal is likely to result in adverse consequences for recruitment and thus have long-term negative consequences for roach population abundance. Thus, any proposed river management practices that seek to assist flood risk mitigation and maintain river access for boats and anglers ought to consider, during the initial planning phase, their direct and indirect consequences for the fish community (Dawson & Haslam 1983; Johnstone 1986; Bass & Collett 1996; Stanford et al. 1996). IBMs can thus provide the evidence base for this, with the IBM used here demonstrating that river management practises can have minimal impacts for fish growth and recruitment when they are not applied indiscriminately.

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7. Discussion

7.1 The individual based model

The findings, recommendations and conclusions of this investigation are based on the assumption that the final IBM was parameterised in such a manner that it correctly reflects reality. Thus, its predictions should be robustly validated under a pattern-oriented modelling approach (Grimm & Railsback 2005, 2012). Finally, in order to ensure that the management recommendations ultimately produced by the model are more widely applicable, a comparison should be made between the study site and similar lowland rivers. It was each of these steps that comprised the various chapters of this thesis, and as such, the chapters were presented in that sequence.

Firstly, chapters 2 and 3 were used to parameterise the IBM, specifically in relation to foraging behaviour of juvenile roach. These investigations built on the body of research describing the foraging behaviours and energetics of roach (Persson 1983; Mann et al. 2007; Holker & Breckling 2002; Holker et al. 2002; Hjelm et al. 2003; Holker & Haertel 2006) as well as the functional response of fishes under controlled conditions (Aksnes & Giske 1993; Buckel & Stoner 2000; Delcourt et al. 2006; Murray et al. 2013 (Section 2)). It was shown that roach display a Type II functional response when foraging for larger food items, compared to a Type I response when filter feeding (Jeschke et al. 2004; Murray et al. 2013). This work also allowed for the description of specific behavioural traits that would form many of the forager parameters (Table 5.1a), specifically the reaction distance, swimming speed when foraging, and handling time of food items (Holling 1959; Holker et al. 2002; Smart et al. 2008; Baker at al. 2009; Murray et al. 2013). Chapter 3 went on to describe how the feeding behaviour and behavioural parameters of juvenile roach are further influenced by environmental conditions, particularly turbidity, food item size and habitat complexity in the form of substrate (Real 1979; Romuald et al. 1986; Jeschke et al. 2002; Vollset & Bailey 2011; Section 3.3). These finding should have utility in future model development when more complex feeding behaviour or environmental interactions could be included in the modelled system. For example, the potential increased energetic costs of foraging under the turbid conditions seen during periods of high flow could be accounted for.

The research outcomes of chapter 4 were useful for both the parameterisation and interpretation of the IBM. The data collected at the study site, and described in chapter 4, was used to parameterise the forager, environmental and global parameters used in the model (Table 5.1). The global and environmental data that were collected were then analysed so as to allow the study site to be accurately reflected in the model, with this process easily replicated in order to study similar ecosystems. The relationships between recorded data and simulated parameters were simple and literal, with few interpretative processes involved as the data were being used simply to create parameters that reflect the study site. Parameters that dictated the size and number of patches and stretches may, however, require some judgement and analysis. Similarly, the estimation of the energetic contents of forager diets required greater analysis than the other global and environmental parameters and as such, would require further work when applied to other systems. Given the importance of the bioenergetics to the model outcomes (Figure 5.5; Holker & Breckling 2002; Holker et al. 2002; Holker & Haertel 2006), when parameterising the IBM, careful consideration is recommended before collecting drift and/ or benthic invertebrates, or when describing the relationship between the two. This is also true when collecting site or habitat specific data on invertebrate size and species composition.

The forager parameters collected and described in Chapter 4 were designed and selected to represent roach physiology, bioenergetics and foraging behaviour. As such, the parameters should remain unchanged between populations, with the exception of differences between lentic and lotic diets, and associated foraging behaviours (Schiemer & Wieser 1992). However, forager parameters related to initialising the simulated population, for example in terms of initial mass, population age composition and distribution within the virtual environment, should be tailored to the specific site under investigation and based on recorded data, so as to ensure an accurate representation within the model. The analysis performed on forager data collected at the study site may serve as a basis for future work, simulating alternative sites, allowing models to be developed using the same model framework.

The outcomes of Chapter 4 on the investigations into the population patterns of roach in three UK lowland rivers provided insight into the degree to which the model

outcomes and recommendations might be more broadly applicable than just the study site. In the case of growth rates and habitat utilization metrics (i.e. suitability indices), there were no significant or marked differences between the three rivers for either 0+ or 1+ roach. Furthermore, the roach size data collected at the study site were used in conjunction with information from published literature to describe the weight and size of the foragers, as well as how these changed over time (Cryer et al. 1986; Papageorgiou 2006). The habitat suitability indices produced in Chapter 4 also provided insight into the habitat associations of the simulated roach, with the findings being highly consistent with other studies (Persson 1987; Brabrand & Faafeng 1993; Holker et al. 2002; Schulze et al. 2006; Martin et al. 2010). Finally, the collection and analysis of scale samples outlined in Chapter 4 were used to describe the growth rates and length at the end of growth season of the roach population. Regarding the scale data collected at all three rivers, these were used to compare the growth rate and growth increments of the three populations. The scale samples collected from the study site as part of this investigation were used in subsequent model validation, comparing predicted growth rates to growth rates estimated from back-calculation of scale samples (Horppila & Nyberg 1999; Ibanez et al. 2008; Stillman & Goss-Custard 2010; Beardsley & Britton 2012; Grimm & Railsback 2012).

A key outcome of Chapter 4 at the study site was the recruitment pattern of roach over time and its relationship with growth rates, climatic variables and habitat availability at the end of their first summer. In common with roach populations generally, the study population of roach was dominated by a few strong year classes, whose high rate of recruitment into the adult stock would have heavily influenced subsequent population abundances and the number of adult spawners (Mann 1991; Cowx & Frear 2004). Roach recruitment patterns are principally a product of fish survival during their first year of life, a period when high mortality occurs through stochastic events, such as episodic periods of significantly elevated flow, that result in displacement and low survival, or through predation by aquatic and aerial predators (Mills 1981; Garner 1996; Copp 1997a; Allouche & Gaudin 2001; Nunn et al. 2003). In both cases, mortality is directly influenced by body size (as a result of prior growth rates) (Mann & Bass 1997; Ohlberger 2006; Nilsson & Bronmark 2000) and physical habitat characteristics (for example the presence of slack water or in-stream

macrophytes) (Copp 1997b; Pinder 1997; Schulze et al. 2006; Martin et al. 2010). Thus, roach recruitment success is at least partially a function of their growth rates in their first summer of life, with associated climatic influences and habitat availability being important determinants, with the latter often influenced by river management policies.

Chapters 5 and 6 produced crucial outcomes in terms of a parameterised and validated IBM for the modelled roach population, and the management recommendations arising from scenario testing using the finalised model. The description of the IBM, as well as the analysis required to develop the MORPH framework using data collected from a representative system, was described using the ODD protocol (Grimm & Railsback 2012), with the model itself being implemented to ensure simplicity, accessibility and general applicability. The model was successfully validated using a pattern-oriented modelling approach (Grimm & Railsback 2005, 2012). Comparisons were made between specific growth rates (SGR) predicted by the model and observed at the field site derived from back-calculated growth rates and population means over the corresponding growth season for 1+ roach and literature values under similar environmental conditions for 0+ roach (Section 5.3.2). Validation was also performed based on stretch-level distribution patterns in 1+ roach (Section 5.3.3). Further analysis of the model was also performed through sensitivity analysis of each parameter that was not measured directly as part of the investigation (Figure 5.5a,b) and stochasticity analysis, performed to test the variation in output and estimate the number of simulations required for subsequent scenario testing (Figure 5.1a,b,c). Both the sensitivity analysis and stochasticity analysis were based on predicted SGR model output.

The scenario testing and recommendations for management of lowland rivers was the primary research outcome of chapter 6, with a focus on the aspects that represent both the main risk factors to juvenile roach and the most commonly implemented management interventions: macrophyte removal and flow rate regulation. The outcomes of the scenario testing were predictions that in 0+ roach, removal of 75% of in-stream macrophyte cover would result in reduced growth rates and final lengths at the end of the growth season (Figure 6.1). Removal of macrophyte cover above 75% was predicted to cause more severe reductions in mean SGR, with both 85% and 95%

removal resulting in significant reductions in mean SGR, affecting the vast majority of individuals, with this likely to result in poor recruitment of 0+ roach. These negative consequences were further exacerbated by acute or chronic increases in flow rate (Figure 6.2 a,b,c). No significant negative impacts on growth rate were predicted under management scenarios that involved removal of 50% or less of the available in-stream macrophyte cover. Such scenarios were designed to mimic the removal of in-stream macrophyte cover from only one side of the river as suggested by Garner et al. (1996) or the practice of leaving some refuge or nursery areas as per Dawson & Haslam (1983) and Copp (1997a,b). No significant negative impacts on SGR or final lengths were predicted for the 1+ roach under any management scenario (Figure 6.5). This reflects their reduced vulnerability to increased flow, both in terms of risk of displacement (Mann & Bass 1997) and the increased energetics costs associated with keeping station (Holker 2006; Ohlberger et al. 2006). Similarly, predation poses a lower risk to the larger roach, due to gape-size limitations in both perch and pike predators (Nilsson & Bronmark 1999; Dorner & Wagner 2003). These factors also reduced the importance of macrophyte cover to 1+ roach when compared to 0+ roach. This is reflected in habitat preference and diet shifts associated with body size in juvenile roach (Brabrand & Faafeng 1993; Holker et al. 2002; Hjelm et al. 2003; Schulze et al. 2006; Bogacka-Kapusta & Kapusta 2007; Martin et al. 2010). The relative vulnerability of 0+ versus 1+ roach serves to highlight the importance of the first year of life for growth and therefore, survival and recruitment of roach in heavily modified lowland rivers.

7.2 Overview of management of lowland rivers

Freshwater ecosystems, especially heavily modified systems, are a challenge for managers due to conflicts between stakeholder groups, the complexity of their physical, hydrological and ecological processes, and the associated interactions and outcomes. These conflicts can arguably be more thoroughly addressed through a better understanding of how the processes that occur in freshwater systems, both biotic and abiotic, are altered by river management schemes. Indeed, this research has described how lowland rivers are at the centre of a conflict between their management for societal needs, such as preserving the provision of valuable ecosystem services, and the vital habitat the river provides for aspects of biodiversity. Potential solutions and compromises in river management may be informed through predictions of

management impacts, such as the predictions made by a validated IBM. These predictions are important as whilst the motivation for better management usually exists, there is often a lack of scientific consensus on management priorities due to a lack of understanding of the consequences, with waiting for an agreed-upon strategy often resulting in further impacts through inaction (Ludwig et al. 1993). Furthermore, there is growing impetus to move from single-goal river or fisheries management towards holistic freshwater ecosystem management, especially in light of ecological assessments within the Water Framework Directive (Hatton-Ellis 2008; FAO 2012). In this Chapter, the outcomes of the previous research will be discussed in the context of freshwater management of lowland rivers, the limitations of the investigation will be described and suggestions made on the future direction of management of lowland and heavily modified rivers in the UK generally, and the River Stour specifically.

7.3 Current management regimes on heavily modified lowland rivers and the study site
The current management objectives on the heavily modified River Stour are to maintain the provision of ecosystem services and similar anthropocentric requirements such as channel navigability, bankside access, recreational fishing, water abstraction, dilution of sewage outflow and management of flood risk (Garner et al. 1996; Downs & Thorne 2000). Meeting these management objectives must now also be aligned to meeting the requirements of the Water Framework Directive (EU 2000). As described in Chapter 1, the WFD is based on assessment of ecological status where freshwaters are assessed using a five tiered system, from High (undisturbed) to Bad (relevant biological communities absent), and where water bodies fail to meet Good status, a management and remediation plan is required. Where water bodies, such as the study site, have been altered by anthropogenic activities to the point where restoration is not feasible, then the WFD requires these heavily modified waters to reach their maximum ecological potential. The biological quality element of the WFD is assessed by measuring metrics of phytoplankton, other aquatic flora, macroinvertebrates and fish, with often only the most sensitive element assessed (Hatton-Ellis 2008). This is often the fish community, with a range of metrics measured to deduce ecological status, including the presence of type-specific species and their abundance (Schmutz 2004; Pont et al. 2007; Schmutz et al. 2007).

Current management practices undertaken on the River Stour, designed to maintain provision of the primary ecosystem services, follow two main interventions: the removal of in-stream macrophytes and the regulation of flow rate. Managed by the Environment Agency, best practice policy on in-stream macrophyte removal concentrates on limiting its impact through considered use of the timing and patterns of macrophyte removal (RSPB et al. 2001; Agate & Brooks 2003; Britt et al. 2003; SEPA 2009). For example, avoiding macrophyte removal during the breeding seasons of birds and spawning of fish, usually by postponing management from summer cutting to autumn cutting, is recommended (RRC 2002; Agate & Brooks 2003). It is also recommended to consider the pattern or extent of macrophyte removal, so as to reduce ecological impact whilst maintaining management objectives. Various patterns have been recommended, from removing all the macrophytes from one side of the river and leaving the other side intact, with this alternating each year (Garner et al. 1996). Other options include removing the majority of macrophytes from both sides and the open channel, whilst selecting a few areas to act as refuges for wildlife, either in selected off-channel areas or even individual, larger plants where feasible (Dawson & Haslam 1983; Copp 1992). Environment Agency good practice also recommends cutting in patches, as opposed to a 'blanket cut' of all macrophytes. With the areas left uncut varying between years (RSPB et al. 2001; Britt et al. 2003; SEPA 2009), performed in conjunction with maintaining riparian vegetation, and leaving some sections unaltered (in-channel, riparian and terrestrial), then a mix of undisturbed terrestrial, semi-aquatic and aquatic plants could be preserved with the potential for high benefits for biodiversity, including within the fish community. Nevertheless, observations on the weed cutting practises in the River Stour, aligned with anecdotal evidence from Fishery Officers in the Environment Agency Area in which the River Stour is located, suggest such best and good practice approaches are not always considered in full and a more indiscriminate approach tends to be adopted.

Best-practice methods may also be used to limit the impact of modified flow regimes on ecosystem health, and fish communities and their populations, given that the fish populations of heavily modified rivers are prone to deleterious impacts on their juvenile fish due to, for example, the effects of high flows that arise through canalisation and the alteration of river courses to become wider, deeper and straighter (Schmalz et al. 2008).

This is compounded by the use of water in industry and population centres, resulting in periods of high flow and low flow, with an increased magnitude between Q10 and Q90, and rapid changes in flow rate. Mitigation of these effects include the adoption of fish-sensitive flow regimes where the periods of high flow are limited to below critical velocities, given that the ability of a fish to hold station in flows is dependent on body length (Mann & Bass 1997), whilst considering the refuge effects of off-channel refugia and macrophyte cover (Copp 1992; Merritt et al. 2010), and limiting the risk of flooding during periods of high discharge. Similarly, high pulses or rapid changes in flow rate are avoided where possible (EA 1999; Balkham et al. 2010). Conversely, in systems such as the study site where water abstraction occurs, care should be taken to ensure there is always a minimum flow rate to limit siltation effects, ensure sufficient oxidation and the dilution of effluents or pollutants (Pyrce 2004; Hannaford & Buys 2012). Environment Agency management guidance recommends the construction of baffles in sections of riverine systems where high flow is expected to impact the ability of fish to hold station in the open channel. Such baffles are usually constructed within culverts of gradient > 5 % to slow water velocities to more acceptable levels (EA 1999; CIWEM 2007; Balkham et al. 2010). Similarly, to ensure sufficient flow upstream and downstream of culverts, Environment Agency practice is to, wherever possible, modify the structure of culverts so as to promote a more natural bed profile, and improve flow regime and variability (SEPA 2006; CIWEM 2007; Balkham et al. 2010). At the study site, a similar approach is applied to the weir and pumping station (Section 4.3.2) so as to ensure sufficient flow, whilst considering the consequences of high flow, rapid changes in flow and the management of flood risk.

7.4 Impact of current management regimes on roach populations

The recruitment success of a year-class of roach tends to be determined in their first year of life, with their first growth season (from emergence from the egg in May/ June through to approximately October when temperatures decrease) critical for individuals to realise the lengths and body reserves necessary to successfully survive the winter months (Mills 1981; Bystrom & Garcia-Berthou 1999; Nunn et al. 2003). However, cutting and removing in-stream macrophytes reduces available egg-laying sites and nursery habitats occupied by larval and juvenile fishes, thus increasing their risk of displacement due to increased flows, poor growth and even starvation through reduced

food item availability, and increased predation risk through reduced refugia (Mills 1981;Copp 1997b; Nunn et al. 2003, 2007). In-stream macrophytes also affect local hydrology and channel characteristics (Dawson 1989; Garner 1996), often resulting in reduced flow rates. Together with the influence of macrophytes, flow rate varies as a result of factors including river discharge, channel characteristics, depth and substrate characteristics (Acreman & Ferguson 2010; Hannaford & Buys 2012). As such, flow rate can affect fish directly through increased energetic costs when swimming or keeping station (Ohlberger et al. 2006; Liao 2007). High flow also increases risk of displacement, with smaller, juvenile fish being more vulnerable than adults (Mann & Bass 1997). Increased river discharge and flow also results in increased turbidity (Goransson et al. 2013) which may affect foraging behaviour (Diehl 1988; Chapter 3). These effects of turbidity, energetic costs and displacement of smaller fish also occur as a result of sharp increases in flow, often as a result of cessation of water abstraction or the use of sluices and automated weirs. Finally, reduced flow rate can cause negative consequences for fish through reduced connectivity of habitat networks, including nursery sites and off-channel areas.

Consequently, if there is a desire for river managers to maximise roach recruitment, then consideration of their growth and recruitment during the critical first summer of life is vital (Schmutz 2004; Pont et al. 2007; Nunn et al. 2010; Acreman & Ferguson 2010). Conversely, the management regimes described above, whilst maintaining the river function for flood defence and abstraction, are more likely to reduce roach recruitment through their elimination of areas of refugia and their impact on flow rates. Thus, there was an outstanding requirement for an assessment tool that provides insight into how these management practices impact roach recruitment rates through processes such as their growth rates so that management can adapt their practises according to these insights.

7.5 River management recommendations
The management objectives of in-stream macrophyte removal and flow rate regulation (Section 1.5; Section 4.3.2) were selected so as to improve recruitment of cyprinid fish, primarily roach. This would be achieved by reducing the impact of environmental stressors at the site through attempting to maximise growth rates in 0+ and 1+ fish, the

key development stages during which there is very high mortality rates (Mills 1981; Diamond 1985; Beardsley & Britton 2012). As described in Section 7.3, maintaining some in-stream macrophyte cover and regulating river flow was expected to reduce the negative consequences of predation and higher flow rates. The impact of a range of potential management scenarios were tested as part of the scenario testing of the parameterised and validated IBM (Chapter 6). As previously described (Section 6.2.12), the simulated management scenarios involved removing a proportion of all the in-stream macrophyte cover at the study site (Table 6.1). These scenarios were simulated under normal flow rates as well as under a higher flow regime and a normal flow regime with acute periods of very high flow.

The results of the scenario testing (Chapter 6; Section 7.1) showed that in 0+ roach, under normal flow conditions, the specific growth rate was reduced, compared to the unaltered, original model output, only when a significant proportion of the in-stream macrophytes in the modelled river system were removed (75% or greater). The remaining scenarios, where less macrophyte cover was removed, revealed that SGR was not significantly reduced. Similarly, when flow rate was increased, but no macrophyte removal occurred, the SGR was not significantly affected. The effect of reduced specific growth rates in 0+ roach when significant amounts of in-stream macrophyte cover were removed was further compounded under scenarios of simultaneously increased flow rate. Similar effects of management regime were seen in changes to body length at the end of the simulated growth season in 0+ roach. A relationship between length and year-class strength has been previously described (Nunn et al. 2003, 2007; Britton et al. 2004; Chapter 4) whereby it was suggested a 0.5 mm decrease in mean population length at the end of the first growth season resulted in a reduction in the YCS value by 6. The predicted reductions in mean population length of approximately 4.5 mm, would therefore represent a substantial decrease in YCS (54), particularly when using this index, a strong year class has a value of 100 (i.e. it is a strong year class that will be represented in disproportionately high abundances in the population in subsequent years). Thus, the effect of this management regime is potentially reducing a relatively strong year class to a weak year class, substantially reducing the number of adult fish able to spawn and thus alter future population dynamics, as well as reducing the number of fish available for angling exploitation. The potential reduction in roach population

abundance is likely to also impact the assessment of ecological status according to the fish fauna, given that roach are a type-specific species.

The same scenario testing, performed on larger, older, age 1+ roach did not show the same levels of reduced specific growth rate or body length at the end of the simulated growth season. While there was some variation in SGR and body length between the scenarios, including macrophyte removal combined with altered flow rate, no significant variation from the original model output was observed (Figure 6.5). While current river management practices related to in-stream macrophyte removal and regulation of flow rate (Section 7.2) may influence river hydrology, sedimentation rates, macroinvertebrate and fish communities (Gregg & Rose 1982, 1985; Madsen et al. 2001), the outcomes of scenario testing (Chapter 7) predict a limited influence on 1+ roach. While growth and survival are likely to be affected under more extreme conditions (Fladung et al. 2003; Holker & Haertel 2004; Ohlberger et al. 2006), providing that current practice is followed (EA 1999; Agate & Brooks 2003; Britt et al. 2003; CIWEM 2007; SEPA 2009), then 1+ roach and ecologically similar cyprinid fishes should not be considered sensitive to these changes, even in heavily modified rivers.

Conversely, negative consequences for smaller, 0+ roach were observed above a high threshold of macrophyte removal, with this compounded by increased flow rates. Given the role of recruitment and potential population consequences of relatively high or low year-class strengths in roach (Mills & Mann 1985; Nunn et al. 2007), it is recommended that a threshold or 75% or greater in-stream macrophyte removal is not exceeded. Current good practice is to only cut and remove in-stream macrophytes where necessary, with this often focussing on the open channel of the river or for bank-side access. During development works, channel shaping or dredging operations, however, it is likely that this high threshold of 75% of total macrophyte cover being removed would be exceeded. If this is to occur at the same time as other forms of disturbance, including increased flow rates or turbidity, it is expected that this would impact roach growth and recruitment. Therefore, it is recommended that management practices seek to limit their impacts on 0+ roach, by ensuring sufficient in-stream macrophyte cover is conserved within the system, especially if other disturbances are taking place. While management

activities may preclude predetermined removal of a certain proportion of macrophyte cover or dictating which areas may be left undisturbed, it is recommended that refuge areas are maintained that are designed to promote the growth and recruitment of cyprinid fish (Dawson & Haslam 1983; Copp 1992; Zarkami et al. 2012). As such, previous management suggestions, including removal of macrophytes from a single side of the river, or maintaining small stands of macrophytes or off-channel sections (Dawson & Haslam 1983; Copp 1997a; Garner, Bass & Collet 1996) are validated and reinforced by the results of the model scenario testing on 0+ roach.

7.6 Limitations and future work

The research outcomes of the previous chapters were used in model construction, parameterisation, validation or to inform the resulting management recommendations. It is, however, possible that some of these stages may have produced erroneous results that would limit the utility of the model predictions or management recommendations. Such a possibility could arise as a result of the complexity of the model and the reliance on a large number of parameters required to describe the system. Combined with the interactions between the parameters, this complexity makes understanding the underlying processes that create the population level patterns inherently and increasingly difficult (Grimm & Railsback 2005). However, it is this lack of a defined process pathway that benefits the individual-based approach. As patterns emerge at the population level from interactions between individuals, there is no explicit definition of how a population should respond to changing environmental conditions. IBM models are created from the bottom-up (as opposed to from the top-down); as such, the vast majority of assumptions at the individual level in this model (e.g. roach feeding behaviour and bioenergetics) were derived from published studies (Persson 1983; Karjalainen 1997; Holker et al. 2002; Holker & Breckling 2002; Holker & Haertel 2006; Papageorgiou 2006; Bogacka-Kapusta & Kapusta 2007) or under controlled conditions, with the experimental findings consistent with current understandings of roach foraging behaviour (Hjelm et al. 2003; Section 2.4, 3.4). By using empirical, published research, there is greater confidence in the findings and outcomes than if assumptions of feeding behaviour and bioenergetics were used solely during this investigation.

Whilst model validation was performed, further validation could be achieved by using more patterns collected from additional small-scale fieldwork or lab-based experiments. By assuming that the modelled foragers behave like real riverine roach, it can be assumed that they would behave as per their real-life counterparts under well-controlled artificial conditions. This is especially true if conditions were used that accurately reflected a realistic environment. Experiments conducted under controlled conditions, for example in artificial streams or flumes might also overcome some of the weaknesses in the field-based collections of environmental parameters recorded as part of this investigation (e.g. estimates of benthic invertebrate densities). Similar to how some of the forager parameters (reaction distance, handling time and swimming speed during food item capture) were parameterised, the virtual environment in the model could be parameterised to represent artificial conditions so that roach behaviour and population patterns of real fish could be used to validate the model predictions using the same approach as in chapter 5.

While additional validation is possible, the value and robustness of the current validation patterns used as part of this investigation was considered sufficient. The project design of collecting data from complementary fieldwork allowed for the collection of site-specific environmental, global and forager parameters to create the virtual environment and initialise the population. Patterns predicted by the model were compared directly to the patterns observed in the real roach in the form of stretch-level distribution and length from scale back-calculation at the study site. It should be noted that whilst validation was explicitly described in Chapter 5, the predicted patterns made in Chapter 6 may also be interpreted as additional patterns for validation as, although weak patterns, they are still acceptable under a 'pattern-orientated modelling' approach (*c.f.* Grimm & Railsback 2005). Specifically, in Chapter 6, the predictions of decreased mean population specific growth rates under increased flow rates and reduced in-stream macrophyte cover agree with predicted patterns in accordance with established theories on roach habitat preferences and bioenergetics (Persson 1983; Holker et al. 2002; Holker & Breckling 2002; Holker & Haertel 2006; Schulze 2006; Garcia-Berthou 2010; Martin et al. 2010).

There are several potential improvements that could be performed to improve the utility and potential of the IBM including the addition of forager mortality as a result of predation and displacement, with this being coupled with a transition from a closed to an open system, allowing emigration and immigration of foragers. Similarly, the simulation period could be increased from the duration of the summer growth period to include a whole year time frame, during which the foragers and environment change markedly (Fladung et al. 2003; Nunn et al. 2003; Hannaford & Buys 2012). Finally, the IBM could be built upon to include more specific stages in the roach life cycle, including spawning behaviour, as these life stages influence the feeding, growth, habitat selection and bioenergetics of roach (Holker & Breckling 2001; Sagnes & Statzner 2009; Nunn et al. 2010). However, environmental conditions during the winter months, namely increased river discharge, turbidity, velocity and water depth (Berrie 1992), may represent difficult conditions under which to collect sufficiently accurate environmental and population data. One solution would be to estimate the environmental conditions and roach populations trends from data recorded during the milder, subsequent spring period, using calibration based on known relationships between environmental and roach growth, habitat selection and bioenergetics. Similarly, Approximate Bayesian Computation (Beaumont et al. 2002; Jabot et al. 2013) could be used to parameterise the unrecorded winter period.

The lack of forager mortality in the current IBM is one of the foremost areas of potential improvement. While individual mortality in the roach population would not cause significant changes, due to the limited role of density-dependence effects in the simulated roach, it may still alter population patterns and could increase the utility of the model when investigating the impacts of environmental change on the population. This approach would, however, be best suited to a virtual system that was simulated as an open system, not the current closed system used, whereby any forager mortality would simply reduce the total population of roach, with no immigration from outside the system. If forager mortality was to be incorporated into this model as part of future work it would most likely be combined with the emigration function in MORPH (Stillman 2008). Furthermore, estimating deaths, especially from predation and consequently mortality rates, is very difficult to achieve using non-invasive field observations (Vetter 1988; Hewitt et al. 2007) and was intentionally excluded due to the

lack of sufficient information or appropriate patterns to parameterise the behaviour. Estimating natural mortality in fish populations presents a considerable challenge for all fisheries population models, despite the important role it plays (Hewitt & Hoenig 2005). Although alternatives are described by Hewitt et al. (2007) and Pauly (1980), another alternative exists in the Metabolic Theory of Ecology (MTE) as detailed by Brown et al. (2004) and Sibly et al. (2013). MTE also provides the potential for collaboration between other science disciplines in the future as the field develops.

Simulating an entire year, or multiple years, is a potentially useful development to increase the utility of the model beyond small-scale, fishery management towards longer-term management at local, regional and national scales, for example the inSTREAM model developed by Railsback et al. (2009) or the bioenergetics modelling by Holker & Breckling (2001, 2002, 2005). The MORPH model developed as part of this investigation is already capable of simulating longer periods of time, providing parameterisation is achieved for the winter and spring seasonal periods. Similarly, the methods used by the model to simulate growth and allometric shift in diet and behaviour could be extended beyond the differences between 0+ and 1+ fish, to include older fish. The model would be more relevant as a conservation tool if simulated foragers were modelled to reach sexual maturity and display spawning behaviour, adding simulated population dynamics to the potential predictions and patterns used for validation. This would be especially useful under the current application of the model as river managers would be provided with a new tool for managing spawning behaviour and egg laying, with these aspects of roach reproduction complimenting the current emphasis on recruitment. This model would, however, be highly complex and its validation extremely challenging.

7.7 Conclusions

In addition to the management recommendations (Section 7.4) and research outcomes (Section 7.5), the following, more general conclusions can be made from the research:

1. The MORPH IBM modelling framework and platform is robust and easily adaptable to new environments and animal species. It has been successfully used to model the responses of coastal birds and Salmonid fish in chalk streams and has now been adapted to cyprinid fish populations in a lowland river environment. Given the increased complexity of modelling fish bioenergetics, in comparison to birds in terrestrial ecosystems, due to temperature-dependent growth, increased size dimorphism and changes in foraging behaviour with allometric diet shift, there is potential for simplification of the model to increase accessibility, as with the WADER MORPH framework (West et al. 2011).

2. This investigation has also shown the value and utility of IBMs and MORPH for investigating management issues. Investigations into the impacts of common management practices (Chapter 6) will contribute to a greater evidence-base in management practises.

3. The scenario testing performed is a good example of the model's use for informing river managers under scenarios that cannot be tested directly using habitat-association models. This demonstrates the potential for the model to provide a real contribution to management decisions, as has been seen with IBMs generally in informing the management of a wide range of animals.

7.8 References

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