The importance of *Ranunculus* spp. for juvenile salmonids in lowland rivers

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Statement of originality

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Collaboration and Publications

Chapter 2: Stephen Gregory, William Beaumont, Luke Scott, Rasmus Lauridsen and James Pretty helped with electrofishing, habitat surveys and macroinvertebrate sampling. I performed the majority of the laboratory work to identify macroinvertebrates, with some assistance from Dave Cooling. I completed the data analysis and writing of the chapter myself, with guidance and suggestions from Stephen Gregory, William Beaumont, Luke Scott, Pavel Kratina, Rasmus Lauridsen and Iwan Jones.

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Chapters 3 & 4: Stephen Gregory, Luke Scott, William Beaumont, Rasmus Lauridsen, James Pretty and Iwan Jones helped regularly with the *Ranunculus* manipulation and electrofishing. Stephen Gregory, Luke Scott and James Pretty helped regularly with the habitat surveys and macroinvertebrate sampling. Dave Cooling helped with macroinvertebrate processing in the laboratory. I completed the data analysis and writing of the chapters myself, with guidance and suggestions from Stephen Gregory, Pavel Kratina, Rasmus Lauridsen and Iwan Jones.

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Abstract

Macrophytes could be integral to structuring lowland rivers and providing habitat for juvenile salmonids, but currently there is a lack of quantitative evidence evaluating this role. The aim of this thesis was to quantify the influence of a lowland macrophyte, *Ranunculus*, on juvenile salmonids and their environments in lowland rivers. A catchment-wide correlation study determined salmon and trout densities to be positively associated with *Ranunculus* cover, and velocity heterogeneity, respectively (Chapter 2). I subsequently implemented a spatially-and-temporally replicated *Ranunculus* manipulation experiment in a lowland river carrier. High *Ranunculus* cover supported higher abundances of salmon and trout throughout the summer feeding period. I also identified a strong influence of *Ranunculus* at the beginning of summer, when salmon abundances, site fidelity and increase in body length were highest (Chapter 3). Focusing on the beginning of summer, I then showed that higher total biomass of prey and a larger average size of prey were found in diets of salmon and trout captured in high *Ranunculus* cover, suggesting that *Ranunculus* was facilitating better foraging opportunities. Additionally, the dietary niche overlap between the two species was lowest in high cover, suggesting that abundance of *Ranunculus* reduced interspecific competition. There was a positive effect of *Ranunculus* on the growth rates of salmon, but an effect on trout growth was not detected (Chapter 4). Finally, I evaluated direct and indirect effects of *Ranunculus* on salmon abundance and growth rates (Chapter 5). I showed that salmon abundance was most influenced by the cover supplied by *Ranunculus* directly, but that this effect was mediated through negative influences of water depths and velocities. The positive influence of *Ranunculus* on salmon growth rates, however, was more intricately linked to changes in physical habitat and prey resources driven by *Ranunculus*, than to a direct source of cover. Together, these findings demonstrate a holistic role of *Ranunculus* in a lowland river, and its potential to improve the population viability of at-risk salmonid populations.

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Chapter 1: General introduction

1.1 Introduction

One of the simplest definitions of habitat is ‘a place where an animal lives’ (Morrison *et al.*, 1988). Characteristics of a habitat, such as physical, chemical and biological properties will determine the suitability and effectiveness of habitat for a particular species or population (Morrison *et al.*, 1988; Hayes, Ferreri & Taylor, 1996; Armstrong *et al.*, 2003; Kearny *et al.*, 2006). A habitat provides resources, (e.g. food, shelter), and environmental conditions (e.g. temperature, presence/absence of predators) to promote the occupancy, survival and reproduction of individuals of a given species or population, and can span broad spatial and temporal scales (Morrison *et al.*, 1988; Armstrong *et al.*, 2003; Tyne *et al.*, 2015). A revised description, therefore, considers a habitat to represent the space in which an animal lives, of which habitat effectiveness is modified by the environment that an animal experiences, i.e. physical, chemical and biological factors (Hudson, Griffiths & Wheaton, 1992; Hayes, Ferreri & Taylor, 1996; Kearney *et al.*, 2006).

Vegetation can be integral to shaping habitat, and plant communities play a key role in structuring the environment in both terrestrial and aquatic ecosystems (e.g. Morrison *et al.*, 1988; Steneck *et al.*, 2002; Tews *et al.*, 2004). The ‘keystone structure concept’ (Tews *et al.*, 2004) outlines a keystone structure as a vegetation structure that provides resources, shelter or other essential ‘goods and services’ that are crucial for the viability of one or more species. Loss or reduction in quality of the keystone structure can therefore elicit severe consequences for various taxonomic groups (Tews *et al.*, 2004), a trend that has been identified with the loss of vegetation structures such as seagrasses (Lotze *et al.*, 2006), kelp forests (Steneck *et al.*, 2002), and woodlands (Mac Nally *et al.*, 2009). Understanding how a species or population interacts with key vegetation structures is therefore essential to inform effective conservation strategies. Identifying critical habitats, such as those that support foraging at key life stages (Tyne *et al.,* 2015), can focus management efforts to maximise impact.

The freshwater habitat of juvenile salmonids (Salmonidae) can be considered critical habitat as the population viability as a whole is highly dependent upon the production of sufficient numbers of juveniles of good fitness (Bardonnet & Bagliniere, 2000; Zabel & Achord, 2004; Russell *et al.,* 2012; Armstrong *et al.,* 2018; Gregory *et al.*, 2019). Most salmonids are predominately anadromous, or have anadromous morphotypes (Bardonnet & Bagliniere, 2000, Thorstad *et al.,* 2016). Anadromous salmonids begin life in fresh water, then migrate to sea to grow and mature, before returning to the fresh water to spawn (Figure 1.1), though there is a high degree of plasticity and variation in life history strategies of salmonid populations, i.e. duration spent in the river or at sea (Metcalfe & Thorpe, 1990; Armstrong *et al.,* 1998). Healthy populations of salmonids have irreplaceable ecological value throughout their geographic range. For example, in oligotrophic rivers, the presence of adult salmon carcasses after spawning events deposits essential marine-derived nutrients into rivers (Naiman *et al.*, 2002). These have both immediate and long-term benefits for river productivity, particularly by increasing macroinvertebrate biomass and juvenile salmon densities, growth and genetic diversity (Nislow, Armstrong & McKelvey, 2004; Auer *et al.,* 2018; MacLennan *et al.,* 2019). Salmonids are also of considerable cultural and economic importance. During 2015 in England alone, over 2.5 million days were spent freshwater angling for salmonids, generating over £120 million household income, and contributing to an industry that supported 27,000 full-time jobs (Salado & Vencovska, 2018). Angling can also invoke an understanding of environmental awareness and respect for nature (Peirson *et al.*, 2001). As iconic fish, the presence of salmonids in a river has driven substantial habitat restoration and enhancement efforts to attempt to improve their environment (e.g. Binns, 2004), which can also benefit other inhabitants. In the absence of salmonids, less charismatic species might not attract so much attention and funding to carry out this work.

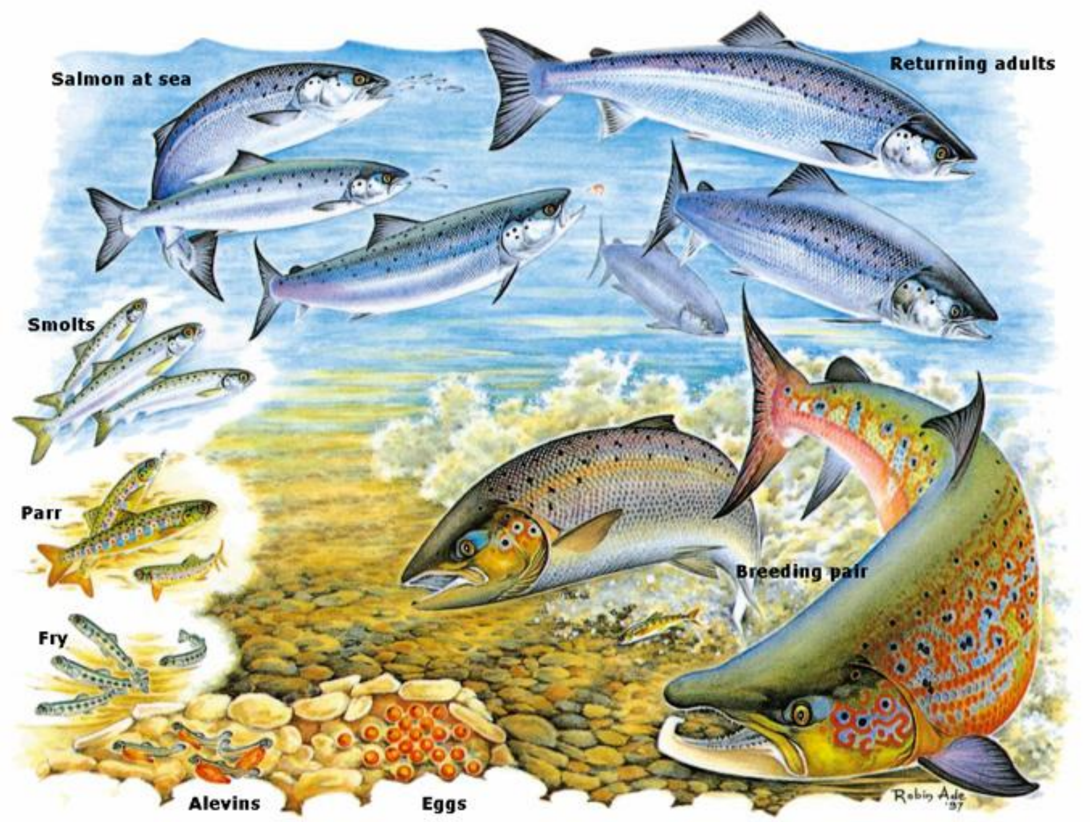


Figure 1.1. Simple representation of the Atlantic salmon (*Salmo salar*) lifecycle, the bottom half of the illustration from 'Breeding pair' to 'Parr' represents the freshwater phase of the life cycle, 'smolts' transition between fresh water and salt water and mature and grow at sea. From *Atlantic salmon lifecycle*, Atlantic Salmon Trust and Robin Ade, available online at http://ness.dsfb.org.uk/salmon-lifecycle/.

Wild fish stocks globally have been impacted by increasing human populations and the resulting incessant resource use, energy production, water usage and habitat manipulation (see Gordon *et al.*, 2018 for a review). Specifically, juvenile salmonid populations have suffered from decreased habitat connectivity and quality in freshwater environments due to threats such as barriers to migration paths (Mills, 1989), intensification of agricultural and abstraction, leading to fertiliser and sediment run off, and low flow events (Wood and Armitage 1999; Soulsby *et al.,* 2001; Cotton *et al.,* 2006; Riley *et al.,* 2006, 2009). Consequently, along with overexploitation and climatic-induced threats in the marine environment (Chaput, 2012; Reid *et al.,* 2018), populations of salmonids have experienced dramatic declines in productivity in recent years, none so more widespread than Atlantic salmon (*Salmo salar* hereafter salmon), which suffered a population crash throughout its geographic range in the late 1980-90's, with many regional populations still yet to recover (Parrish *et al.,* 1998; Russell *et al.,* 2012). A temporal decline in numbers of young-of-year juvenile salmon and the size of these individuals has been identified through long-term monitoring of populations in the UK and France (Gregory *et al.,* 2017). This trend could be indicative of poor freshwater habitat conditions and have occurred more frequently than thought due to the limited number of rivers with intense monitoring programs. The size attained as a juvenile salmon has the potential to impact survival processes throughout an individual's lifetime (Zabel & Achord, 2004). During their first summer in fresh water, increased size can increase the range of prey items a salmon can consume, decrease the range of predators that can consume it, and ensure sufficient energy reserves prior to unfavourable winter conditions (Werner & Gilliam, 1984; Keeley & Grant, 1997; Finstad *et al.,* 2004; Armstrong *et al.,* 2018). Furthermore, a greater size at the time of smoltification increases the likelihood of that individual surviving the marine environment and returning to fresh water to spawn (Armstrong *et al.,* 2018; Gregory *et al.,* 2019). Identifying those freshwater habitats that maximise both the number and size of juveniles could have considerable influence on declining or reduced salmon populations.

The distribution of Atlantic salmon ranges from the western North Atlantic basin by North America to the eastern North Atlantic basin, as far south as Portugal and as north as Russia (ICES 2018). Generalising management of salmon habitat across rivers is rarely possible owing to the great variation in salmonid rivers and complexity in how they function (Armstrong *et al.,* 1998), particularly between dynamic upland river and more stable lowland river systems. While the relative importance of habitat features might vary among river systems (e.g. Morantz *et al.,* 1987; Maki-Petays *et al.,* 1997), it is possible to ascertain generic habitat characteristics that will promote suitable habitat conditions. Habitat use by juvenile salmonids in upland rivers is well studied, and habitat complexity is a reoccurring key habitat characteristic (e.g. Quinn & Peterson, 1996; Dolinsek *et al.,* 2007; Venter *et al.,* 2008). Increased in-river structural complexity can provide essential shelter from predators and harsh environmental conditions, create heterogenous water velocities to exploit for foraging, increase productivity of macroinvertebrate prey and visually isolate fish from competitors (Diehl, 1992; Sand-Jensen & Mebus, 1996; Johnsson, Rydeborg & Sundstrom, 2004; Venter *et al.,* 2008). Habitat restoration efforts frequently focus on restoring structural complexity to degraded upland rivers by placement of large substrate such as boulders or woody debris (Crook & Robertson, 1999). However, in lowland rivers, which are physically more stable systems, large substrates are naturally absent (Berrie, 1992). Instead, the central element structuring the functional characteristics of lowland rivers is aquatic plants (Sand-Jensen, 1998; Gurnell, 2014; Baattrup-Pedersen *et al.,* 2018).

Submerged macrophytes in particular can be considered as key habitat structures owing to their great influence on the dynamics of freshwater systems (Bronmark & Weisner, 1992). They provide essential structural complexity to provide substrate for epiphytes and macroinvertebrates (Gregg and Rose 1982; Diehl, 1992), shelter for juvenile fish (Maki-Petays *et al.,* 1997), and heterogeneous habitats via altering flow dynamics (Sand-Jensen & Mebus, 1996; Wharton *et al.,* 2006). The structuring role of macrophytes is well researched in standing bodies of water (e.g. Diehl, 1992; Diehl & Kornijow, 1998; Law *et al.,* 2019), but less work has been devoted to in-situ studies of macrophytes in flowing water. There is also a lack of empirical evidence quantifying relationships between macrophytes, habitat characteristics of lowland rivers and juvenile salmon populations. Current relevant studies rely heavily on assumption rather than quantitative evidence. For example, by comparing salmonid communities and macrophyte abundance in sites with and without riparian canopy, and assuming that responses observed in salmonids are related to macrophytes, without directly testing this relationship or considering alternative habitat variables that could have influenced salmonids (Riley *et al.,* 2009; McCormick & Harrison, 2011). It follows that increasing habitat complexity will influence more aspects of salmonid behaviour and ecology, making it difficult to tease out individual effects. However, due to their strong influence on the freshwater habitat, macrophytes are likely to be a crucial habitat characteristic for promoting healthy juvenile salmonid populations, and further research to quantify this role in lowland rivers is required.

A potential candidate to quantify this relationship between salmonids and macrophytes is to study the dominant macrophyte in lowland salmonid rivers, *Ranunculus* subgenus *Batrachium* or the water crowfoots (herein known as *Ranunculus*, Figure 1.2). *Ranunculus* are a group of submerged, fine-leaved macrophytes (Cotton *et al.*, 2006) considered to be a significant macrophyte in lowland rivers for their roles in providing refugia for macroinvertebrates and fish, and structuring habitat by altering water flow dynamics, water depth and sediment deposition (Armitage & Cannan, 2000; Wright et al 2002; Cotton *et al.*, 2006; Gurnell et al 2006; Wharton *et al.*, 2006). While the influence of *Ranunculus* on certain individual habitat variables is well studied in experimental set ups, e.g. water velocity (Sand-Jensen, 1998; Sand-Jensen & Mebus, 1996), it is relatively unknown how *Ranunculus* interacts with multiple habitat characteristics to influence lowland salmonid populations. As these characteristics are likely to interact and shape relative influences of each other on juvenile salmonids, so there is a necessity to direct research into these dynamics. *Ranunculus* habitats occur in many European streams and rivers and were designated by the European Community Directive on Conservation of natural and Semi-Natural Habitat as a key habitat to protect (Haslam, 1978; Dawson & Szoszkiwicz, 1999). As macrophytes are integral to structuring lowland rivers, application of findings from this thesis have a wider reach on lowland salmonid populations throughout their range.

1.2 Study location – the river Frome, Dorset, UK

The study river chosen to perform my investigations was the river Frome, a lowland river with salmonid populations and abundant macrophyte communities. The river Frome (total catchment area 414 km^2) in the county of Dorset is located on the southern English coast (Figure 2.1). It rises in chalk at Evershot (Lat. 50°50'24"N; Long. 2°36'12"W) and runs over chalk, clay, sand and gravel substrate for approximately 70 km before entering the sea at Poole harbour (Armitage *et al.*, 2001; Gregory *et al.*, 2019). It is one of southern England’s chalk streams and is considered

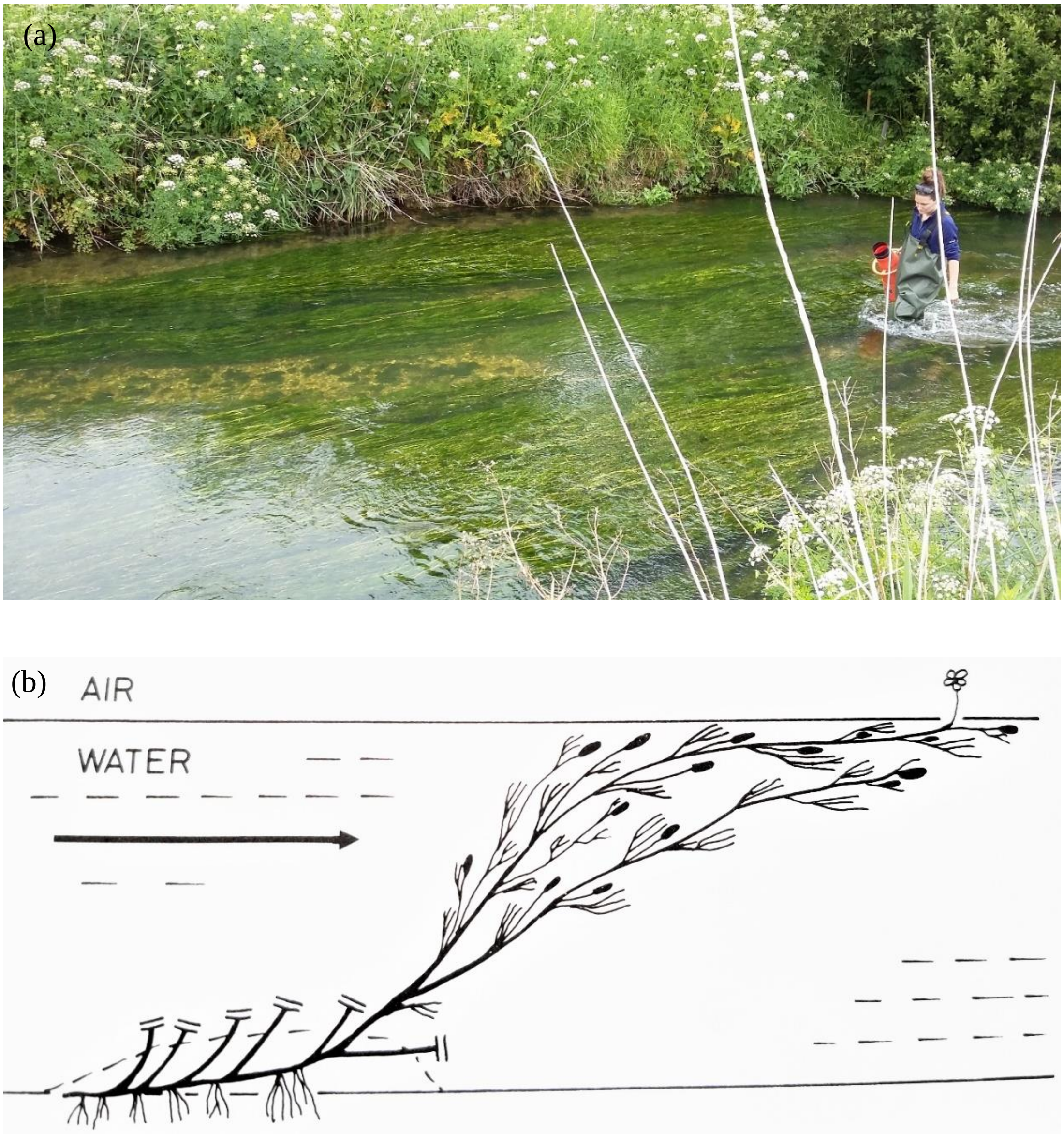


Figure 1.2. *Ranunculus* in a lowland river , (a) high *Ranunculus* cover during summer on the river Frome. The plants establish patchily across the riverbed to create a heterogeneous mosaic of habitat, (b) a simplified cross-section of a typical *Ranunculus* plant in the water column, from Dawson, 1979. One main stem is depicted, with associated lateral stems and emergent flower; the position of other main stems are indicated by short double lines. The

dashed line around the plant illustrates silt beneath which the basal region of the plant is buried, and direction of water flow is indicated by the arrow.

more semi-natural than that majority of lowland rivers, with a diverse geomorphology such as braided sections in parts of the middle and lower reaches (Cotton *et al.*, 2006). These reaches have been designated as a Site of Special Scientific Interest. Historically it is associated with prime salmon fishing in Britain, and fisheries are still a valuable resource (Welton, Beaumont & Ladle, 1999). As well as salmonid species, the river supports many other fish species, including grayling, (*Thymallus thymallus*), pike, (*Esox lucius*), dace, (*Leuciscus leuciscus*), roach, (*Rutilus rutilus*), minnow, (*Phoxinus phoxinus*), bullhead, (*Cottus gobio*), stone loach, (*Barbatula barbatula*), three-spined stickleback, (*Gasterosteus aculeatus*), eel, (*Anguilla anguilla*) sea lamprey, (*Petromyzon marinus*) and brook lamprey, (*Lampetra planeri*). The river Frome was a suitable location for this study as it supports important Atlantic salmon and brown trout (*Salmo trutta*) populations, as well as dominant *Ranunculus* communities (Berrie, 1992). Populations of Atlantic salmon (and recently brown trout) have been extensively monitored on this river using fish counters, trapping, e.g. rotary screw trap, electrofishing, tagging and telemetry. Numbers of adult salmon returning to the river have been quantified for 47 years, smolt production has been estimated for 25 years and estimates of summer juvenile populations have been calculated for the past 14 years (Lauridsen *et al.*, 2017a). Subsequently, there is an extensive existing dataset on the population dynamics of fish, but no complementary records of habitat. Additionally, most juvenile salmon develop for just one year in this river before migrating to sea (Ibbotson *et al.*, 2013), which renders this population vulnerable to poor freshwater conditions.

1.3 Thesis aim and outline

In this thesis I, together with my collaborators, aimed to address the knowledge gap on the role of macrophytes in providing suitable juvenile salmonid habitat in lowland rivers. I define juvenile as 0+ young-of-the-year fish, and salmonids as Atlantic salmon and brown trout in this study (unless noted otherwise). The thesis consists of four data chapters, each written in the format of an extended academic paper:

Chapter 2 Firstly, I began investigations by identifying broad patterns of density-habitat relationships between juvenile salmon and trout densities and key habitat features, including in-stream cover (*Ranunculus*), water velocities and depth, prey abundance, distance from tidal limit, and colonisation potential. By monitoring salmonid densities and habitat variables in late summer throughout the river catchment for three years, I was able to generalise these relationships and identify interspecific differences in habitat requirements. This study advances current understanding of the freshwater habitat requirements of salmonids in lowland rivers and highlights the potential for unexplored factors of velocity heterogeneity and site colonisation potential in habitat studies.

Chapter 3 After identifying an association between *Ranunculus* and salmon densities, and a potential indirect influence of *Ranunculus* on trout densities through influences on velocities, I implemented a novel in-river *Ranunculus* manipulation experiment. It ran for two years and aimed to quantify the effect of natural *Ranunculus* communities on wild juvenile salmonid populations (abundance) and individuals (site fidelity and growth). By monitoring populations through the summer and autumn months and utilising Passive Integrated Transponder (PIT) tagging to distinguish recaptured fish, I was able to assess key periods of *Ranunculus* influence and the consequences of inhabiting differing levels of *Ranunculus* cover on body length.

Chapter 4 Good growth in summer months is imperative for juvenile salmonids to survive overwinter and considered to have lasting impacts on the likelihood of individuals completing their life cycle. Many factors influencing juvenile salmonid growth are related to the amount and quality of habitat available to an individual, however there is a paucity of empirical evidence to identify habitat characteristics influential on growth rates, and indeed diet of salmon and trout, in lowland rivers. Using data collected in the *Ranunculus* manipulation experiment, I explore the influence of *Ranunculus* cover on juvenile salmon and trout growth rates, diet, prey electivity and dietary niche overlap between these two sympatric species.

Chapter 5 The in-field experiment identified positive influences of *Ranunculus* cover on both salmon abundance and growth rates, but the mechanisms underlying these relationships remained unclear. Using observed relationships identified in previous chapters, I applied confirmatory path analysis to identify whether these positive influences of *Ranunculus* were likely to be a consequence of a direct effect of habitat, or an indirect effect through influences on the physical habitat, food resources or competition interactions. Bringing together these influences allowed for testing the relative importance of each component and further specify the role of *Ranunculus* in lowland rivers.

Chapter 6 summarises and discusses the findings of this thesis in the context of existing literature. I demonstrate how this thesis has advanced our knowledge of both the holistic role of macrophytes in lowland rivers, and the influence of the dominant

Ranunculus on juvenile salmonid populations. In light of these findings, I offer recommendations for the management of lowland river ecosystems, and suggest areas of further study.

Chapter 2: Above parr: lowland river habitat characteristics associated with higher juvenile salmon and trout densities

2.1 Abstract

Understanding juvenile salmonid habitat requirements is critical for their effective management, but little is known about such requirements in lowland rivers, which include important but unique salmonid habitats. I explored relationships between juvenile Atlantic salmon and brown trout densities, habitat characteristics (in-stream cover, water depth, prey abundance, distance upstream), and two previously unexplored factors - water velocity heterogeneity and site colonisation potential. I related salmonid densities to these characteristics across 18-22 sites of a lowland river in Dorset, UK, in summer of 2015-2017. I collected data using electrofishing, habitat surveys and macroinvertebrate kick-sampling, and calculated the site colonisation potential from visual salmon redd (nest) surveys. Due to a recruitment crash in 2016, models including and excluding this unusual year were explored. Excluding 2016, juvenile salmon densities were strongly positively associated with *Ranunculus* cover and numbers of nearby upstream redds, and negatively associated with distance upstream from the tidal limit. Trout densities were positively associated with velocity heterogeneity, indicating a potential indirect influence of *Ranunculus* mediated by water velocity. When including 2016, year had the largest effect on densities of both species, highlighting the impact of the recruitment failure. These findings uncover interspecific differences in the freshwater habitat requirements of juvenile salmonids in a lowland river. Previously unexplored factors, velocity heterogeneity and site colonisation potential, had high explanatory power, highlighting their potential application in future studies. Moreover, the results show that temporal replication and recruitment dynamics are important considerations when exploring species-habitat associations. I suggest that *Ranunculus* cover can become an important management tool in conservation of lowland salmonids.

2.2 Introduction

Freshwater ecosystems host a disproportionately high richness of animals and plants but are among the most threatened ecosystems globally (Lundberg *et al.*, 2000; Reid *et al.*, 2018; Sala *et al.*, 2000). The degradation of freshwater habitats, through water pollution, flow modification and impoundments, is considered a leading cause of species loss and declines in population densities (Dudgeon *et al.*, 2006; Reid *et al.*, 2018). Diadromous fish species, such as anadromous salmonids, are particularly vulnerable, because they face the combination of increasing threats in both freshwater and marine environments (Friedland *et al.*, 2009, Reid *et al.*, 2018), and have suffered unprecedented population declines in recent decades (ICES, 2017). An understanding of freshwater habitat use by juvenile salmonids and resulting density-habitat relationships is therefore crucial for effective habitat conservation and management of salmonid populations.

The availability of suitable habitats and food resources in the freshwater environment is essential for maintaining healthy populations of juvenile salmonids (Poff & Huryn, 1998), such as Atlantic salmon (*Salmo salar*, hereafter salmon parr) and brown trout (*Salmo trutta*, hereafter trout parr). The summer life-stage occurs between two critical survival periods for parr: the emergence and establishment of summer feeding territories by salmonid fry that is controlled by strong density-dependent processes (Pender & Kwak, 2002), and overwintering of parr during a period of low prey abundance and deteriorating abiotic conditions (Armstrong *et al.*, 2003, McCormick & Harrison, 2011). The summer months are critical for parr feeding and growth (Wankowski & Thorpe, 1979), and optimal summer habitats should therefore promote efficient foraging, while allowing predator and competitor avoidance. The most important habitat variables for salmonid parr during the summer growth period are proposed to be: in-stream cover, stream substrate, water depth and velocity (Heggenes, 1990). Indeed, most studies have considered only these four habitat characteristics, but have found contrasting – potentially species- and context-specific – relationships. Moreover, few of these studies have focused on lowland rivers (but see Riley *et al.,* 2006, 2009).

In-stream cover provides essential shelter for juvenile salmonids and is considered the most important single site attribute in determining salmonid abundance (Milner, 1982; Gries & Juanes, 1998). An abundance of cobbles and boulders contribute to requirements for "good" parr habitat in upland rivers (Semple, 1991), and provides complex habitats with refugia from water flow, predators and competitors (Cunjak, 1988; Venter *et al*., 2008). Aquatic vegetation can also provide shelter, particularly in summer and autumn months. The smallest size-class of trout parr were found in high cover of aquatic vegetation in an upland river (Maki-Petays, *et al.,* 1997), and salmon parr can occupy vegetation during the night in a lowland chalk stream (Riley *et al.*, 2006). Although very high macrophyte cover could reduce habitat heterogeneity and suitability for salmonid parr, in the absence of large substrate, aquatic vegetation may provide essential cover and shelter for both salmon and trout parr.

Salmon parr are commonly associated with shallow to intermediate water depths in lowland (Riley *et al*., 2006) and upland (Morantz *et al*., 1987) river systems. Trout parr are associated with a greater range of habitats than salmon, but most frequently with deeper habitats along river margins (Armstrong *et al.,* 2003; Riley *et al.,* 2006). Both species may utilise deeper pools in the absence of potential competitors and predators (Gibson, 1993; Maki-Petays, 1997). Although there is an overlap in water velocities preferred by both juvenile salmon and trout, salmon tend to inhabit faster flowing waters than trout (Heggenes, Bagliniere & Cunjak, 1999; Riley *et al.,* 2006), and it is recognised that salmon parr can hold station in higher water velocities than trout (Heggenes, Saltveit & Lingaas, 1996; Riley *et al*., 2006).

Water velocity can also influence salmonid foraging behaviour. Both salmon and trout are opportunistic feeders, seeking drifting and benthic prey depending on their availability (Gibson, 1993; Poff & Huryn, 1998), although trout actively search for prey more frequently than salmon (Bardonnet & Bagliniere, 2000). When seeking drifting macroinvertebrates, salmonids utilise heterogeneity in velocity to minimize the energy cost of foraging by maintaining station in an area of low velocity adjacent to fast flows that are carrying macroinvertebrate prey (Cunjak, 1988; McCormick & Harrison, 2011; Morantz *et al.,* 1987). While causal relationships between habitat characteristics and changes in flow (e.g. boulders and low velocity refuges in upland rivers) have been proposed (Cunjak, 1988; Venter *et al.,* 2008), to my knowledge, no study of salmonid habitat use has related any measure of velocity heterogeneity or patchiness to juvenile salmon densities.

Salmonids – particularly salmon - undergo ontogenetic shifts in both behaviour and habitat use during their freshwater stages (Folt *et al*., 1998). Upon emergence from spawning redds, fry often disperse downstream in search of habitat suitable for their growth and development. Maximum dispersal distances range from a few hundred metres (e.g. Crisp, 1995) to a few kilometres (e.g. Beall *et al.*, 1994), dependent on conspecific density and habitat availability (Bardonnet & Bagliniere, 2000). Using fine-scale data, a positive relationship between available redd area and local salmon parr densities was identified (Teichert *et al.*, 2011), although as salmon fry were considered to be limited dispersers in this study (<20 m), these results may not be representative of all wild populations. Although the presence and proximity of redds are likely to affect colonisation potential and the density of summer parr, no rigorous study of juvenile salmonid habitat use has tested proximity among the different habitats required for different salmonid life stages.

Lowland rivers differ from many upland river systems because: (1) they are physically more stable habitats and typically have a similar gradient throughout the river catchment (Ibbotson, *et al.*, 2013), (2) they are low-energy systems (Berrie, 1992), and (3) they lack the large substrate (i.e. rocks and boulders) typically used by juvenile salmonids as cover and refuge from high flows in upland rivers. Consequently, submerged macrophytes, such as the water crowfoots (*Ranunculus* subgenus *Batrachium*, hereafter *Ranunculus*), play a particularly important structuring role in these rivers (Riley *et al.*, 2006; McCormick & Harrison, 2011).

Here, I provided a comprehensive analysis of the relationships between characteristics of lowland river habitats, and densities of salmon and trout parr. Habitat characteristics included in-stream vegetation (*Ranunculus*) cover, water depth, velocity, and prey availability (macroinvertebrates). I also considered two hitherto overlooked characteristics, namely velocity heterogeneity, and the presence and proximity of salmon redds (colonisation potential), to draw a more complete picture of the habitat requirements of juvenile salmonids in lowland rivers. Additionally, distance from tidal limit was included to account for differences in the accessibility of sites to migrating adults, which could influence the distributions of juveniles the following summer. Based on the previous research, I hypothesised the following relationships for both species: (1) a strong positive influence of *Ranunculus* cover on salmonid densities (albeit to a threshold), (2) that fast water velocity had a strong positive effect on salmon densities, but a negative effect on trout (3) a negative influence of water depth on salmon, and a positive influence on trout densities, (4) a positive effect of prey abundance on salmonid densities, (5) a strong positive influence of velocity heterogeneity on salmonid densities, and additionally for salmon, (6) a strong positive influence of the number of salmon redds found directly upstream on observed salmon densities.

2.3 Methods

2.3.1 Study sites and sampling

The river Frome, Dorset, and its tributaries are considered the most westerly of the UK chalk streams. The river is inhabited by salmon and trout populations of regional significance (Berrie, 1992; Lauridsen *et al.*, 2017a), with salmon stock estimates annually reported to the International Council for the Exploration of the Seas (ICES, 2017). Trout populations in the river Frome (and, therefore trout parr sampled in this study) represent individuals with resident and anadromous life histories.

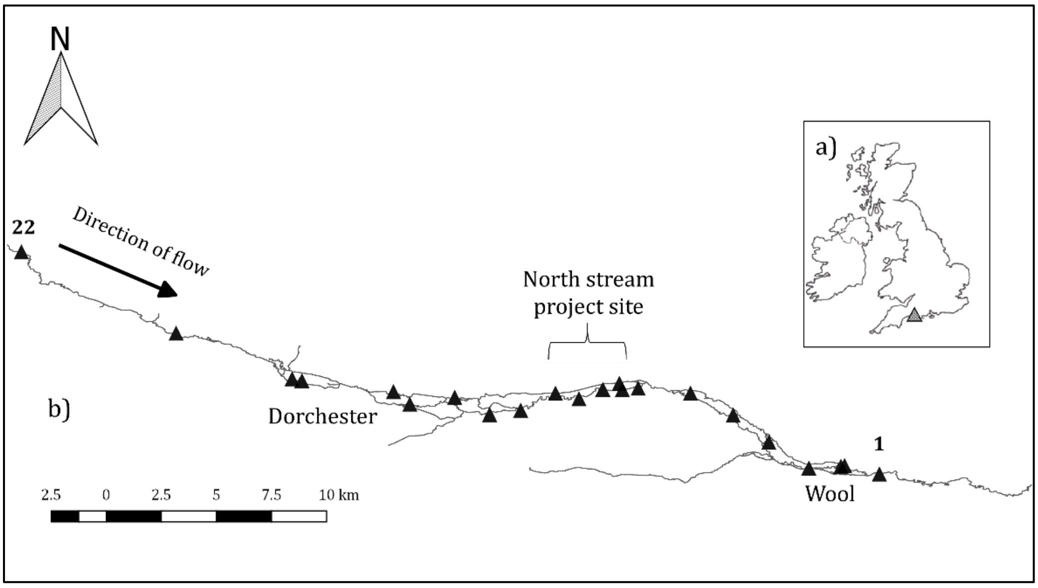


Figure 2.1. Study sites. a) Location of river Frome in Dorset, UK; b) study site locations along the river Frome (1 = most downstream site; 22 = most upstream site); section of river where juvenile salmonid diet sampling took place in a separate study on the North stream.

To determine the relationships between habitat characteristics and the summer density of juvenile salmonids, I sampled habitat characteristics, macroinvertebrates and juvenile salmonid populations at 18-22 sites on the river Frome (Figure 2.1). Sampling occurred during August and September for three years (2015-2017). Sampling sites were approximately 100 m in length, varied in physical characteristics, and were selected to represent contrasting habitat, representing natural variation in *Ranunculus* cover throughout the river catchment (Table S2.1).

The habitat at each sampling site was surveyed in five evenly-spaced quadrats (0.5 m x 0.5 m) distributed along each of ten evenly-spaced transects across the wetted width of the river. Within each quadrat, water depth was measured, the cover of *Ranunculus* plants was estimated visually as a percentage, and the water velocity was estimated visually as one of five categories (1 = 0-25 cm s^{-1}; 2 = 25-50 cm s^{-1}; 3

= 50-75 cm s^{-1}; 4 = 75-100 cm s^{-1}; 5 > 100+ cm s^{-1}). Specifically, water velocity was estimated by comparing visually the surface water changes around a wooden meter stick, i.e. how far up the stick the bow wave reached and the amount of turbulence the stick created. Although this measure was subjective, the estimates were all done by a single observer and were considered sufficiently objective to allow comparisons between quadrats within sites, between sites and over time. Percentage cover of other species of macrophytes, bryophytes and submerged riparian vegetation was also estimated in each quadrat, but they were not present with sufficient frequencies or quantities to be considered in statistical analyses.

Aquatic macroinvertebrates were sampled with standardized effort once per site using a 180 sec kick-sample with a pond net (net size: 25 x 25 cm; mesh aperture: 1 mm). Kick-samples covered the area of each site and sampled all habitats in proportion to their occurrence (Wright, 1997). The distribution of effort for the kick-samples was determined *a priori* from water depth, velocity and macrophyte assemblages observed during habitat surveys. Kick-samples were preserved in 70% ethanol solution and transported to the laboratory where they were washed with a 500 µm pore sieve prior to sorting and identification. All specimens were identified to the lowest practical taxonomic level (usually species), except Oligochaeta (sub-class), Hydrachnidae (family), Simuliidae (family) and Chironomidae (tribe). All habitat and macroinvertebrate samples were collected at least two hours prior to the surveying of fish populations to limit lasting disturbance to macrophyte beds, sediment and fish communities.

Standard quantitative k-pass depletion electro-fishing was used to estimate densities of juvenile (0+) salmon and trout (Hilborn & Walters, 1992). There were too few older juvenile salmonids (1+) to be considered in this study, as the majority of anadromous individuals migrate to sea after their first year in the river (Ibbotson *et al.*, 2013). I used between two and five fishing passes as required to achieve a depletion of > 50% in the numbers of fish caught per pass. Pulsed DC was used where the output waveform was a square-wave fished at 50 Hertz, ~200 volts and 25-30% duty cycle. Electro-fishing was carried out using a single anode (380 mm diameter) and cathode (3000 mm long). These settings are known to return high salmonid parr capture rates and cause <1% mortality rates on the River Frome (W. Beaumont, pers. comm., August 2015). Captured fish were sedated, identified to species, had their fork length (L_F: to age fish) measured to the nearest mm, and a scale sample taken from between the dorsal fin and lateral line (used if aging by L_F was inconclusive). After processing, all fish were released back into the river section where they were captured. Processing was carried out by licenced personnel under a UK Home Office A(SP)A licence (PPL 30/3277). Additional data were available for salmon redds (but not for trout): GPS locations of redds on the main river and major tributaries for the 2014/15 and 2016/17 spawning seasons (River Frome salmon spawn around New Year) were collected by the Environment Agency (subcontractor, Casterbridge Fisheries, Ltd) in January/February 2015 and 2017. No data were available for the 2015/16 spawning season because surveys were prevented by high water levels and poor weather.

2.3.2 Data preparation

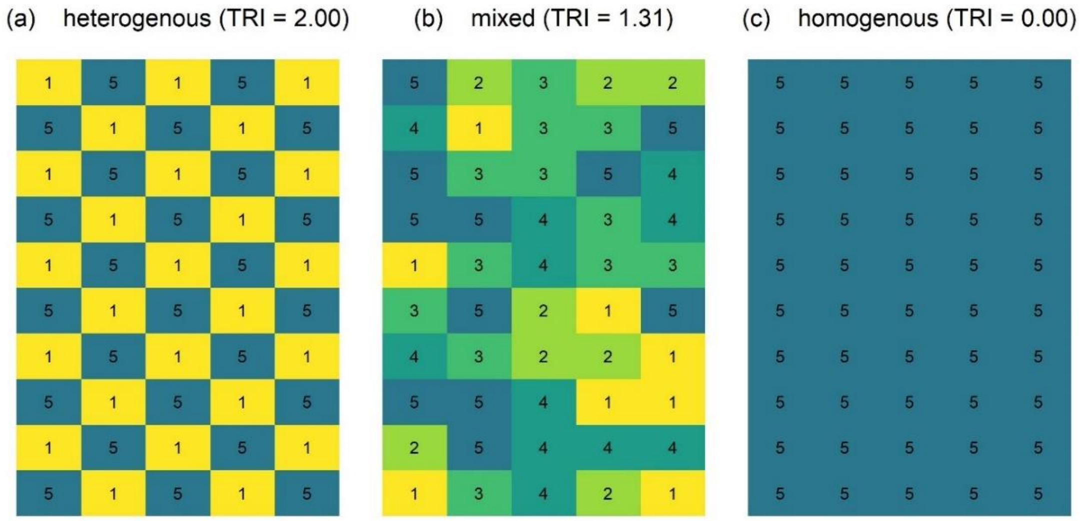
Fish were aged using L_F distribution and scale samples where necessary (Figures S2.1 – S2.2; max 0+ salmon L_F: 129 mm; max 0+ trout L_F:150 mm). The k-pass removal method used to calculate fish abundance estimates and associated 95%

confidence intervals uses the maximum likelihood model of Carle and Strub (1978) and assumes that (1) the population is closed, (2) effort is constant between passes, and (3) the probability of capture for an animal is constant for all animals and samples. It was reasonable to assume constant capture probability within each site because the same personnel undertook all fishing within a site and fishing passes were undertaken successively. Fish density estimates were obtained by dividing the fish abundance estimate for a site by the site area (site length x mean channel width).

The variable *depth* was normally distributed and required no transformation. *Ranunculus* cover was a proportion and arcsine transformed according to $(asin(x/100) \times 2/\pi)$, where x is the explanatory variable. To select a summary statistic that best represented explanatory variables (measured at the quadrat-level) at the site-level, the mode, median and mean of the transformed explanatory variable were compared visually with its empirical distribution: the mean was chosen to represent *Ranunculus* cover and the median to summarise *depth*.

As trout parr are considered to inhabit slower water than salmon, and have not been reported in habitats with velocities greater than 50 cm s^{-1} (Heggenes, Saltveit & Lingaas, 1996; Riley *et al.*, 2006), I grouped velocity categories 3, 4 and 5 (50 – 100+ cm s^{-1}) to represent the faster velocities used by salmon and avoided by trout. The site-level proportions of fast velocity were calculated as the proportions of quadrat measurements of the respective categories and arcsine transformed as above. To represent heterogeneity in site-level velocity, I aimed to capture the difference in velocity between neighbouring quadrats. The mean steepness of gradients in velocity between adjacent quadrats was calculated for all quadrats with a complete set of eight neighbours (Figure 2.2), using the Terrain Ruggedness Index (TRI: Wilson *et al.*, 2007) and implemented in R package raster. TRI was calculated as

$\sum|x[-5]-x[5]|/8$. Absolute values of TRI were averaged across all quadrats and used to represent velocity heterogeneity at the site-level.



(a) heterogenous (TRI = 2.00)

1	5	1	5	1
5	1	5	1	5
1	5	1	5	1
5	1	5	1	5
1	5	1	5	1
5	1	5	1	5
1	5	1	5	1
5	1	5	1	5
1	5	1	5	1
5	1	5	1	5

(b) mixed (TRI = 1.31)

5	2	3	2	2
4	1	3	3	5
5	3	3	5	4
5	5	4	3	4
1	3	4	3	3
3	5	2	1	5
4	3	2	2	1
5	5	4	1	1
2	5	4	4	4
1	3	4	2	1

(c) homogenous (TRI = 0.00)

5	5	5	5	5
5	5	5	5	5
5	5	5	5	5
5	5	5	5	5
5	5	5	5	5
5	5	5	5	5
5	5	5	5	5
5	5	5	5	5
5	5	5	5	5
5	5	5	5	5

Figure 2.2. Examples of site-level velocity heterogeneity measures using Terrain Ruggedness Index (TRI) calculations on matrices of fifty estimates (10 transects x 5 quadrats) of velocity categories (1:5): a) maximum heterogeneity between quadrats results in an average TRI value of 2.00; b) a mixture of medium-fast velocity categories between quadrats results in a lower average TRI value of 0.81, as the average heterogeneity is lower; c) maximum homogeneity between quadrats results in an average TRI value of 0.00, as the velocity category at all quadrats is identical.

Abundance of aquatic macroinvertebrates is not necessarily the best measure of salmonid food availability (Folt *et al.*, 1998) as taxa found frequently in kick samples might occur infrequently in the drift and are less available to salmonids, e.g. interstitial fauna (Poff & Huryn, 1998). Frequently consumed aquatic macroinvertebrate species were determined from a separate study undertaken on the North Stream of the river Frome (Figure 2.1) during June and August in 2016 and 2017, where gut contents were obtained from 0+ salmonids (204 salmon and 94 trout). Specimens in the gut contents were identified to the lowest possible taxonomic level (see above) and frequency of prey occurrence calculated for each fish species (Baker *et al.,* 2014). Taxa that were present in at least 25% of all samples were considered to be 'frequently consumed aquatic prey'. For salmon, frequently consumed prey consisted of: *Baetis* spp, Simuliidae, Chironomidae, and *Serratella ignita* (Ephemerellidae). The same taxa were frequently consumed by trout with the addition of, *Gammarus pulex* group, *Hydroptila* spp. and *Hydropsyche* spp. (Table 4.1). The frequently consumed taxa were present in all sites and contributed over 40% of the total abundance for most sites each year (except: sites 8, 10, 15 in 2015 and site 3 in 2017; Table S2.2). The total abundance of the frequently consumed taxa found in the kick samples was calculated to represent the variable *prey abundance*.

For data collected in 2015 and 2017, the GPS coordinates of redd locations and study sites were used to calculate the distances along the river between the downstream starting point of each site and all upstream redds. A vector map of the river Frome was constructed using R package raster and the GRASS GIS functions *r.thin* and *r.to.vect*. Redds and study sites were positioned on the river using GRASS GIS function *v.net* and least-cost (i.e., shortest) distances in km along the river between study sites and each upstream redd were calculated using GRASS GIS function *v.net.distance*. I used reported fish dispersal distances from Beall *et al.,* (1994) as this study represents wild fish dispersal behaviour (using eggs reared in-situ). Based on their estimates of summer downstream dispersal distances of 900 m by the majority of parr (68%), and an upper range of 2400 m, I chose a conservative limit of 1100 m downstream to represent dispersal distances of the majority of parr, whilst also capturing dispersal capabilities of fish that travelled further. I then calculated the number of redds present within 1100 m upstream of a study site to represent the variable *number of nearby upstream redds* (colonisation potential).

I calculated distance between sites and the tidal limit (located at Wareham bypass, approximately 3 km from the river mouth at Poole Harbour) using R package riverdist. Across sites, averages of the explanatory variables did not differ between years, with the exception of *Ranunculus* cover in 2015 relative to 2017 (Figure 2.3 and Table S2.3).

2.3.3 Statistical analysis

The analysis aimed to maximise the potential to draw interspecific comparisons in population density-habitat associations while accounting for both an anomalous year (observed failure in salmonid recruitment in 2016 following high overwinter temperature in 2015-16) and missing data (poor weather conditions prevented salmon redd counting in 2016 and collecting macroinvertebrate data at three sites across 2015 and 2016). I considered the following models to test my hypotheses: (1) models for each species including data from all 3 years but excluding cases with missing macroinvertebrate samples and the *number of upstream redds* explanatory variable, hereafter “3-year models” (n = 56); (2) models for each species excluding the anomalous 2016 data, two cases with missing macroinvertebrate samples and the *number of upstream redds* explanatory variable, hereafter “2-year models” (n = 38); and (3) models for salmon only excluding the anomalous 2016 data and two cases with missing macroinvertebrate samples but including the *number of nearby upstream redds* explanatory variable, hereafter “2-year salmon redds models” (n = 38).

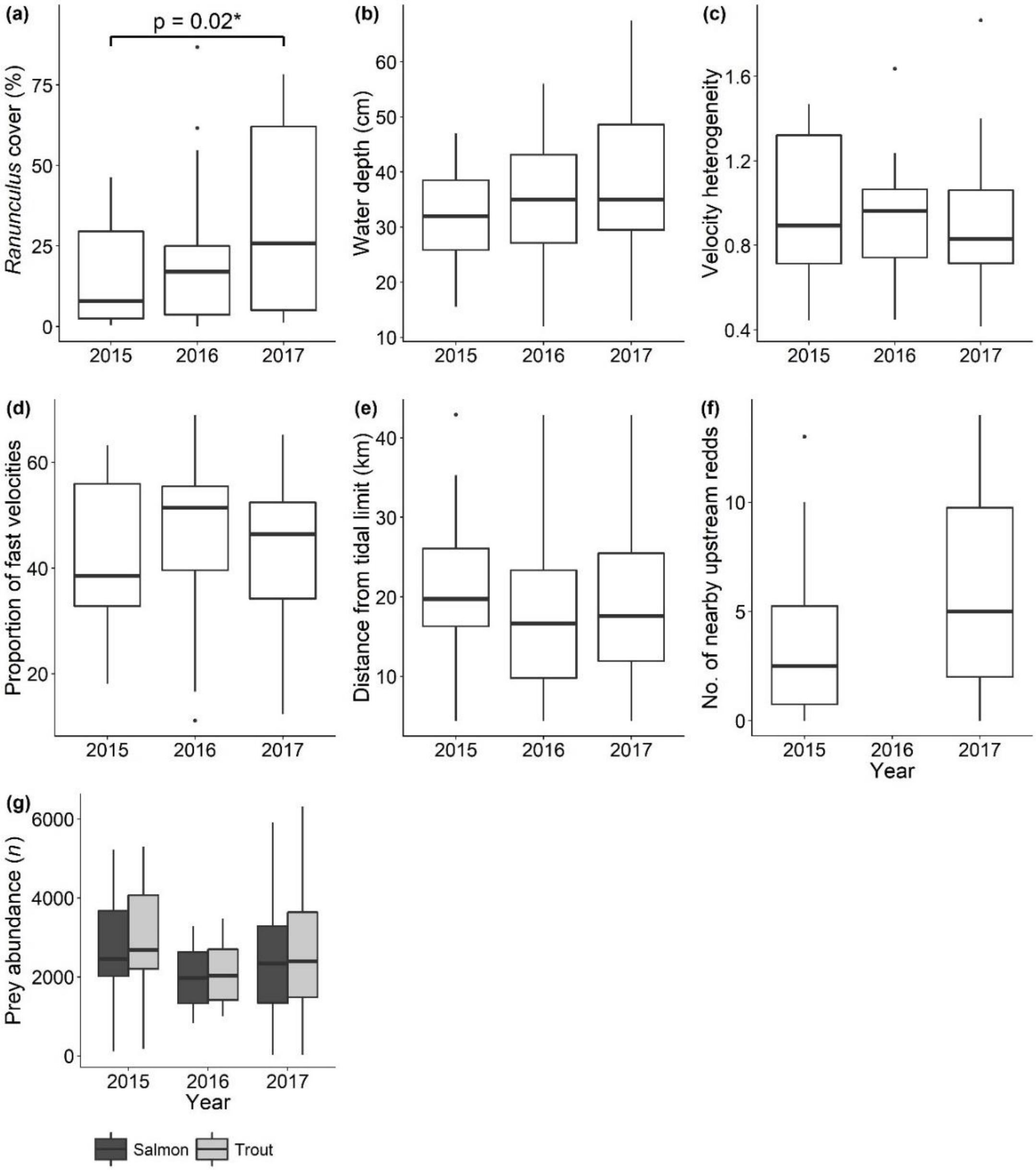


Figure 2.3. Median and interquartile range of environmental variables recorded across all study sites included in subsequent analyses for each year: 2015 (*n* = 16); 2016 (*n* = 18); 2017 (*n* = 22). (a-f) represent environmental variables common to a site; (g) shows abundance of preferred prey items for each fish species. All variables were tested for differences between years; significant differences between years are marked with a *p*-value.

For each collection of models, I considered the two species (salmon and trout) separately due to limiting sample sizes. Linear models tested the effect of the biotic and abiotic explanatory variables that were hypothesised to be important (Figure 2.3) on site-specific estimated juvenile salmonid densities. The models took the general form:

$$y \sim \alpha + \beta X + \epsilon,$$

where y is salmon or trout density, α is an overall fish density, β is a vector of coefficients relating the matrix of explanatory variables X to y, and ϵ is an independent and identically distributed (iid) random normal variate representing model error.

Prior to model fitting, explanatory variables were examined for collinearity (Figures S2.3 – S2.4): Pearson's correlations between pairs of potential explanatory variables $r \geq |0.6|$ were considered highly correlated (Dormann *et al.*, 2013) and models including highly correlated variables were further investigated to decide which explanatory variables to exclude. To compare the effects of variables measured at different scales, numerical explanatory variables were standardised prior to analyses by subtracting their mean and dividing by their standard deviation. I also explored whether the effect of *Ranunculus* was best represented by a linear or quadratic relationship, by developing and comparing univariate models with Akaike's Information Criteria model selection (AICc), corrected for small sample size (Figure S2.5). Models containing a linear or quadratic term of *Ranunculus* were statistically indistinguishable, thus, I included *Ranunculus* as a linear term, providing the most parsimonious model. Where *Ranunculus* was retained in the best-fit model, I implemented post-candidate model comparisons (post-tests), using all best models and additional models fit with a quadratic *Ranunculus* term (replacing the linear *Ranunculus* term, where applicable). This allowed for the selection of the overall best model and to consider whether there was a threshold effect of cover, where *Ranunculus* was important.

Candidate models for the 3-year and 2-year analyses were developed to represent hypotheses of the effects of different combinations of explanatory variables based on original predictions and field observations. Starting with a global model (including all explanatory variables), I removed variables one at a time to test my hypothesis about their importance. Subsequent simpler models included only the variables important for one or both species (designated as important if the difference in ΔAICc between initial models was >1), and as a final step, I tested each variable individually (see Tables S2.4 – S2.5 for full process).

Models were fitted using maximum likelihood and compared using AICc, and the model with the lowest AICc was selected as the final best model. If the difference between two models with the lowest ΔAICc was <2, the models were deemed to be statistically indistinguishable (Burnham & Anderson 2002), and the most parsimonious model was selected. To understand the balance between the generality and specificity of the models, I also calculated the predictive performance using leave-one-out cross-validation (*LOO CV*). The model with the smallest prediction error (*ΔLOO CV*) was assumed to have the greatest predictive ability.

To test for the importance of redds in the 2-year salmon redd analysis, I added the redd variable to the best performing model/s of the 2-year salmon analysis to construct a global candidate model. I then constructed a set of candidate models including different combinations of variables in the global model. Models were fitted and compared as above. Model residuals of the best performing 2-year models for salmon and trout were inspected to ensure they did not violate assumptions of homogeneity, normality and independence. All statistical analyses were conducted in R version 3.4.4 (R Development Core Team, 2018).

2.4 Results

2.4.1 3-year models

Mean densities of juvenile salmon were higher than densities of juvenile trout across all years and the lowest mean densities for both species occurred in 2016 (Figure 2.4). Eighteen candidate models were fitted to the 3-year fish data and compared (Table 2.1). The four best models at predicting juvenile salmon densities were statistically indistinguishable (ΔAICc <2), all of which included a *year* effect. As *Ranunculus* was retained in two of these models, six post-test comparisons were implemented (Table 2.1). The most parsimonious of the post-test models, and therefore the best overall model, was Model PS6, which included the effects of *year* and *distance from tidal limit* and explained 29% of variance in salmon densities (Table 2.1). The addition of *Ranunculus* as a linear term in Model PS3, and as a quadratic term in Model PS4 explained more variance ($R_{adj}^2 = 0.30$ & 0.33, respectively), and a combination of adding a quadratic term of *Ranunculus* and *prey abundance* explained the most variance ($R_{adj}^2 = 0.34$), although the prediction error for all six models was equal (*ΔLOO CV* = 0.004). The parameters *proportion of fast velocities*, *velocity heterogeneity* and *depth* were not retained in the best-fit salmon models (Table 2.1).

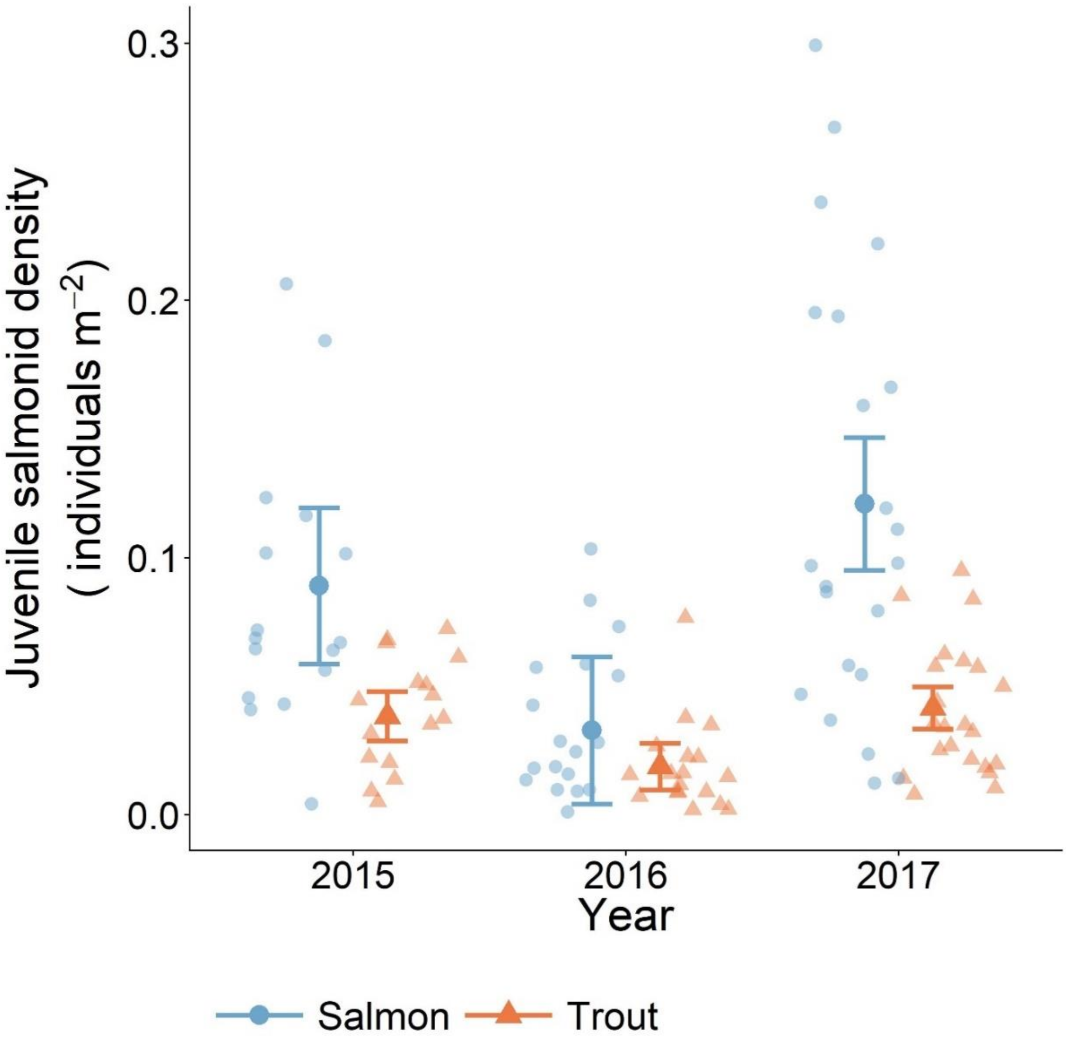


Figure 2.4. Marginal effect of year on estimated juvenile salmon (circles) and trout (triangles) densities in the top performing 3-year models (PS6, 17) as determined by AICc model selection. Points are mean estimates, and error bars are the 95% confident interval. Raw density estimates are illustrated as jittered transparent circles and triangles for salmon and trout respectively.

Table 2.1. 3-year models: Information statistic summary for the fit of 18 candidate models to the 3-year juvenile salmon and trout density data. Model parameters include: Y – Year, R – *Ranunculus*, D – Depth, FV – Fast velocity, VH – Velocity heterogeneity, P – Prey abundance, DS – Distance from tidal limit. K is the number of model parameters. Rows in bold represent the best fitting models selected by AICc for each species.

Hypothesis tested	Candidate models		Salmon					Trout				
	Model no.	Model terms	AICc	ΔAICc	K	σ	R^2_{adj}	AICc	ΔAICc	K	σ	R^2_{adj}
Candidate model selection												
Global model	Global	Y + R + D + FV + VH + P + DS	-140.4	8.54	8	0.06	0.28	-268.6	8.42	8	0.02	0.35
DS is not important	1	Y + R + D + FV + VH + P	-138.9	10.03	7	0.06	0.24	-267.7	9.25	7	0.02	0.32
P is not important	2	Y + R + D + FV + VH + DS	-141.5	7.49	7	0.06	0.27	-270.1	6.88	7	0.02	0.35
VH is not important	3	Y + R + D + FV + P + DS	-143.2	5.75	7	0.06	0.29	-258.8	18.13	7	0.02	0.21
FV is not important	4	Y + R + D + VH + P + DS	-143.1	5.82	7	0.06	0.29	-270.5	6.47	7	0.02	0.36
D is not important	5	Y + R + FV + VH + P + DS	-142.3	6.63	7	0.06	0.28	-271.0	5.96	7	0.02	0.36
R is not important	6	Y + D + FV + VH + P + DS	-142.2	6.77	7	0.06	0.28	-269.7	7.27	7	0.02	0.35
Y is not important	7	R + D + FV + VH + P + DS	-130.9	18.04	6	0.07	0.09	-258.4	18.61	6	0.02	0.17
VH & A both important	8	Y + R + DS + VH + P	-144.9	4.00	6	0.06	0.29	-272.8	4.18	6	0.02	0.36
VH not as important as P	9	Y + R + DS + P	**-147.3**	**1.67**	**5**	**0.06**	**0.30**	-263.5	13.44	5	0.02	0.23
P not as important as VH	10	Y + R + DS + VH	-146.5	2.42	5	0.06	0.29	-274.3	2.62	5	0.02	0.36
VH & P not important	11	Y + R + DS	**-148.9**	**0.00**	**4**	**0.06**	**0.30**	-263.4	13.58	4	0.02	0.20
R most important	12	Y + R	-145.2	3.78	3	0.06	0.24	-261.5	15.44	3	0.02	0.15
D most important	13	Y + D	**-147.3**	**1.61**	**3**	**0.06**	**0.27**	-261.0	15.93	3	0.02	0.15
FV most important	14	Y + FV	-145.0	3.95	3	0.06	0.23	-265.8	11.15	3	0.02	0.22
DS most important	15	Y + DS	**-148.9**	**0.05**	**3**	**0.06**	**0.29**	-263.7	13.22	3	0.02	0.19
P most important	16	Y + P	-143.9	5.07	3	0.06	0.22	-262.0	14.96	3	0.02	0.16
VH most important	17	Y + VH	-143.7	5.22	3	0.06	0.22	**-277.0**	**0.00**	**3**	**0.02**	**0.36**
Post – candidate model comparisons on top performing model/s (post-tests)												
Mod S9: R performs better than R^2	PS1	Y + R + DS + P	-147.3	2.32	5	0.06	0.30	-	-	-	-	-
Mod S9: R^2 performs better than R	PS2	Y + R^2 + DS + P	**-148.6**	**0.94**	**6**	**0.06**	**0.34**	-	-	-	-	-
Mod S11: R performs better than R^2	PS3	Y + R + DS	**-148.9**	**0.65**	**4**	**0.06**	**0.30**	-	-	-	-	-
Mod S11: R^2 performs better than R	PS4	Y + R^2 + DS	**-149.6**	**0.00**	**5**	**0.06**	**0.33**	-	-	-	-	-
Mod S13: D most important	PS5	Y + D	-147.3	2.26	3	0.06	0.27	-	-	-	-	-
Mod S15: DS most important	PS6	Y + DS	**-148.9**	**0.70**	**3**	**0.06**	**0.29**	-	-	-	-	-

Juvenile trout densities were best described by Model 17, which contained the terms *year* and *velocity heterogeneity* and explained 36% of the variance in densities (Table 2.1). As *Ranunculus* was not retained in the best model, no post-test comparisons were performed. No other candidate model explained more variance or had a lower prediction error ($\Delta LOO\ CV < 0.0004$). The parameters *proportion of fast velocities, depth, prey abundance* and *distance from tidal limit* were also not retained in the best-fit trout models (Table 2.1).

Both salmon and trout densities were strongly influenced by *year*, whereby the effect was driven by the negative influence of 2016 when juvenile salmonid populations were unusually low, relative to 2015 and 2017 (Figures 2.4 and 2.5). Salmon density was negatively associated with *distance from tidal limit*, with density estimates decreasing the further upstream the sites were located (Figure 2.5a). Juvenile trout density also increased with increasing *heterogeneity in velocity* (Figure 2.5b).

2.4.2 2-year models

When 2016 data were omitted, *depth* was strongly correlated with *Ranunculus* ($r = 0.63$). As *Ranunculus* is likely to be important as salmonid habitat and because its presence is associated with increased water depths (Franklin, Dunbar & Whitehead, 2008), *depth* was excluded and *Ranunculus* was retained in the model selection.

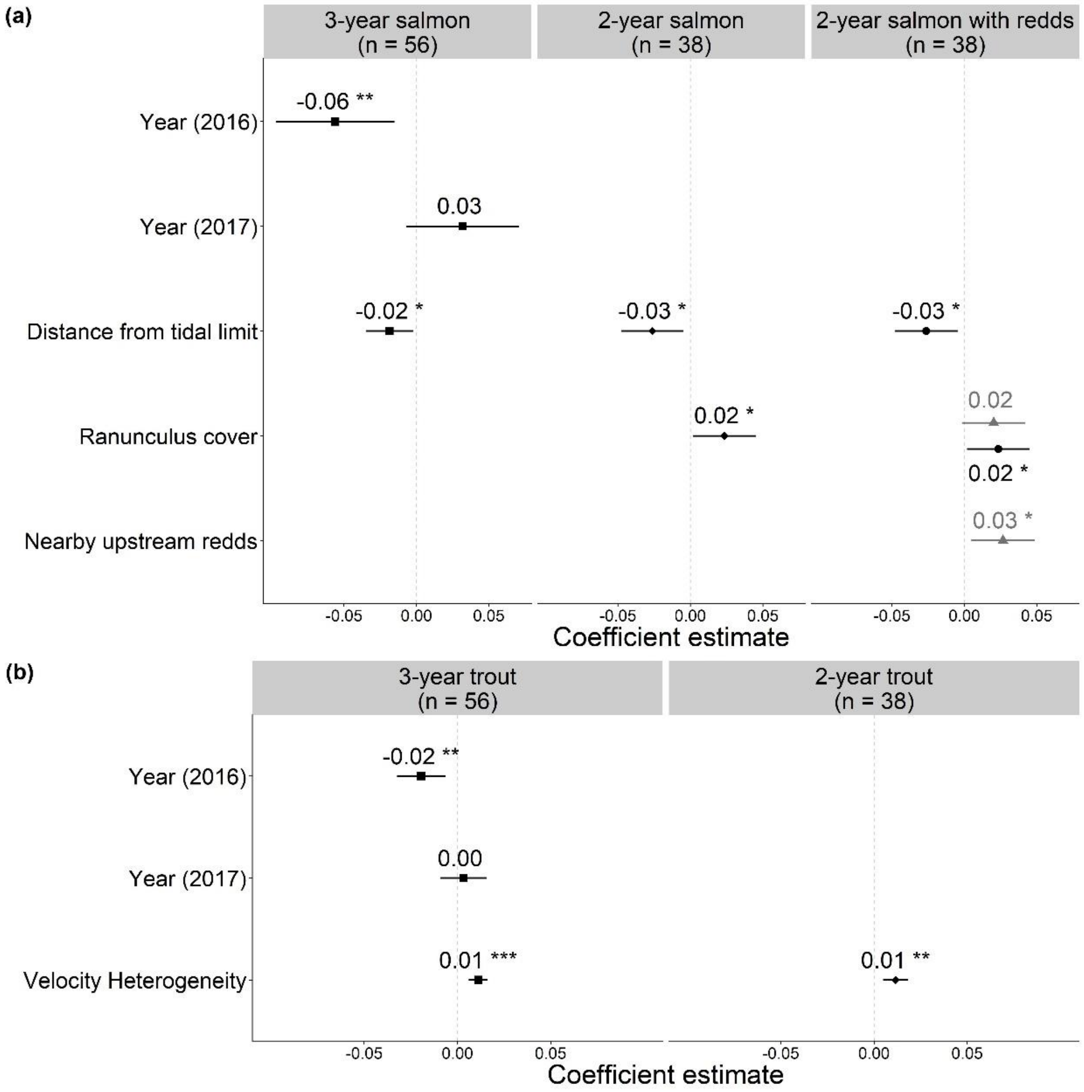


Figure 2.5. Coefficient estimates for explanatory variables retained in the best 3-year and 2-year model for (a) salmon and (b) trout. Best-fit 2-year redd models are also shown for salmon. 2015 is the reference level for year estimates. Points illustrate mean estimates (■ 3-year model; ♦ 2-year model; ● 2-year salmon redd [Model 1]; ▲ 2-year salmon redd [Model 2]), lines are 95% confidence limits, and values denote the estimate and significance levels (* p < 0.05, ** p < 0.01, *** p < 0.001).

Table 2.2. 2-year models: Information statistic summary for the fit of 19 candidate models to the 2-year juvenile salmon and trout density data. Model parameters include: Y – Year, R – *Ranunculus*, FV – Fast velocity, VH – Velocity heterogeneity, P – Prey abundance, DS – Distance from tidal limit. K is the number of model parameters. Rows in bold represent the best fitting models selected by AICc for each species.

Hypothesis tested	Candidate models		Salmon					Trout				
	Model no.	Model terms	AICc	ΔAICc	K	σ	R^2_{adj}	AICc	ΔAICc	K	σ	R^2_{adj}
Candidate model selection												
Global model	Global	Y + R + FV + VH + P + DS	-81.1	10.58	6	0.07	0.11	-173.9	8.13	6	0.02	0.23
DS is not important	1	Y + R + FV + VH + P	-80.7	11.00	5	0.07	0.06	-173.5	8.53	5	0.02	0.18
P is not important	2	Y + R + FV + VH + DS	-84.1	7.64	5	0.07	0.14	-174.3	7.70	5	0.02	0.20
VH is not important	3	Y + R + FV + P + DS	-84.1	7.61	5	0.07	0.14	-167.9	14.08	5	0.02	0.05
FV is not important	4	Y + R + VH + P + DS	-84.3	7.39	5	0.07	0.14	-175.0	7.00	5	0.02	0.21
Y is not important	5	R + FV + VH + P + DS	-83.9	7.86	5	0.07	0.13	-176.2	5.75	5	0.02	0.24
R is not important	6	Y + FV + VH + P + DS	-80.6	11.13	5	0.07	0.05	-175.2	6.75	5	0.02	0.22
VH & P important	7	R + DS + VH + P	-86.9	4.86	4	0.07	0.16	-177.3	4.72	4	0.02	0.22
FV & P important	8	R + DS + FV + P	-86.7	5.06	4	0.07	0.15	-170.5	11.54	4	0.02	0.07
VH & FV important	9	R + DS + VH + FV	-86.6	5.14	4	0.07	0.15	-176.4	5.63	4	0.02	0.20
VH important	10	R + DS + VH	-89.1	2.57	3	0.07	0.17	-178.8	3.15	3	0.02	0.22
P important	11	R + DS + P	-89.5	2.24	3	0.07	0.18	-173.3	8.74	3	0.02	0.09
FV important	12	R + DS + FV	-89.1	2.59	3	0.07	0.17	-171.5	10.45	3	0.02	0.05
DS important	13	R + DS	**-91.7**	**0.00**	**2**	**0.07**	**0.19**	-173.0	9.01	2	0.02	0.05
R most important	14	R	-88.5	3.21	1	0.07	0.09	-173.0	9.01	1	0.02	0.01
FV most important	15	FV	-86.0	5.75	1	0.07	0.03	-174.6	7.42	1	0.02	0.05
DS most important	16	DS	-89.6	2.14	1	0.07	0.11	-174.1	7.89	1	0.02	0.04
P most important	17	P	-84.1	7.64	1	0.08	<0.01	-173.5	8.54	1	0.02	0.02
VH most important	18	VH	-84.3	7.39	1	0.08	<0.01	**-182.0**	**0.00**	**1**	**0.02**	**0.22**
Post – candidate model comparisons on top performing model/s												
Mod S13: R performs better than R^2	P1S	R + DS	**-91.7**	**1.30**	**2**	**0.07**	**0.19**	-	-	-	-	-
Mod S13: R^2 performs better than R	P2S	R^2 + DS	**-93.0**	**0.00**	**3**	**0.06**	**0.25**	-	-	-	-	-

Subsequently, 19 candidate models were fitted to the 2-year fish data and compared (Table 2.2). Model 13, including the effects of *Ranunculus* and *distance from tidal limit,* was the best model at explaining salmon densities. Post-test comparisons included this model with and without a quadratic *Ranunculus* term. The two post-test models were statistically indistinguishable and as the most parsimonious, Model P1S was the best overall performing model (Table 2.2). Including *Ranunculus* as a quadratic term explained more variance in salmon densities than Model P1S (R^2_{adj} = 0.25 & 0.19, respectively), but the prediction error was identical for both models (*ΔLOO CV* = 0.005). The parameters *proportion of fast velocities*, *prey abundance*, *velocity heterogeneity* and *year* were not retained in the best models (Table 2.2).

The juvenile trout densities were best described by Model 18, with *velocity heterogeneity* as the only model term (Table 2.2). As *Ranunculus* was not retained in the best model, no post-test comparison was performed. Model 18 explained 22% of the variance in trout densities and had the lowest prediction error of all candidate models tested (*ΔLOO CV* = 0.0004). Model residuals of Model 18 did not violate any assumptions (Figure S2.6).

2.4.3 2-year salmon redd models

Eight candidate models that included *number of upstream redds* as an explanatory variable were fitted to the 2-year salmon data and compared (Table 2.3). The six best models were statistically indistinguishable (ΔAICc <2) and all included an effect of *Ranunculus*. The two most parsimonious models, Models 1 and 2, performed equally well ($R^2_{adj} = 0.19, \Delta LOO\ CV = 0.005$), and, in addition to a linear *Ranunculus* term, included *distance from tidal limit* and *number of nearby upstream redds* respectively. Model 1 was the same best model in the 2-year analysis. Including *Ranunculus* as a quadratic term rather than a linear term explained more variance in salmon density (Table 2.3). The most variation was explained by Model 4 ($R^2_{adj} = 0.28$), which included *distance from tidal limit, number of upstream redds* and a quadratic *Ranunculus* term, though the prediction error for all candidate models was equal (*ΔLOO CV* = 0.005). Model residuals of Models 1 and 2 did not violate any assumptions (Figure S2.6).

Table 2.3. 2-year salmon redd models: Information statistic summary for the fit of 8 candidate models to the 2-year juvenile salmon density data, including number of nearby upstream redds as an explanatory variable. Model parameters include: R – *Ranunculus*, DS – Distance from tidal limit, RD – Number of nearby upstream redds. K is the number of model parameters. Rows in bold represent the best fitting models selected by AICc.

Hypothesis tested	Candidate models		Salmon				
	Model no.	Model terms	AICc	ΔAICc	K	σ	R^2_{adj}
Global model	Global	R + DS + RD	**-91.3**	**1.68**	**3**	**0.07**	**0.22**
RD not important	1	R + DS	**-91.7**	**1.30**	**2**	**0.07**	**0.19**
DS not important	2	R + RD	**-91.7**	**1.31**	**2**	**0.07**	**0.19**
RD most important	3	RD	-90.8	2.22	1	0.07	0.14
R^2 performs better than R	4	R^2 + DS + RD	**-92.6**	**0.39**	**4**	**0.06**	**0.28**
RD not important, R^2 performs better than R	5	R^2 + DS	**-93.0**	**0.00**	**3**	**0.06**	**0.25**
DS not important, R^2 performs better than R	6	R^2 + RD	**-92.2**	**0.85**	**3**	**0.07**	**0.23**
R not important	7	DS + RD	-90.2	2.84	2	0.07	0.16

2.4.4 Direction and strength of habitat effects

Marginal effects plots visualise the relationships between salmonid densities and individual habitat variables, when holding the effects of other model parameters constant (Figures 2.6 and 2.7). The best 2-year salmon redd models and 2-year trout model were used to assess habitat effects on fish densities in years of regular recruitment (i.e. excluding the unusual year). The residuals of the best models do not violate the linear model assumption of normality (Figure S2.6).

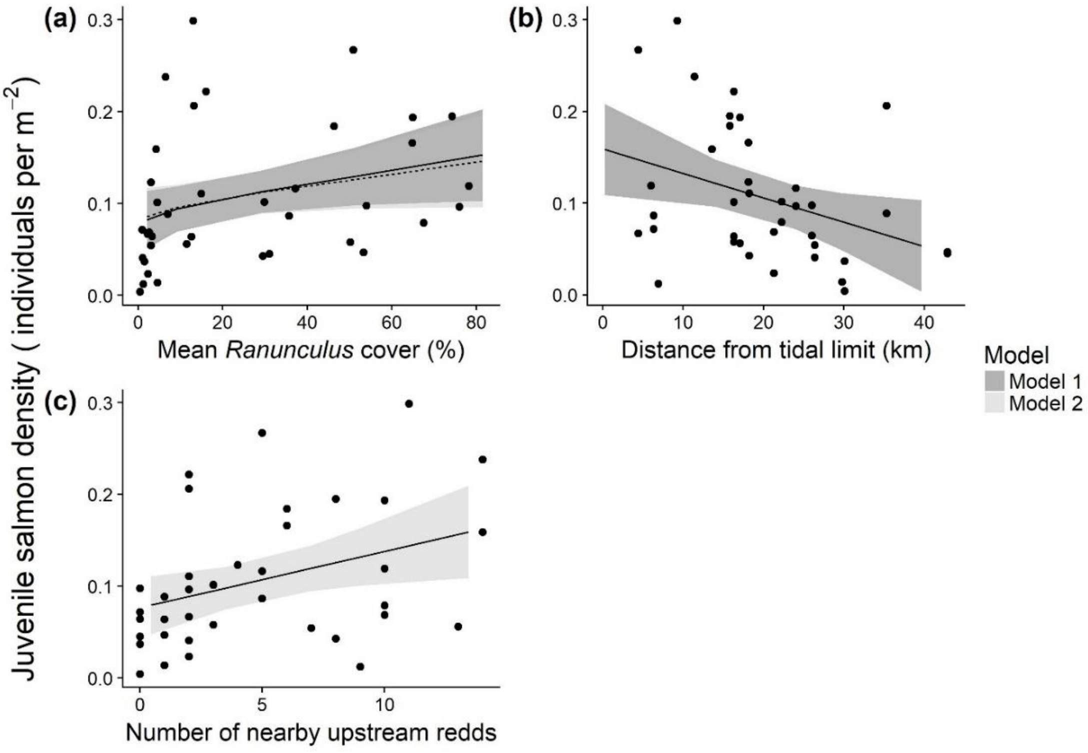


Figure 2.6. Relationships between juvenile salmon density and (a) mean *Ranunculus* cover, (b) distance from tidal limit, and (c) number of upstream redds, the explanatory variables retained in the top two performing 2-year salmon redds models, (Models 1 and 2) as determined by AICc. The black line is the mean estimated effect, the shaded grey area is the standard error of the estimated effect, and black points are observed salmon densities at individual sites.

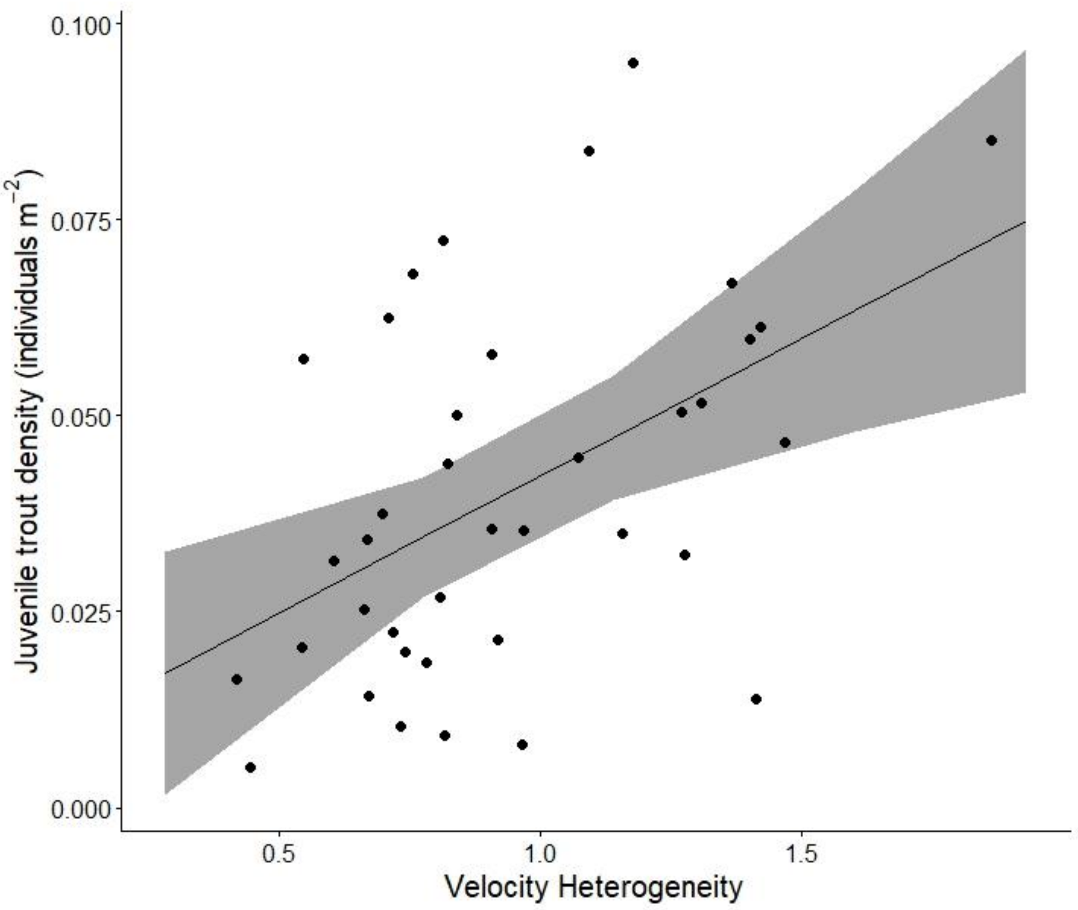


Figure 2.7. Relationship between juvenile trout density and velocity heterogeneity, the explanatory variable retained in the top performing 2-year trout model (Model 18) as determined by AICc. X-axis scales from 0 (indicating constant velocity) to 2 (indicating high velocity heterogeneity): see Figure 2.2. The black line is the mean estimated effect, the shaded grey area is the standard error of the estimated effect, and black points are observed trout densities.

The first 2-year salmon redd model (Model 1) showed that *Ranunculus* was positively associated, whereas *distance from tidal limit* was negatively associated with salmon density (Figure 2.6). The 95% confidence intervals of the effects *Ranunculus* and *distance from tidal limit* did not overlap with zero (Figure 2.5a). The second 2-year salmon redd model (Model 2) showed that *Ranunculus* and *number of nearby upstream redds* were positively associated with salmon density, though the

95% confidence interval of the *Ranunculus* effect did intercept zero (Figure 2.5a). Salmon density was higher in sites with higher *Ranunculus* cover and more redds upstream, but was lower in sites located further upstream of the tidal limit (Figure 2.6). The 2-year trout model showed a strong positive association between the *velocity heterogeneity* and trout density (Figure 2.7) and the 95% confidence interval of the effect did not overlap with zero (Figure 2.5b).

2.5 Discussion

The densities of juvenile salmon and trout were associated with different summer habitat characteristics. Juvenile salmon density was positively associated with *Ranunculus* and site colonisation potential, and negatively associated with distance upstream, whereas juvenile trout density was strongly positively associated with velocity heterogeneity. These findings highlight the different habitat requirements of each species and indicate how juvenile summer habitat might be managed to maximise salmonid densities in lowland rivers.

When incorporating a poor recruitment year in the analyses, year had the largest effect on both salmon and trout densities, emphasising the importance of recruitment dynamics in studies of species-habitat associations and of temporal replication to identify potential effects. The strong negative effect of 2016 conditions on salmonid density corresponded with a juvenile salmon recruitment crash across England and Wales following an unusually wet and warm winter thought to have caused high egg and alevin (pre-emerged salmonid) mortality (ICES, 2017). As trout in southern chalk streams spawn between late December and early January (Mann, Blackburn & Beaumont, 1989) it is possible that the extraordinary winter of 2015/16 also affected trout egg and alevin survival, leading to low densities of juvenile trout the following year.

The importance of recruitment is further emphasised, as proximity to salmon redds had a positive influence of juvenile salmon densities highlighting that, in addition to habitat characteristics, the colonisation potential of a site might determine juvenile population sizes. Although salmon fry are capable of greater dispersal distances from redds to summer habitats (Beall *et al.*, 1994), the results suggest that fry move downstream only as far as adequate feeding grounds. Hence, maintaining appropriate summer habitats close to suitable spawning areas would have the greatest benefit for the juvenile salmonids. It also suggests that where that mosaic of spawning and summer habitat is missing, knowledge of annual distributions of salmon redds would allow for more focused habitat conservation and improvements at sites with high colonisation potential.

A recent study of long-term salmon redd distributions on the River Frome found the highest densities of redds within the middle reaches of the river, and that these aggregations increased under low-flow conditions, where access to upper reaches might be limited (Parry *et al.*, 2017). Although salmon fry can migrate to summer habitats upstream of their redd, the majority of juveniles disperse downstream (Beall *et al.*, 1994). If most recruitment occurs in the middle reaches, it is plausible to expect higher juvenile densities to be found at sites located in the lower to middle reaches of the river. Recruitment distribution, therefore, could explain the importance of distance from tidal limit at describing salmon densities, and why lower densities were associated with sites further upstream.

Ranunculus cover was positively associated with juvenile salmon density. Several potential mechanisms could drive this relationship. When comparing 0+ salmon densities between exposed sites with macrophytes and shaded sites without macrophytes but extensive canopy cover, McCormick and Harrison (2011) found higher salmon densities in the exposed sites. While canopy cover is thought to protect stream fish from aerial predators, thereby maximising foraging and minimising vigilance behaviour (Johnsson, Rydeborg & Sundstrom, 2004), McCormick and Harrison’s results suggest that macrophytes afford adequate protection from aerial predators. Moreover, *Ranunculus* can provide necessary structural complexity throughout the water column to reduce predation (Diel & Kornijow, 1997) and reduce the visual capacity of competitors, thereby promoting smaller, more numerous 0+ salmonid territories (Imre *et al.*, 2002). For example, an in-river experiment found that increasing habitat complexity (through addition of boulders) resulted in higher 0+ salmon population densities via decreases in territory size (Venter *et al.*, 2008). Larger substrates, such as boulders, are absent from lowland rivers, but perhaps *Ranunculus* provides a comparable level of habitat complexity.

These results are consistent with findings on other river systems that highlight the importance of mixed water velocities for juvenile salmonids, which promote energy-efficient foraging (Morantz, *et al.*, 1987; McCormick & Harrison, 2011). Velocity heterogeneity influenced trout density in all years (including 2016), suggesting that it could be an important habitat requirement, irrespective of conspecific density. However, salmon densities were not influenced by heterogeneity in velocity, and perhaps instead utilise the structure and prey resources of *Ranunculus* in lowland rivers. Additionally, as trout can be more active predators than salmon (Bardonnet &

Bagliniere, 2000), they might be more likely to use different velocities whilst foraging.

Certain habitat variables associated with juvenile salmonid densities (Heggenes, 1990) were not important in this study, suggesting that their relative influence differs between lowland rivers and other river types. For example, deeper water and in-stream cover are thought to be essential for juvenile trout (Milner, 1982; Gries & Juanes, 1998; Heggenes, *et al*., 1999), yet neither water depth nor *Ranunculus* cover was associated with higher trout densities. Large substrates act as important velocity refuges (Cunjak, 1988) and increase habitat heterogeneity (Venter *et al.,* 2008). Lowland rivers, however, lack coarse substrate and sediment is generally finer than in other river systems (Armstrong *et al.,* 2003). In the absence of coarse substrate, the ability of *Ranunculus* beds to slow water through hydraulic drag within the plant stands (Franklin, Dunbar & Whitehead, 2008), might enhance velocity heterogeneity in lowland rivers and, therefore indirectly influence trout densities. Neither salmon nor trout densities were influenced by fast water velocities in this study, which contrasts with suggestions that juvenile salmon use faster flowing water, and juvenile trout use slower flowing water (Riley *et al.,* 2006; McCormick & Harrison 2011). The lack of influence of these measures of water velocity and depth on either species suggests opportunistic habitat use based on available habitats, which may occur more readily in rivers with fewer multi-cohort assemblages (Maki-Petays *et al*., 1997).

Macroinvertebrate prey abundance was not important in describing observed densities of either fish species. Riley *et al.,* (2009) suggested that habitat that offers refuge might be more imperative than prey resource, as densities of juvenile salmon and trout responded to increases in aquatic and marginal vegetation, rather than increases in macroinvertebrate biomass. Alternatively, the measure of macroinvertebrate prey availability that I used might not have been representative, perhaps because the benthic sampling under-represented prey accessible to drift-feeding salmonids (McCormick & Harrison, 2011). Although not directly quantified in this study, competitors and predators could also influence the density of juvenile salmonids. While some studies report that competition affects habitat use of juvenile salmonids, particularly interspecific competition between salmon and trout (Bardonnet & Bagliniere, 2000), others suggest these species have different niches (Davidson *et al*., 2010). Density-dependence effects on juvenile salmonids are thought be most influential within the first three months post-redd emergence, as juveniles establish feeding territories (Pender & Kwak, 2002). The timing of this study sampling, approximately five-six months post-emergence, is likely to have recorded density-habitat relationships that have developed after an earlier phase of intraspecific competition. This study also assumed that summer habitat associated with higher densities of juvenile salmonids allows for predator avoidance. If predation caused high mortality at a particular site, there would be lower juvenile densities present and the findings from that site would indicate habitat unsuitable to support high juvenile density.

In conclusion, this study (i) describes summer habitat characteristics that promote high densities of juvenile salmon and trout in lowland chalk streams, (ii) highlights how juvenile salmonid density-habitat relationships may be context-specific and dynamic associations, and (iii) demonstrates the potential of previously unexplored habitat characteristics, velocity heterogeneity and salmon redds, to better describe juvenile salmonid densities. Both an unexpected recruitment crash during this study and the importance of proximity to redds further demonstrate the need to consider the influence of recruitment to habitat patches when exploring species-habitat associations, to avoid misrepresenting the importance of habitat characteristics. Most importantly, this finding, together with the strong influence of distance upstream, stresses the importance of the spatial configuration of habitats for different life stages. This conclusion is pertinent to the conservation of the fish populations studied here, and more widely. Finally, *Ranunculus* appears to be a key habitat characteristic for juvenile salmonids, whether acting directly or indirectly to influence their densities, and these findings are likely to be applicable to other low-energy lowland salmonid streams where *Ranunculus* play a pivotal role in structuring aquatic habitats. Its role should be studied further to ascertain the mechanisms driving the observed relationships, and its potential as a conservation tool for lowland salmonid populations.

Chapter 3: Take cover! Higher summer *Ranunculus* cover supports more, better-growing salmonids

3.1 Abstract

Habitat complexity creates physical river conditions that provide, for example, energy-efficient foraging, abundant prey resources and structures for refuge, and therefore suitable habitat for juvenile salmonids. In upland rivers, large structures, such as boulders and woody debris, create heterogenous habitats but these structures are absent from low-energy, lowland rivers. It has been hypothesised that macrophytes create habitat complexity in lowland rivers, and thereby influence juvenile salmonid populations, however there is a paucity of empirical evidence supporting this theory. I performed a novel spatially- and temporally- replicated in-river *Ranunculus* manipulation experiment, to test the influence of this dominant lowland river macrophyte, on abundance, site fidelity and growth rates of juvenile Atlantic salmon and brown trout. Through planting and removing existing *Ranunculus* plant stands in nine sites (20 m in length), I achieved a *Ranunculus* cover gradient throughout a two-year experimental period. Both juvenile salmon and trout abundances were highest in high *Ranunculus* cover throughout summer. By monitoring the salmonid populations throughout summer and autumn months, I identified the beginning of summer as a period of key influence of *Ranunculus* cover on abundance, site fidelity, and individual body size growth in juvenile salmon. Additionally, no other habitat characteristic (water depths, velocity and prey biomass) outperformed *Ranunculus* cover at explaining the variation in any of the salmonid responses. These findings can help prioritise conservation efforts for at-risk salmonid populations by ensuring healthy macrophyte communities during summer.

3.2 Introduction

Habitat heterogeneity is known to enhance coexistence across many taxa (MacArthur & MacArthur, 1961, Tews *et al.,* 2004). Environments with a range of habitats provide different niches (Tews *et al.,* 2004), enhance productivity (Hall *et al.,* 2018), and positively influence somatic growth rates (Quinn & Peterson, 1996). Consequently, safeguarding habitat complexity has become a central concept in conservation of freshwater and marine ecosystems (Kovalenko, Thomaz & Warfe, 2012). Aquatic macrophytes often support abundant and diverse aquatic communities (Warfe & Barmuta, 2006) and are considered drivers of structural complexity, particularly in standing waters (Diehl, 1992).

Macrophytes can influence habitat conditions predominately by interacting with water flow. Flow resistance by macrophytes slows velocities within and behind the plant stands, providing a flow refuge for fauna, retaining organic matter and increasing water depths (Sand-Jensen, 1998; Gurnell *et al.,* 2006; Wharton *et al.,* 2006). Water flow around the plant stands increases (Sand-Jensen & Mebus, 1996; Gurnell *et al.,* 2006), thus adjacent patches of heterogeneous velocities are formed. Complex structural architecture of the plants themselves can provide more surface area for attachment, and interstitial space for predator avoidance (Diehl & Kornijow, 1998; Warfe & Barmuta, 2006). Macrophytes, therefore, influence aquatic communities via multiple pathways, and might be essential to provide habitat complexity in low-energy lowland rivers, which typically lack substantial substrate (Berrie 1992).

Salmonids are ecologically, culturally and economically important fishes throughout their entire geographic range (Elliott, 1994; Peirson *et al.,* 2001). However, wild populations of anadromous salmonids, such as Atlantic salmon (*Salmo salar*), have declined over the last few decades (ICES, 2018), due to increased threats in both the freshwater and marine ecosystems (Chaput, 2012; Reid *et al.,* 2018). Some freshwater populations of juvenile salmon have recently been declining in both number and individual body size (Gregory *et al.,* 2017; ICES, 2018). This could render salmon more susceptible to elevated threats in the marine environment, reducing the likelihood of individuals returning to fresh water to spawn (Gregory *et al.,* 2019). Considerable research effort has been dedicated to understanding habitat use of salmonids in freshwater ecosystems in recent years, in a bid to inform effective habitat management and safeguard at-risk salmonid populations. This body of work has shown that habitat complexity is important for juvenile salmonid productivity (Hall *et al.,* 2018), over-winter survival (Quinn & Peterson, 2011), and densities and territory size (Venter *et al.,* 2008). However, much of this research has focused on high-energy, upland rivers, and the role of large substrates, such as tree roots, boulders and large woody debris (Morantz *et al.,* 1987; Venter *et al.,* 2008). In contrast, very little is known about the role of habitat heterogeneity in lowland rivers that are physically more stable and lack large substrates. Aquatic macrophytes may provide key structural complexity in these lowland rivers (Berrie, 1992; Warfe & Barmuta, 2006), particularly during the summer months of the highest salmonid growth and peak in macrophyte biomass.

Juvenile salmonids feed and grow during the productive summer months, before facing high over-winter mortality caused by low prey availability and unfavourable abiotic conditions (Wankowski & Thorpe, 1979; Armstrong *et al.,* 2003; McCormick & Harrison, 2011), and larger individuals are more likely to survive over winter than smaller conspecifics (Quinn & Peterson, 2002). The presence and abundance of dominant macrophytes in lowland rivers has been positively associated with summer densities of juvenile salmon (Chapter 2), although the mechanisms governing this relationship remain unclear. Juvenile trout can be found in areas with high cover of aquatic vegetation (Maki-Petays *et al.*, 1997), and in areas of high velocity heterogeneity (Chapter 2) during summer months, which could represent an indirect effect of macrophytes on juvenile trout, through the influence of macrophytes on flow dynamics. In lowland rivers, macrophytes can provide refuges from predators, as well as visual isolation from competitors (Imre *et al.*, 2002; McCormick & Harrison, 2011). Furthermore, the structural complexity of the macrophytes might create habitat patches with different water depths and velocities, to allow sympatric species such as salmon and trout to coexist, as well as supporting high abundances of macroinvertebrate prey (McCormick & Harrison, 2011). Dominant macrophytes in lowland rivers, such as *Ranunculus* (subgenus *Bactrium,* hereafter *Ranunculus*), could therefore provide essential summer habitat for viable populations of juvenile salmonids.

To understand the role of *Ranunculus* cover in supporting juvenile salmonid populations in lowland rivers, I performed a spatially-and-temporally replicated in-river *Ranunculus* manipulation experiment. To my knowledge, this is the first study to experimentally manipulate macrophytes to demonstrate their importance as habitat for salmonids. I tested the influence of *Ranunculus* cover on abundances of juvenile salmon and trout populations across an experimentally induced gradient of *Ranunculus* cover. I also tested whether the amount of *Ranunculus* cover influenced the site retention rate of juvenile salmonids, and if so, whether the consequences of remaining in a particular amount of *Ranunculus* cover were positive or negative for individual growth rates. To further ascertain the importance of *Ranunculus*, I also compared the relative importance of *Ranunculus* cover to other habitat variables pertaining to water depth, velocity, and prey availability. I tested the following hypotheses:

1. There are higher juvenile fish abundances, a higher site retention rate, and greater individual growth rates in sites with higher *Ranunculus* cover.
2. The positive impacts of *Ranunculus* cover on all fish response variables diminish with the onset of *Ranunculus* senescence in autumn, and so the influence of *Ranunculus* cover changes over time.
3. Where *Ranunculus* cover was found to influence a fish response, it explains more variation in the fish data relative to other habitat characteristics of water depth, velocity, and prey availability.

3.3 Methods

3.3.1 Study location and experimental design

I imposed the *Ranunculus* manipulation experiment over two years (2016-17) in the North stream, a carrier of the lowland river Frome, Dorset, UK (Figure 3.1). This river section has abundant *Ranunculus* beds and supports high densities of juvenile Atlantic salmon and brown trout, whilst the physical habitat characteristics are homogenous relative to the main river, allowing experimental treatments to be replicated across the similar environmental conditions. Three spatial blocks, approximately 100 m in length and with mean channel width of 7.1 m (±0.3 SE), were selected in locations with the highest similarity of habitat. Within each block, the experimental treatments were applied to three sites, 20 m in length, that lacked riparian cover but had natural *Ranunculus* beds (mean site cover ranged from 5 – 32 %).

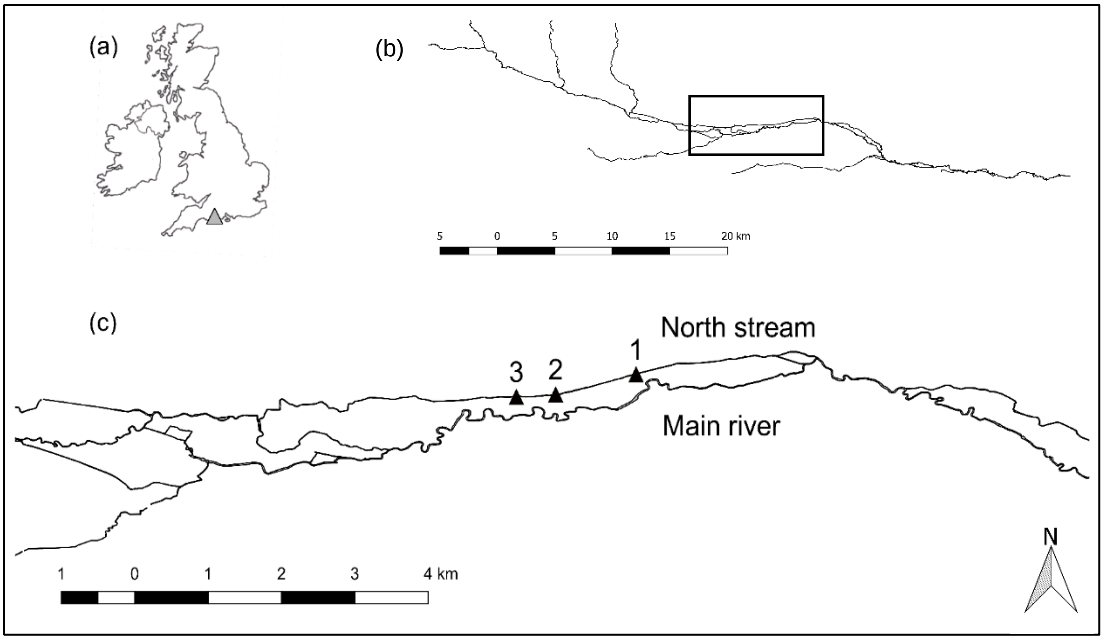


Figure 3.1. Study location. (a) location of the river Frome in Dorset, UK; (b) location of experiment in the river Frome catchment; (c) location of the three experimental blocks on the North stream (3 most upstream – 1 most downstream).

(a) 

(b) 

Figure 3.2. Post-manipulation river sites in March 2016 in (a) a high *Ranunculus* cover treatment level, and (b) a low *Ranunculus* cover treatment level.

To achieve a gradient of *Ranunculus* cover, three levels of *Ranunculus* treatment manipulation, low (<10 %), medium (30-40 %) and high (>60 %) cover, were assigned to the sites within each block using a Latin square design (Bradley, 1958, Figures 3.2 - 3.3). There was no difference in mean *Ranunculus* cover between sites of differently assigned treatments prior to the initial *Ranunculus* manipulation in 2016 (one-way ANOVA: $F_{2, 6} = 0.174$, $p = 0.844$). I imposed the treatment manipulation at the beginning of spring (March/April) each year when the *Ranunculus* plant beds were recovering from the winter period. To achieve the target percentage cover of each treatment level, some *Ranunculus* plant stands were removed, by digging out plants and roots with the minimum disturbance possible. These plants were re-planted into the sites with natural *Ranunculus* cover lower than the required treatment level, and their roots were covered with existing bed sediments. Buffer strips of 5 m on either side of the site were created by cutting existing *Ranunculus* stands back, to minimise any edge effects of adjacent habitat on the experimental sites (Figure 3.3). Treatment levels were maintained over the course of the experiment until the natural plant senescence at the end of summer. At sites that did not require plant maintenance, I simulated maintenance disturbance by walking through the sites and disturbing sediment.

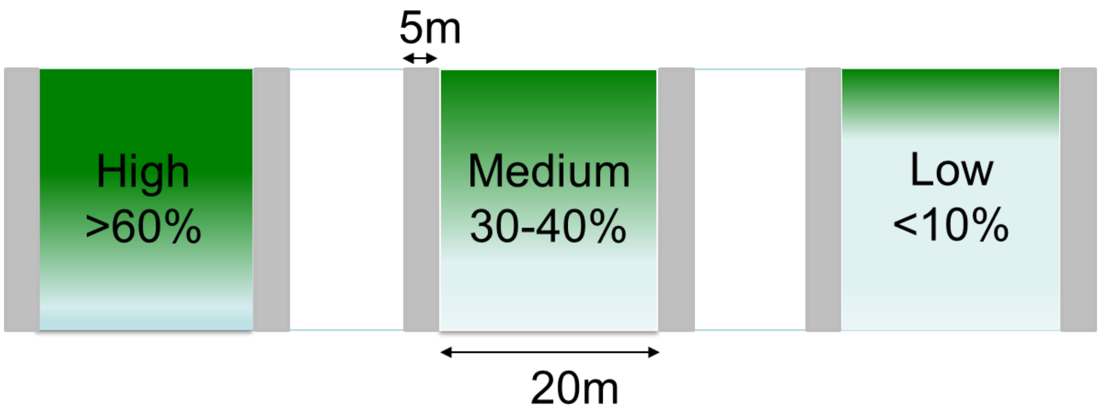


Figure 3.3. Schematic of an experimental block with three sites (20 m in length) of different assigned *Ranunculus* cover treatments (high, medium, low) and the associated desired amount of cover. Grey strips either side of the site represent the buffer strips (5 m in length).

3.3.2 Sampling methods and data preparation

Ranunculus and habitat variables

To determine the effect of the treatment manipulation on *Ranunculus* cover throughout the duration of the experiment, I monitored *Ranunculus* cover at 25 quadrats per site every six weeks from the initial manipulation in March 2016, until December 2017. Quadrats (0.5 x 0.5 m) were evenly spaced across five evenly spaced transects spanning the stream channel wetted width. Percentage cover of *Ranunculus* cover was estimated in each quadrat. All other explanatory variables, including key habitat characteristics, macroinvertebrate biomass and composition, and fish responses were monitored at six-week intervals during late summer to autumn of each year coincident with the four occasions when *Ranunculus* cover was determined between June - October. Wetted channel width (m) was measured at each transect, averaged at the site, and multiplied by site length (20 m) to calculate site area. Site area was subsequently used in the fish abundance analysis (see Section 3.3.3 *Effect of Ranunculus cover on salmonids*). To determine the importance of habitat variables relative to that of *Ranunculus* cover, at each quadrat water depth was measured (cm), and water surface velocity was estimated visually as one of five categories [1 = 0-25 cm s^{-1}; 2 = 25-50 cm s^{-1}; 3 = 50-75 cm s^{-1}; 4 = 75-100 cm s^{-1}; 5 >100 cm s^{-1}]. I calculated the site-level proportion of fast velocities as the proportion of velocity categories 3, 4 and 5 recorded in quadrats at a site. The steepness in velocity gradients between a quadrat and its neighbouring quadrats was calculated using the Terrain Ruggedness Index (TRI, Wilson *et al.,* 2007, see Section 2.3.2 for TRI equation). Absolute values of TRI were averaged to represent site-level velocity heterogeneity.

Macroinvertebrate prey biomass

To determine available prey biomass, aquatic macroinvertebrates were sampled from benthic substrates at three random locations within each site on the four sampling occasions during the fishing period. Samples were collected using a Surber sampler (0.25 m x 0.25 m, mesh aperture 250 μm), where the substrate was disturbed by hand for 30 seconds. Samples were preserved in 70 % ethanol solution for sorting, identification and body size measurements. All macroinvertebrate specimens were identified to the lowest taxonomic resolution possible (usually species), except Oligochaeta (sub-class), Hydrachnidae (family), Simuliidae (family) and Chironomidae (tribe), and counted to determine total abundances per sample. I also measured either the body length, head width or the largest body dimension of up to 30 randomly selected individuals of each taxon and used published length-mass relationships (Table S3.1) to estimate the mean biomass of each taxon. I then multiplied the mean biomass by the abundance of each taxa to estimate a total biomass of each taxon per sample. The biomass of all taxon was summed to generate the total macroinvertebrate biomass of each sample, and I averaged across the three samples per site to estimate mean macroinvertebrate biomass. I adapted the mean macroinvertebrate biomass measure to represent biomass of frequently consumed aquatic prey. This was considered a more informative measure of prey availability, as benthic Surber samples can sometimes misrepresent prey taxa available to juvenile salmonids (Poff and Huryn, 1998). I used frequently consumed prey taxa identified in the diets of salmon and trout in this river (see Section 2.3.2 for full details on identifying frequently consumed prey). I then subset the mean macroinvertebrate biomass measure for each fish species to include only these taxa, and produced a variable of *prey biomass*.

Fish abundance, retention rates and growth

To determine 0+ juvenile salmon and trout abundance and biometrics I electro-fished each experimental site on the four sampling occasions during the fishing period each year. Fishing took place three days after each habitat survey and macroinvertebrate sampling to allow fish populations to recover from the disturbance as well as to minimize the effect of the habitat damage. To maximise capture efficiency, stop nets were set at the downstream and upstream limits of the site, thus preventing fish migrating in and out of the site during fishing. Details of the equipment and settings used for electrofishing are given in section 2.3.1 *Study sites and sampling*. I electro-fished in an upstream direction, capturing and removing all individuals encountered, known as an electro-fishing *pass*. Sites were fished repeatedly until two consecutive passes yielded zero salmonid captures, indicating that all catchable salmonids present in the site had been removed. After each pass, salmon and trout were identified and the abundance of each species caught at each site were recorded. Each individual was sedated, measured (fork length, to nearest mm), and marked with a PIT tag (12.5 mm length, 2.12 mm diameter; Biomark, Idaho, USA). I inserted the

PIT tag into the body cavity and clipped the adipose fin as an external identification of capture. Fish smaller than 60 mm in length were not tagged to avoid detrimental effects on growth or survival (Richard *et al.,* 2013). On recapture, PIT tag codes were read at the time of processing using a handheld reader (Biomark HPR plus) to identify individuals. After processing, fish were transferred to a holding bin filled with cold, aerated river water, and released back into the site of capture once all fishing passes had been completed. All procedures were carried out by licenced personnel under a UK Home Office A(SP)A licence (PPL 30/3277).

An unusually wet and warm winter over the 2015/16 spawning season resulted in poor recruitment of juvenile salmonids on a national scale, including on the river Frome (ICES, 2017, Chapter 2). Indeed, fishing in June 2016 returned low numbers or no juveniles across all sites in blocks 2 and 3. To augment low salmon captures, in July 2016 I electro-fished and caught 300 juvenile salmon in nearby sections of the main river, mostly in the section that runs parallel to the north stream study site (Figure 3.1). Fifty salmon were translocated in aerated holding tanks into each site in blocks 2 and 3. I used June fish data in calculations of site retention rate and growth rates of recaptured individuals, but excluded these June abundance data from all other analyses. In total, throughout the study, 803 juvenile salmon with mean length 86.1 mm (range: 60 – 124 mm), and 391 juvenile trout with mean length 90.6 mm (range: 60 – 133 mm), were captured.

Tagged individuals that were caught in the same site in at least two consecutive sampling occasions were defined as recaptures and assumed to have been exposed to the site-specific *Ranunculus* cover for the period between sample occasions (approximately six weeks). In June of both years, some fish were caught that were too small to be tagged (fork length <60 mm), therefore I acknowledge the potential bias of fish tagged in June and re-caught in August to represent larger individuals in the population. I also consider that larger individuals may be more dominant, which could influence an individual's ability to hold a territory and thus, our measure of site retention rate. However, there was no difference between treatments of the proportion of untagged (smaller fish) to tagged (larger fish) individuals in June (Linear model, $F_{2, 11} = 0.39$, $p = 0.69$), so any effect of this bias should be consistent across all treatment levels. For growth rate analyses, as the majority of fish were only recaptured once, I subset the recapture data to only include fish at the time of their *initial capture* and their *first recapture*. *Initial captures* ($t - 1$) could include the sample occasions in June, August and September, and *first recaptures* (t) could include the sample occasions in August, September or October. I expected that the initial size of the individual could influence their growth rate as given the same amount of resources, a smaller individual has the potential to grow more relative to a larger individual. I accounted for this influence of initial body size by calculating the relative growth rate of individuals, $((L_r - L_c)/L_c) \times 100$, where L_r and L_c were the fork length of an individual at first *recapture*, and initial *capture*, respectively. Multiplying the calculation by 100 gave the percentage increase in length from the initial size.

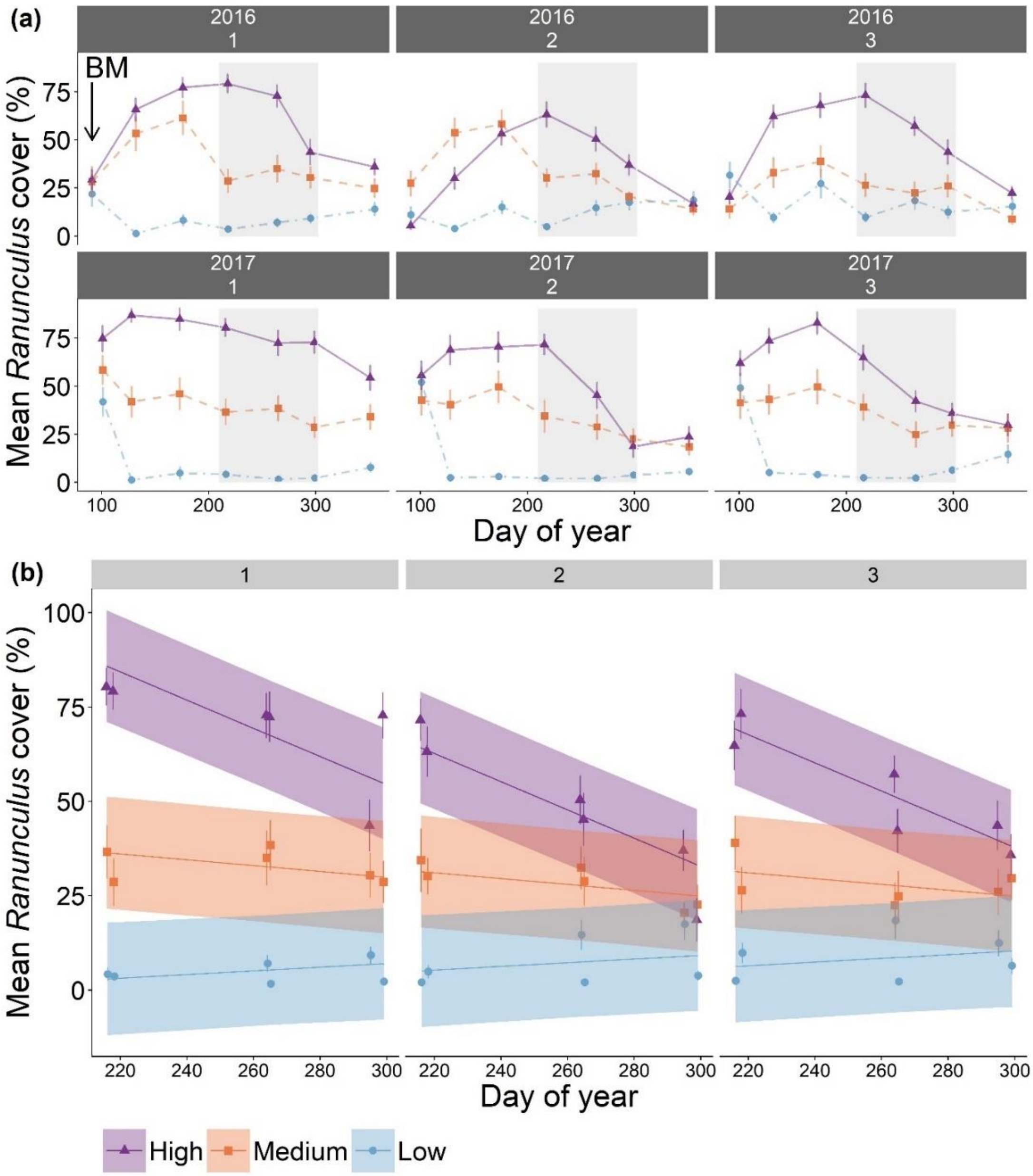


Figure 3.4. Mean observed *Ranunculus* cover in ▲ High, ■ Medium, and ● Low treatment levels, (vertical lines around the mean show the standard error) during (a) all sample occasions (*n* = 3,150), including before manipulation. Rows of plot indicate each year (2016 & 2017), and columns illustrate individual blocks (1-3), shaded grey area highlights the fishing period (August-October), BM = before manipulation, and (b) the fishing period (*n* = 1,350) with predicted *Ranunculus* cover overlaid in transparent ribbons (solid line is the mean predicted value, shaded area is the lower and upper 95% confidence intervals), columns illustrate individual blocks (1-3). Predicted *Ranunculus* is taken from the linear mixed effects model describing *Ranunculus* cover during the fishing periods (Model R1).

3.3.3 Statistical Analyses

Effectiveness of experimental manipulation

First, I aimed to determine if the experimental manipulation treatment resulted in measurable and sustained differences in all three levels (high, medium and low) of *Ranunculus* cover. Using quadrat-level *Ranunculus* cover measurements from sample occasions during the fishing period (n = 1,350), I constructed a linear mixed effects model to describe the observed *Ranunculus* cover as a function of variables that represented the experimental design (*block, treatment*, *year* and *day of year*). The experiment included periods of natural *Ranunculus* growth and senescence, which resulted in dynamic changes to *Ranunculus* cover through both years (Figure 3.4). Consequently, I tested the interaction between *treatment* and *day of year* to capture changes in *Ranunculus* cover through time. I included a quadrat nested in site random effect structure to account for multiple quadrat measures taken within sites, and at the same sites over time. To determine whether there was any difference in the treatment replicates between each experimental block, I constructed a linear model to describe the variation in observed *Ranunculus* cover as a function of the main effects of *block* and *treatment* and their interaction. The *Ranunculus* manipulation was successful and achieved a gradient of cover throughout time with which to test the influence of *Ranunculus* on juvenile salmonid response variables, although I note that this gradient diminished with the natural senescence of *Ranunculus* in autumn (Figure 3.4a). The fixed effects explained 40% (R_C^2 = 55%) of the variation in *Ranunculus* cover during the fishing period (August – October) and all parameters were statistically important, with the exception of the main effects of *block* and *year* (Table 3.1a). There was a strong, positive effect of the medium and high treatments on *Ranunculus* cover relative to the low treatment, and *Ranunculus* cover in high treatments appeared to decline most over time relative to low or medium treatments (Figure 3.4b). There was significant *block x treatment* interaction (Table 3.1b), which appeared to be driven by *Ranunculus* cover being on average lower in the high treatment sites of blocks 2 and 3, relative to block 1, highlighting the among-replicate variation in the manipulated variable (Figure 3.4b). Having confirmed the effectiveness of the manipulation, I then used *Ranunculus* cover as a continuous explanatory variable for all subsequent analyses. Using direct measurements of *Ranunculus* cover in the analysis instead of the three categorical levels can reduce a chance of obtaining spurious results as there was variation in the data among replicates (Damgaard, *et al.*, 2018).

Table 3.1. Effects of the experimental manipulation on *Ranunculus* cover during the fishing period (August to September) in both years (n = 1,350). Summary statistics for, a) the linear mixed effects model describing *Ranunculus* cover, and b) the linear model testing for an effect of a *block* x *treatment* interaction on achieved *Ranunculus* cover between the experimental replicates.

Model Parameter	*Sum Squares*	*Mean Squares*	*Df*	*F value*	*Pr(>F)*
a)					
Treatment	73854	36927	2	68.2	<0.01
Day of year	25811	25811	1	47.7	<0.01
Block	1208	604	2	1.1	0.42
Year	1262	1262	1	2.3	0.13
Treatment x Day of year	45662	22831	2	42.2	<0.01
b)	16274	8137	2	390.9	<0.01
Block	563937	281969	2	11.3	<0.01
Treatment	29169	7292	4	10.1	<0.01
Block x Treatment					

Effect of Ranunculus cover on salmonids

Salmonid abundance (a count producing integers, including zeros), site retention rate (a rate derived from counts, including zeros), and growth rate (a measure derived from measurements, including zeros) were each modelled assuming appropriate and different error structures, and separate models were constructed for each fish species. Salmonid abundance (n = 54) was described as a function of the explanatory variables outlined below using a negative binomial regression (log-link function) to account for overdispersion in the abundance data, which might otherwise introduce heteroscedasticity in the regression residuals, violating the homoscedasticity assumption of a Poisson regression, or indeed a linear regression on *a priori* calculated (possibly log-transformed) salmonid density (O'Hara & Kotze, 2010; Warton, Wright & Wang, 2011). To account for variation in abundance due to differences in habitat size, log site area (m^2) was included in the model as an offset (O'Hara & Kotze, 2010). This effectively models salmonid abundance per unit site area and does not introduce any additional parameters (Kery & Royle, 2016). Although there were differences in site areas, reassuringly, there was no difference in site area between the treatment levels (Linear model: $F_{2, 51} = 0.97$, $p = 0.38$), that might have confounded a response in salmonid abundance to *Ranunculus* cover had I not included an offset of site area. I also down-weighted occasions when no salmonids were captured (n = 4/54) because zero captures do not contribute to estimating the effect of the explanatory variables on abundance. Data were weighted by vector w whereby

$$w = \begin{cases} 0, & y = 0 \\ 1, & y > 0 \end{cases}\text{'}$$

which effectively removes zero captures from the estimation of effects of explanatory variables on response variable *y*. Site retention rate (*n* = 54) was modelled as a rate based on the numbers of tagged individuals at time *t-1* (June, August, September) that were recaptured in the same site at time *t* (August, September, October) in a binomial regression (logit-link) to ensure the expected rate was bounded between 0 and 1, as a function of explanatory variables outlined below. I used this approach rather than calculating rates directly from the data because some sites had zero fish at time *t*-1, which would have resulted in data loss because it is not possible to divide by zero. I down-weighted occasions with few tagged individuals in time *t-1*, by the number of fish caught in time *t-1*, because there were fewer fish to accurately estimate the site retention rate. For example, if two fish were caught in Site 1, and 25 fish were caught in Site 2, these data would be weighted by 2 and 25, respectively. Growth rates of recaptured salmon (*n* = 173) and trout (*n* = 85), were described in a linear mixed effect model as a function of the explanatory variables outlined below.

Model development

Block was the experimental replicate and treating it as a random factor would have allowed generalisations beyond the specific blocks measured for this experiment. However, observations of salmon abundance in block 1 differed greatly from blocks 2 and 3, which were very similar. Consequently, I treated *block* as a fixed factor to capture this difference in salmonid abundance. It might have been desirable to include a site random effect to account for site-specific differences in measurements taken through time. However, this was not possible where response variables were measured at the site level because there was only one site – and therefore only one salmonid abundance measure - for each treatment within a block, i.e. the estimation of the site-specific effect would have been confounded with the site-specific abundance measure. Instead, I tested for the relative importance of the habitat variables (water depth, water velocity and prey biomass) to explore whether site-specific differences in other measurable variables were effective at explaining salmonid responses.

To test for an effect of the experimental manipulation on the salmonid abundance, I included main effects of *Ranunculus cover, month*, *block* and *year* and an interaction between *Ranunculus cover* and *month.* The same main effects were included in the models for site retention rate and growth rate, with *period* replacing *month* to represent the period of time between the fish being first captured and recaptured. *Ranunculus cover* was averaged across the periods (i.e. June to August) to represent mean site-level cover for the duration of the period. As body size measurements were taken from multiple recaptured individuals at each site, I had sufficient data, i.e. more than one measurement per site, to include a random effect of *site* in this analysis to account for any variation in growth rates that could be caused by site-specific differences.

To test whether *Ranunculus* cover explained more variation in salmonid abundance, site retention rate and growth rate than other habitat variables, I simplified the initial model for each response to include only statistically significant parameters. Using these simplified models, I included additional main effects of *water depth, proportion of fast velocities*, *velocity heterogeneity* and *prey biomass*, both with and without the *Ranunculus* main effects and interactions to test for the relative importance of the key habitat variables. To represent habitat characteristics during periods for the site retention rate and growth rate analyses, I averaged site-level measures of the habitat variables across the periods. All nine candidate models were compared for each response with AIC model selection, and the best (and most parsimonious) fit model was selected based on the smallest AIC value (Burnham & Anderson, 2002).

Prior to model fitting, I used Pearson's correlation to examine all explanatory variables for collinearity. I found that no pairs were highly correlated ($r \geq |0.6|$, Dormann *et al.,* 2013, Figures S3.1 – S3.2). To compare the effects of variables measured at different scales, proportional explanatory variables were arcsine transformed according to $(asin(x/100) \times 2/\pi)$, where x is the explanatory variable, and then standardised by dividing by their standard deviation. All numerical explanatory variables were standardised prior to analyses by subtracting their mean and dividing by their standard deviation. All statistical analyses were performed in R version 3.4.4 (R Development Core Team, 2018), using packages lmerTest (Kuznetsova, Brockhoff & Christensen, 2017) and MASS (Venables & Ripley, 2002). Model performance and goodness of fit statistics were produced using packages MuMin (Barton, 2009), pscl (Jackman 2017). Model residuals were inspected to check assumptions of homogeneity, normality and independence.

3.4 Results

3.4.1 Salmonid abundance

Salmon

Salmon abundance was significantly influenced by *Ranunculus cover*, and this positive influence did not change over time (Table 3.2a). The model explained over 75% of the variation in salmon abundance (R^2_{ML} = 0.77). Marginal effects plots (Figure 3.5) showed that salmon abundances were positively influenced by

Ranunculus cover for most of the fishing period, though the strength of the effect differed (Figure 3.5a). Salmon abundances were strongly positively related to *Ranunculus cover* in August, but this effect weakened in September. By the end of the fishing period, in October, there was little effect of *Ranunculus cover* on salmon abundance (Figure 3.5a). This corresponds with the decline in *Ranunculus* cover over time, especially in sites with high and medium manipulation levels, which resulted in similar levels of *Ranunculus* cover observed across most sites by the end of the fishing period (Figure 3.4b). This pattern also corresponded with a decline in salmon abundances over time. Salmon abundances differed among blocks (Table 3.2a), with higher abundances reported in block 1 relative to blocks 2 and 3 (Figure 3.5b). There was no effect of *year* on salmon abundance (Table 3.2a, Figure 3.5c).

Table 3.2. Effects of the experimental manipulation on salmon and trout response variables. Parts (a) and (b) show analysis of deviance summaries for the negative binomial regression describing variation in fish abundance, and the binomial regression describing variation in site retention rate, respectively. Part (c) shows the analysis of variance summary for the linear mixed effect model describing growth rate of recaptured individuals.

		Salmon					Trout				
		Df	*Deviance*	*Residual Df*	*Residual deviance*	*Pr(>Chi)*	*Df*	*Deviance*	*Residual Df*	*Residual deviance*	*Pr(>Chi)*
(a)											
Abundance (n = 54)	Ranunculus	1	66.4	48	169.9	<0.01	1	9.3	35	96.7	<0.01
	Month	2	39.2	46	130.7	<0.01	2	8.5	33	89.1	0.01
	Block	2	77.3	44	53.4	<0.01	2	17.7	31	71.4	<0.01
	Year	1	2.1	43	51.3	0.15	1	34.2	30	37.2	<0.01
	Ranunculus x Month	2	3.0	41	48.3	0.22	2	0.4	28	36.9	0.82
(b)											
Site retention rate (n = 54)	Ranunculus	1	98.1	46	1964.7	<0.01	1	3.8	38	432.4	0.05
	Period	2	311.8	44	1652.8	<0.01	2	129.9	36	302.6	<0.01
	Block	2	327.0	42	1325.9	<0.01	2	12.4	34	290.2	<0.01
	Year	1	25.2	41	1300.7	<0.01	1	1.1	33	289.1	0.30
	Ranunculus x Period	2	503.2	39	797.5	<0.01	2	44.6	31	244.5	<0.01
		Df	*Sum sq*	*Mean sq*	*F value*	*Pr(>F)*	*Df*	*Sum sq*	*Mean sq*	*F value*	*Pr(>F)*
(c) Growth rate (Salmon n = 173 Trout n = 85)	Ranunculus	1	60.3	60.3	1.0	0.34	1	1.3	1.3	0.0	0.86
	Period	2	3998.8	1999.4	33.2	<0.01	2	571.4	285.7	7.0	<0.01
	Block	2	56.7	28.3	0.5	0.65	2	263.9	131.9	3.2	0.09
	Year	1	13.0	13.0	0.2	0.64	1	0.3	0.3	0.0	0.93
	Ranunculus x Period	2	927.1	463.6	7.7	<0.01	2	36.2	18.1	0.4	0.64

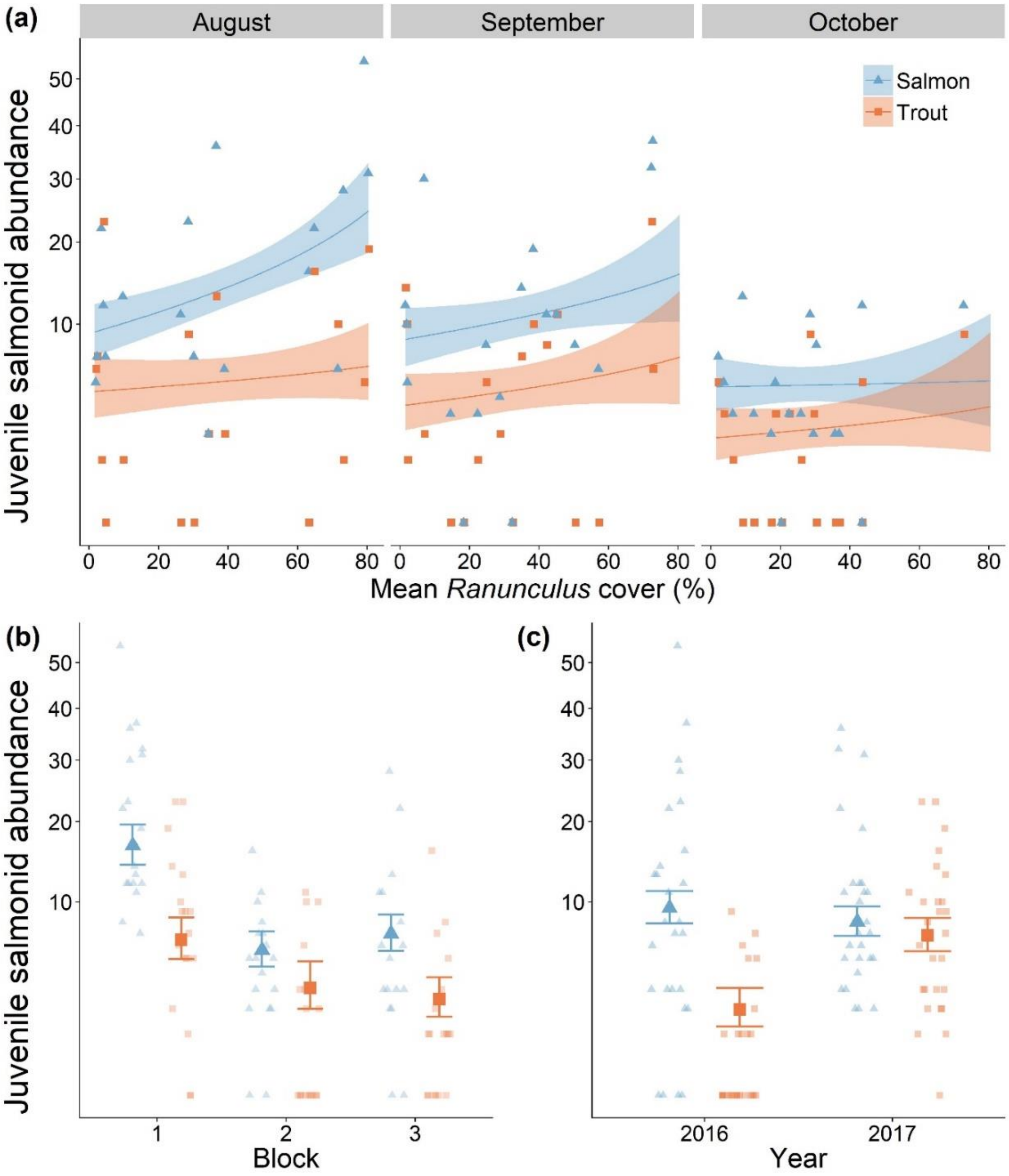


Figure 3.5. Influence of (a) *Ranunculus* cover during different months, (b) block and (c) year on juvenile salmonid abundance. In (a) the solid line is the mean estimate and shaded area denotes the 95% confidence intervals. In (b) and (c) points are the mean estimates and errors bars denote the 95% confidence intervals. On all plots, the smaller triangles and squares show the observed abundance data for each species; these are displayed as jittered points on the discrete x axis. The y axis is on a square-root scale for visual clarity.

Of the nine candidate models testing importance of alternative habitat variables (Table S3.2a), three models were statistically indistinguishable, as the difference in

AIC (ΔAIC) was < 2 (Table 3.3a). The most parsimonious of these models was the original simplified model SA1. The other two best performing models included an additional main effect of *prey biomass* (model SA5), and *velocity heterogeneity* (model SA4), respectively. Visualising the marginal effects of these additional main effects showed salmon abundance to be weakly positively associated with *prey biomass* ($P = 0.05$, Figure S3.5a), and weakly negatively associated with *velocity heterogeneity* ($P = 0.06$, Figure S3.5b).

Trout

Trout abundances were significantly influenced by *Ranunculus cover*, and this positive effect did not change over time (Table 3.2a). Trout abundance declined steadily over time, and abundances were higher in block 1 relative to blocks 2 and 3, and in 2017 relative to 2016 (Table 3.2a, Figure 3.5). The model explained 52% of the variation in trout abundance.

Of the nine alternative habitat variable candidate models (Table S3.3a), three models were statistically indistinguishable, as the difference in AIC (ΔAIC) was < 2 (Table 3.3a). One of these was the original model TA1. The other two best performing models included a main effect of *water depth* instead of *Ranunculus cover* (model TA6), and *velocity heterogeneity* instead of *Ranunculus cover* (model TA8), respectively. Trout abundance was positively associated with *water depth* ($P = 0.04$, Figure S3.6a), and with *velocity heterogeneity* ($P = 0.05$, Figure S3.6b).

Table 3.3. Maximum-likelihood comparison statistics of model fits with *Ranunculus* cover main effects and interactions to alternative habitat variable main effects. Part (a) displays top three negative binomial regression models that best explain variation in juvenile fish abundance. θ = dispersion parameter, R^2_{ML} = maximum likelihood pseudo-R^2. Part (b) displays top three binomial regression models that best explain variation in site retention rate. D^2 = percentage of deviance explained. Part (c) displays top three linear mixed effect regression models that best explain variation in growth rate of salmon between initial capture and first recapture. Mixed effects models also included a random effect of *site*. Table is ordered from the best performing model (model with the lowest AIC) from each analysis.

Mod	**Model terms**	**Model fit**		**Comparison**			**Performance**	
(a)	*Abundance*							
	Salmon (n = 54)	θ	logLik	K	AIC	ΔAIC	R^2_{ML}	
SA5	Ranunc, Month, Block, PreyBiom	19.3	-135.5	6	290.1	0.0	.77	
SA4	Ranunc, Month, Block, VelHet	20.2	-135.7	6	290.6	0.5	.76	
SA1	Ranunc, Month, Block	15.5	-137.3	5	291.1	0.9	.75	
	Trout (n = 54)							
TA6	Block, Month, Year, Depth	11.1	-89.5	6	198.2	0.0	.52	
TA1	Ranunc, Block, Month, Year	10.8	-89.9	6	198.9	0.8	.52	
TA8	Block, Month, Year, VelHet	11.0	-89.9	6	199.0	0.8	.51	
(b)	*Site retention rate*							
	Salmon (n = 54)	Dev	logLik	K	AIC	ΔAIC	D^2	
SR3	Ranunc, Period, Block, Year, Ranunc x Period, VelHet	780.0	-1400.1	9	2825.4	0.0	62.2	
SR2	Ranunc, Period, Block, Year, Ranunc x Period, Depth	785.6	-1403.0	9	2831.0	5.6	61.9	
SR5	Ranunc, Period, Block, Year, Ranunc x Period, PreyBiom	791.1	-1405.7	9	2836.5	11.1	61.9	
	Trout (n = 54)							
TR5	Ranunc, Period, Block, Ranunc x Period, PreyBiom	229.8	-561.0	8	1144.0	0.0	47.3	
TR1	Ranunc, Period, Block, Ranunc x Period	245.2	-568.7	7	1156.5	12.5	43.8	
TR3	Ranunc, Period, Block, Ranunc x Period, VelHet	243.3	-567.7	8	1157.5	13.5	44.2	
(c)	*Growth rate*							
	Salmon (n = 173)	σ	logLik	K	AIC	ΔAIC	R^2_M	R^2_C
SG3	Ranunc, Period, Ranunc x Period, FastVel	7.4	-573.5	6	1166.1	0.0	.64	.68
SG5	Ranunc, Period, Ranunc x Period, VelHet	7.6	-585.3	6	1189.7	23.5	.58	.67
SG2	Ranunc, Period, Ranunc x Period, Depth	7.5	-585.9	6	1190.8	24.7	.52	.72

3.4.2 Site retention rate

Salmon

Site retention rate of juvenile salmon was significantly influenced by *Ranunculus cover* and all other model parameters (Table 3.2b), and the model explained 61% of the total deviance. The strength and direction of the effect of *Ranunculus* cover on site retention rate changed through time (Figure 3.6a). There was a strong, positive effect of *Ranunculus cover* on site retention rate between June-August, when the proportion of salmon remaining in high *Ranunculus* cover sites was more than double that of salmon remaining in low *Ranunculus* cover sites. Between August-September, site retention rate was influenced less by *Ranunculus cover* than the previous period. During September-October, the direction of the effect had reversed, suggesting that site retention rate was higher in low *Ranunculus* cover sites. Site retention was higher in block 1, relative to blocks 2 and 3, and higher in block 2 relative to block 3 (Figure 3.6b), and slightly higher in 2017 compared with 2016 (Figure 3.6c).

Of the nine alternative habitat variable models (Table S3.2b), the best performing model according to AIC model selection was the full model with the additional main effect of *velocity heterogeneity* (model SR3), which explained slightly more deviance than model SR1 (D^2 = 62 %, Table 3.3b). The effect of *velocity heterogeneity* on site retention rate was positive ($P < 0.01$, Figure S3.7), suggesting that salmon were more likely to remain in sites with mixed water velocities.

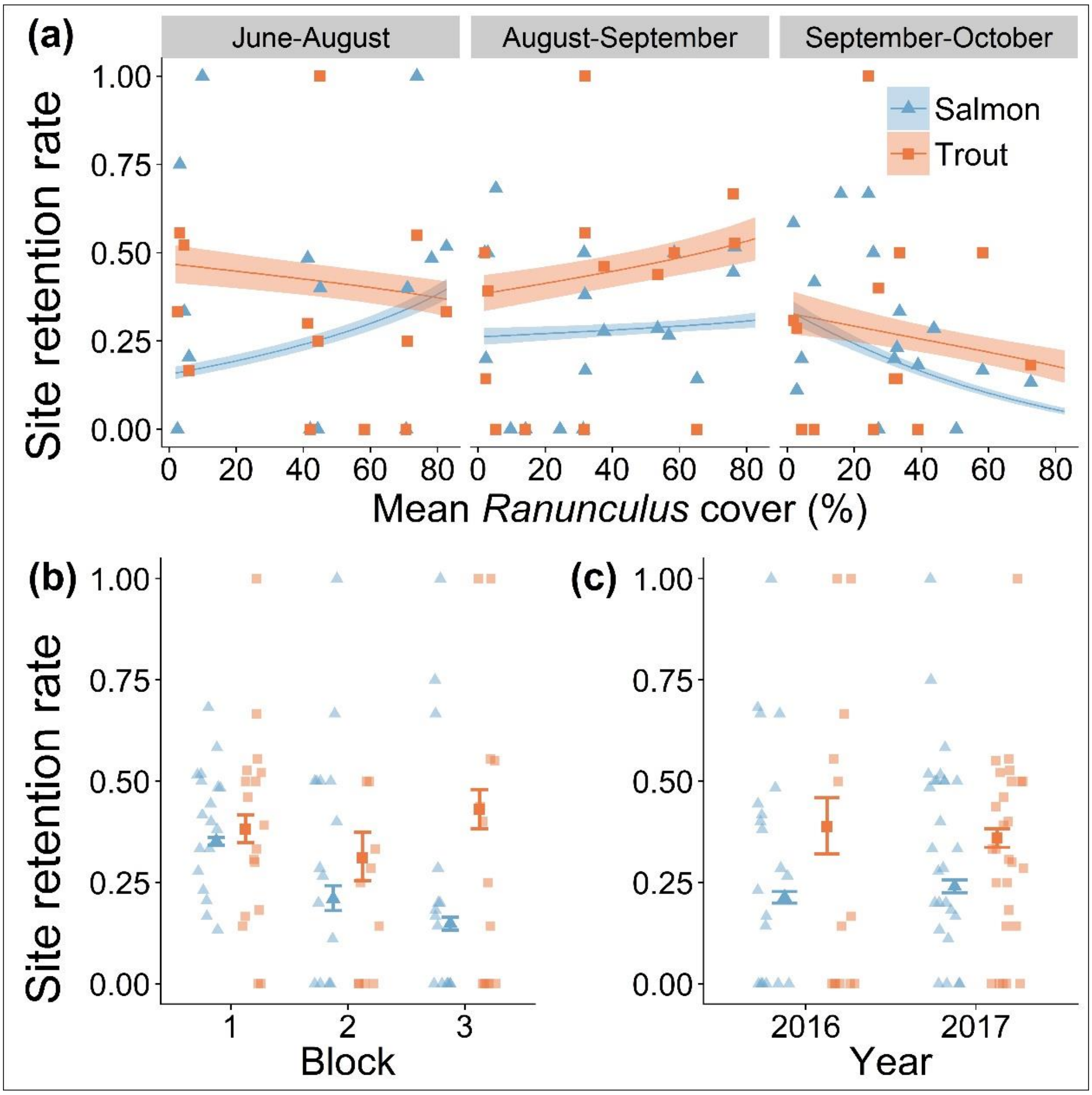


Figure 3.6. Influence of (a) *Ranunculus* cover during different periods, (b) block and (c) year on variation in site retention rate of juvenile salmon and trout (i.e. the proportion of tagged individuals that were recaptured in the same site in the following sample event). In (a), the solid line is the mean estimate and shaded area denotes the 95% confidence intervals. In (b) and (c) points are the mean estimates and errors bars denote the 95% confidence intervals. On all plots the smaller triangles and squares show the observed site retention rate for each species, 20 data points are omitted from each plot where no individuals were tagged at a site in the first sample event. Points are jittered on the discrete x axis.

Trout

Site retention rate of juvenile trout was significantly influenced by *Ranunculus cover* (Table 3.2b), and the model explained 44% of the total deviance. The effect of *Ranunculus cover* differed between periods (Table 3.2b). There was a negative relationship between trout site retention rate and *Ranunculus cover* between June-August, suggesting that trout were more likely to remain in a site with low *Ranunculus* cover (Figure 3.6a). This relationship reversed direction between August-September when the average site retention rate was highest and there was a strong positive influence of *Ranunculus cover*. The lowest site retention rate occurred between September-October, with a weak negative influence of *Ranunculus cover*. Site retention differed between blocks (Table 3.2b), and was highest and lowest in blocks 3, and 2, respectively (Figure 3.6b). Site retention rates did not differ between years (Table 3.2b, Figure 3.6c). Overall, site retention rates appeared to be higher for juvenile trout relative to juvenile salmon (Figure 3.6).

Of the nine alternative habitat variable models (Table S3.3b), the best performing model (TR5) as selected by AIC comparison was the original model, with an additional main effect of *prey biomass*. Model TR5 explained 3% more of the total deviance than model TR1 (Table 3.3b). The influence of *prey biomass* on site retention rate was negative ($P < 0.01$, Figure S3.8), suggesting that trout were less likely to remain in sites with high prey biomass.

3.4.3 Growth rates

Salmon

Salmon growth rates was significantly influenced by *Ranunculus* differently between each *period* (Table 3.2c). The fixed effects of the model explained 58% of the variation in growth rates, and the random effect of *site* explained a further 7% of the variation. There was a positive effect of *Ranunculus cover* between June-August, which reversed direction between August-September, and remained negative between September-October (Figure 3.7a). Overall the change in body size was greatest during the beginning of the fishing period. There was no effect of *block* or *year* on the change in body size (Table 3.2c, Figures 3.7b and c).

Of the nine alternative habitat models (Table S3.2c), the best performing model was the original model with the additional main effect of *proportion of fast velocities* (model SG3, R_M^2 = 64%, Table 3.3c). The effect of *proportion of fast velocities* on the change in body size was positive ($P < 0.01$, Figure S3.9), suggesting that changes in salmon body size were greater in sites with fast velocities.

Trout

Growth rates of recaptured trout individuals were not influenced by *Ranunculus cover*, though did differ over time (Table 3.2c). The significant effect of *period* was driven by lower average growth rates between September-October relative to the previous periods. Growth rates were not influenced by *block* or *year* (Table 3.2c), and the fixed effects of the model explained 36% of the total variation in the response. As neither the main effect nor interaction involving *Ranunculus cover* were important at explaining variation in the growth rates of trout, I did not compare the importance of *Ranunculus* cover relative to alternative habitat characteristics.

No candidate models tested excluding the main effect and/or interactions of *Ranunculus cover* performed better at describing any of the salmon or trout responses according to AIC comparison (Table 3.3). Model residuals did not violate assumptions of homogeneity, normality or independence (Figures S3.3 - S3.4).

3.5 Discussion

This is the first in-field habitat manipulation of naturally occurring macrophytes demonstrating the potential of increased *Ranunculus* cover to support larger populations of both juvenile salmon and trout at the reach scale. By monitoring the salmonid populations throughout summer and autumn months, I have identified when *Ranunculus* cover is most important for fish abundance, site retention rate, and individual body size growth during summer.

Juvenile salmon and trout were more abundant in sites with higher *Ranunculus* cover during the summer and autumn months, suggesting that *Ranunculus* is important habitat for salmonids in lowland rivers. This is consistent with studies where high densities of juvenile salmon (Chapter 2), and trout (Maki-Petays *et al.,* 1997) have been found in rivers with high cover of aquatic vegetation. This positive influence of *Ranunculus* could be driven by directly providing cover, or indirectly by introducing heterogeneity to the physical habitat. Submerged macrophytes increase the structural complexity to provide protection from both aerial and aquatic predators (Diehl & Kornijow, 1998, McCormick & Harrison, 2011), as well as visual isolation from competitors hence creating a higher density of territories (Imre *et al.,* 2002).

There was a steady decline in both salmon and trout populations across all sites during the fishing period. The duration of the experiment is likely to have captured

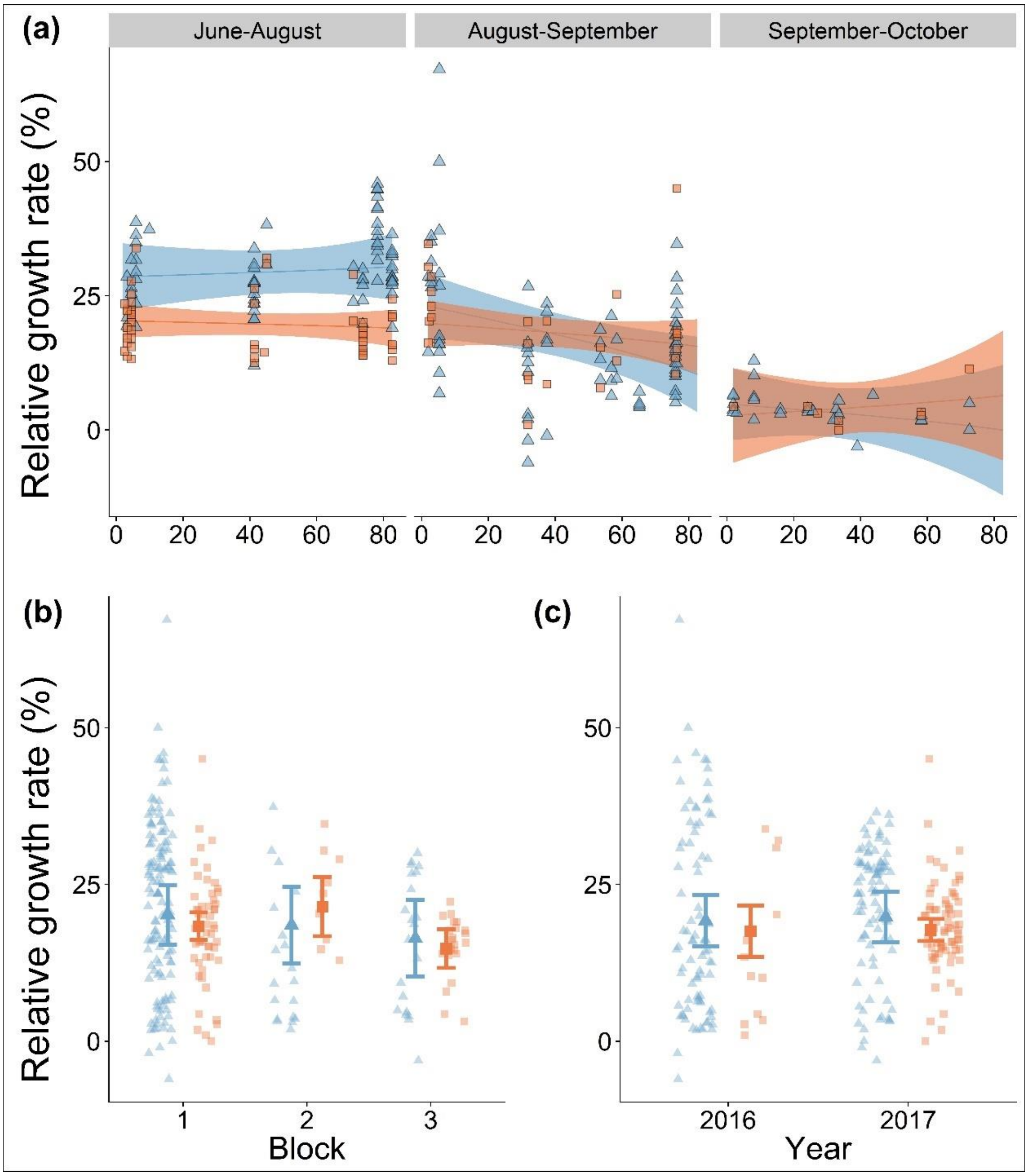


Figure 3.7. The influence of (a) *Ranunculus* cover during different periods, (b) block and (c) year on the relative growth rates of salmon and trout that were recaptured in the same site after six weeks. In panel (a), the solid line is the mean estimate and grey shaded area denotes the 95% confidence interval. In panels (b) and (c) points are the mean estimates and errors bars denote 95% confidence interval. In all plots the solid circles are the observed growth rate, these are jittered where the x axis is discrete.

autumn migration of juvenile salmonids, when a substantial proportion of juveniles move downstream (Ibbotson *et al.*, 2013). Downstream movement of juvenile salmon on the river Frome peaks between October and November (Pinder *et al.*, 2007), which could explain why I caught fewer fish in October. Factors known to trigger movement in the smolt life stage, such as water temperature and time of day, have been found to play no detectable role in this autumn downstream shift (Riley, Eagle, & Ives, 2002), however discharge has been associated with downstream movements (Aarestrup, Birnie-Gauvin & Larsen, 2016). Environmental cues, such as lack of suitable resources in summer habitats to meet energy demands of larger, dominant fish could drive this migration (Huntingford *et al.*, 1992). Supply of in-stream cover has also been suggested as a driver of autumn habitat shifts (Ibbotson, *et al.*, 2013), and the steady decline in salmonid abundances in this study corresponded with the gradual decline in *Ranunculus* cover as the plants began to senesce in autumn. This suggests that *Ranunculus* cover provides essential habitat for juvenile salmonids, possibly through its association with abundant macroinvertebrate resources, and as its availability declines, fish are required to seek alternative habitats elsewhere.

There were interspecific differences in the influence of *Ranunculus* on the probability of an individual remaining in a site. The effect of *Ranunculus* on the site retention rate of salmon was positive between June and August, but had less influence between August and September. This change in strength of effect could have occurred because salmon were most abundant in high *Ranunculus* cover sites in August, which might have intensified intraspecific competition. Conversely, trout were more likely to be recaptured in sites with high *Ranunculus* cover between August and September, when salmon abundances had begun to decline, which could represent an impact of interspecific competition. Where juvenile salmonid abundance is high, or resources become limiting, larger individuals are thought to drive smaller subordinates to disperse away to habitats with less competition (Elliott, 1994). However, competition has been found to have little effect on site fidelity and dispersal of juvenile salmon, and that mobile individuals are not necessarily of lower fitness (Steingrimsson & Grant, 2003).

Juvenile salmon remaining in sites with high *Ranunculus* cover between June and August had better growth conditions, as demonstrated by the greatest increase in body size during this period. There are a number of mechanisms that could underlie this significant result. Better growth could be driven by increased food availability, through the increased range of habitats created by *Ranunculus* that might promote abundant macroinvertebrate assemblages (Berrie, 1992), or by increased opportunities to access food resources. The structural complexity may afford enough protection from predators or competitors to devote more time to foraging rather than vigilance or territorial behaviour (Warfe & Barmuta, 2006). Additionally, the steep velocity gradients created though the flow resistance within plant stands, and increase in flows around the plant stands (Gurnell *et al.,* 2002; Whaton *et al.,* 2006) provides opportunity for energy-efficient foraging opportunities, where fish can wait in low-velocity shelters for the adjacent fast velocities to bring prey to them in the water drift (Morantz *et al.,* 1987; Cunjak, 1988).

Irrespective of the causative mechanism, an increase in growth during summer is likely to promote higher survival rates of salmon during summer and subsequent life stages. Greater salmonid body length can increase swimming capability for increased predator evasion and prey capture (Armstrong *et al.,* 2018). A longer length during migration of smolts would allow for avoidance of gape-limited predators, which are abundant in the lower reaches of lowland rivers (Mann, 1982; Lauridsen *et al.,* 2017b; Armstrong *et al.,* 2018). In contrast to salmon, there was no clear effect of

Ranunculus cover on the trout growth during any period, though the trout sample size was low relative to salmon. Trout have been described as more opportunistic and active predators compared with salmon (Bardonnet & Bagliniere, 2000; Dineen, Harrison & Giller, 2007), therefore might depend less on *Ranunculus* cover for prey resources.

No other habitat characteristic outperformed *Ranunculus* cover at explaining the variation in any of the salmonid responses. However, salmon abundances were positively associated with greater prey biomass and lower velocity heterogeneity. More individuals can be supported by a larger source of available prey, and increased velocity heterogeneity can provide salmonids with energy efficient opportunities to access this prey (Morantz, *et al.*, 1987). Therefore, I would have expected a positive relationship between velocity heterogeneity and abundances. This expected positive relationship was observed with trout abundance, which is consistent with a catchment-wide study of trout density-habitat relationships that identified velocity heterogeneity as a key characteristic for promoting abundant juvenile trout (Chapter 2). The difference between salmon and trout in response to velocity heterogeneity could indicate niche differentiation between these two sympatric species. Salmon were less likely to remain in a site with greater velocity heterogeneity, and trout were less likely to remain in a site with higher prey biomass. These findings could represent the impacts of increase intra- and inter-specific competition in areas of high salmonid abundance and resource value (Gibson, 1993).

Although I positioned the replicate blocks relatively close together on the same stream to minimise any unmeasured influences, it appeared that block 1 had naturally higher abundances of salmon and trout relative to blocks 2 and 3. Population distribution and abundance at a catchment scale are driven by recruitment dynamics, by availability of and access to spawning habitat (Parry *et al.,* 2017), and distance between spawning habitat and summer feeding territories (Chapter 2). This could suggest areas of successful spawning immediately upstream of block 1. As well as supporting higher abundances of salmon and trout, salmon present in sites within block 1 were more likely to remain in the same site during a sample period, suggesting that these sites supported higher abundance of fish. Yet the change in body size of recaptured salmon and trout individuals did not differ between the blocks. I expected that greater abundances of salmonids would reduce growth potential of individuals due to increased rates of inter and intra-specific competition (Grant and Imre, 2005). However, the habitat provided at block 1 appears to support more individuals without negatively impacting their growth rates.

Ranunculus plants quickly established after the experimental manipulations and were largely resistant to high-flow events shortly after the manipulation. No re-planting was required over the course of the experiment, and I successfully achieved the desired treatment levels of *Ranunculus* cover. The manipulation technique used in this study could therefore be applied to habitat management. Artificial structures can be effective at habitat enhancement for wild salmonids, but are expensive, and can lose effectiveness or be washed away downstream over time (Binns, 2004). Such structures may also be geared towards performing specific function, such as digging pools for trout, or planting riparian canopy to provide terrestrial inputs and overhead cover (Binns, 2004; McCormick & Harrison, 2011). Naturally occurring macrophytes, such as *Ranunculus,* can create complex habitats to structure and support both biotic and abiotic components of salmonid ecosystems, and could be cost-effective alternatives to artificial structures.

Aquatic weed cutting takes place throughout the year to manage against flooding and agricultural run-off, although its effectiveness is assumed, and cutting stimulates further regrowth (Baattrup-Pedersen *et al.,* 2018). The strongest effect of weed cutting on water levels is between July-September, when cutting negatively impacted the ecological status of over a hundred Danish streams (Baattup-Pedersen *et al.,* 2018). In addition to the positive effect of *Ranunculus* cover on abundances of juvenile salmon and trout throughout the summer months, I have identified an important period of influence of *Ranunculus* cover on salmon site fidelity and growth at the beginning of summer. These findings could help prioritise efforts to compromise on timing of weed cuts to benefit stakeholders, and not negatively impact salmonid populations inhabiting rivers structured by *Ranunculus*. Although further research is needed to understand the detailed mechanism/s governing these relationships, this study clearly demonstrates an effect of *Ranunculus* on juvenile salmonid populations in lowland rivers.

Chapter 4: Times o’ plenty: high *Ranunculus* cover is associated with successful juvenile salmonid summer foraging and growth

4.1 Abstract

Good growth during summer months is important if juvenile salmon and trout are to survive overwinter, smoltify, and survive their early marine phase. Many factors are thought to influence juvenile salmonid summer growth, including river conditions and conspecific and heterospecific competitor densities. To a greater or lesser extent, these factors are related to the amount and quality of habitat available to an individual, which provides it all the vital resources, such as food and shelter, it needs to grow and survive. *Ranunculus* is the major habitat component in lowland rivers of southern England, and has the potential to provide vital resources and habitat heterogeneity for juvenile salmonid growth and survival. Yet, empirical evidence to test this hypothesis is lacking. I measured, weighed, and collected the stomach contents of juvenile salmon and trout during June and August over two years from nine river sites that had been subjected to experimental manipulation of *Ranunculus* cover. I also quantified the abundance of available macroinvertebrate prey during the same months at each site in each year. I used these data to calculate salmonid growth rates and characterise their diet selection (compared with what was available) and overlap, and how these measures were affected by the amount of *Ranunculus* cover. I found that salmon realised higher growth under higher *Ranunculus* cover, but that trout did not. Prey biomass and mean prey size in the diets of both salmon and trout were strongly positively influenced by *Ranunculus* cover, suggesting that *Ranunculus* facilitates successful foraging. Dietary niche overlap between salmon and trout was greatest in low *Ranunculus* cover, suggesting increased interspecific competition, possibly due to reduced resouces. This hypothesis was corrobated by greater selection for terrestrial taxa in low *Ranunculus* cover suggesting reduced aquatic food resources. Together, these findings suggest that the growth of salmon,

and to a lesser extent, trout, is positively associated with *Ranunculus* cover, which might be regulating foraging opportunities for high-quality aquatic macroinvertebrate prey.

4.2 Introduction

Conservation strategies for managing declining populations should not only aim to increase numbers, but also the condition of individuals to ensure long-lasting demographic impacts driven by good survival rates and subsequent recruitment (Catlin, *et al.,* 2014; Armstrong *et al.,* 2018; Gregory *et al.,* 2019). Individual condition can be influenced by myriad factors including resouce availability, inter- and intraspecific competition, risk of predation, and habitat structure (Grant & Imre, 2005; Millidine, Armstrong & Metcalfe, 2006; Finstad *et al.,* 2007; Amundsen & Gabler, 2008; Naslund, Sundstrom & Johnsson, 2015), the latter of which can mediate impacts of the other listed factors (Warfe & Barmuta, 2006). In anadromous salmonids, fitness at the juvenile life stage has the potential to impact survival processes throughout an individual's life time (Zabel & Achord, 2004; Armstrong *et al.,* 2018; Gregory *et al.,* 2019). Understanding the role of habitat in promoting juvenile growth and development can ensure the overall viability of salmonid populations through applied management of freshwater habitats.

Salmonids are born in the freshwater environment and typically spend their first summer maximising food intake and growth before entering a winter period of reduced activity (Wankowski & Thorpe, 1979; Heggenes *et al.,* 1993). The following spring, individuals of anadromous species can smoltify and migrate out to sea; in some rivers, this constitutes the majority of the cohort (Ibbotson *et al.,* 2013).

Suitable foraging and growth opportunities for juvenile salmonids are essential during their first summer in fresh water to maximise chances of survival, as increased size reduces risk of predation and ensures sufficient energy reserves to endure harsh winter conditions (Werner & Gilliam, 1984; Finstad *et al.,* 2004; Armstrong *et al.,* 2018). Life history strategies of salmonids can also be governed by availability of food resources and juvenile growth rates. Higher growth rates might result in earlier maturation and smoltification of salmon (Davidson, Letcher & Nislow, 2010), and the body length attained by the time a salmon smoltifies can determine the likelihood of that individual surviving at sea and returning to the river to spawn (Armstrong *et al.,* 2018; Gregory *et al.,* 2019). Food resources appear to play an important role in determing life history strategies in brown trout, though with mixed outcomes. Food restriction on juvenile brown trout in autumn led to reduced signs of smoltifying in individuals that were recaptured in the wild during the following spring (Naslund, Sundstrom & Johnsson, 2015). Conversely, in artificial conditions (e.g. experimental tanks and hatcheries), reduction in food supplies have either had little impact on, or increased, smoltification rate (Jones, Bergman & Greenberg, 2015; Archer *et al.,* 2019).

Maximising growth during the summer and autumn months is imperative to salmonids attaining sufficient growth, as growth potential reduces over the winter months. Available food resources diminish over winter (Keeley & Grant, 2001; French *et al.,* 2014), and lower temperatures during winter reduce metabolic rate, which lessens rates of food digestion or prey capture success (Elliott, 1972, Watz *et al.,* 2014). Behavioural changes occur during winter, notably a switch to nocturnal activity has been observed in both salmon and brown trout (Fraser, Metcalfe & Thorpe, 1993; Heggenes *et al.,* 1993), which might not match up with prey activity and thus reduce accessibility of food resources. Autumn growth rates and body size of individuals prior to the winter period does not influence the over-winter growth rates of juvenile brown trout (Naslund, Sundstrom & Johnsson, 2015), suggesting that the size of the fish does not necessarily equate to higher resource acquisition during winter. Indeed, the switch to nocturnal foraging activity could reduce territory sizes and aggresive activity due to reduced visual acuity (Fraser, Metcalfe & Thorpe, 1993), and so dominance status may have less influence on foraging success among individuals during winter (Heggenes, *et al.,* 1993).

Fast growth during summer and autumn months is driven by net energy gain (Heggenes *et al.,* 1993), and juvenile salmonids therefore are expected to exploit habitats with high energy-efficient foraging opportunities. Efficiency may be maximised by occupying heterogeneous habitat, such as low velocity refuges adjacent to high velocity patches that deliver drifting prey (Morantz *et al.,* 1987), or structures which allow protection from predators and competitors (Finstad *et al.,* 2007), thus individuals may maximise foraging relative to evasive and defensive behaviours. Productive habitats with abundant food resources can support greater growth rates in juvenile salmonids (Naslund, Sundstrom & Johnsson, 2015). Selection of prey items can also influence growth, and consumption of larger prey items is considered more profitable, and linked to faster growth of salmonids (Wankowski & Thorpe, 1979; Keeley & Grant, 1997). Salmonids are gape-limited predators, and both the mouth breadth and gill raker spacing is strongly related to fork length of juvenile salmonids (Wankowski, 1979). There is, therefore, an allometric relationship between the size of a fish and the prey size that it can consume (Keeley & Grant, 1997). Faster growth at the beginning of summer may subsequently maximise feeding and growth opportunities, by increasing the range of prey available to an individual over the summer feeding period.

The densities of con- and heterospecifics can also influence growth of juvenile salmonids, though findings differ across studies, suggesting context-specific effects. Whilst density-dependence generally exerts strong impacts on earlier phases of the salmon life cycle, such as growth and survival of fry (Imre, Grant & Cunjak, 2005), density of potential competitors can have a weak (Davidson, Letcher & Nislow, 2010) or strong and negative (Amundsen & Gabler, 2008) impact on juvenile salmonid growth. Juvenile salmonids compete for food resources via interference (Keeley & Grant, 1995), which can result in broad overlaps in both the prey size and composition among similarly sized salmonid species occupying a habitat (Keeley & Grant, 2001). The intensity of interference competition is proposed to increase with increasing densities of sympatric species, reducing niche overlap between competitors (Llewellyn & Jenkins, 1987), therefore determining niche overlap between species can suggest the mechanisms through which sympatric species coexist.

I have demonstrated that higher *Ranunculus* cover in lowland rivers supports larger abundances of juvenile Atlantic salmon, *Salmo salar,* and brown trout, *S. trutta,* (Chapter 3). However, it is important to understand how the feeding and growth opportunities are influenced by *Ranunculus* habitat structure. The structural complexity of *Ranunculus* provides heterogeneous habitat conditions that could support energy-efficient foraging behaviour, while reducing the risk of predation and competition (Morantz *et al.,* 1987; Diehl & Kornijow, 1998; Sand-Jensen, 1998; Venter *et al.,* 2008; O'Briain *et al.,* 2017). Retention of organic material in the plant stands (Sand-Jensen, 1998; Wharton *et al.,* 2006), and the complex morphology of

Ranunculus (Warfe & Barmuta, 2006) can provide more resources and heterogenous habitat to support abundant and diverse macroinvertebrate communities (Diehl, 1992), on which salmonids prey. Despite an extensive literature on juvenile salmonid growth and diet (e.g. Keeley & Grant, 2001; Grant & Imre, 2005), few studies focused on lowland rivers and the influence of macrophytes in these ecosystems (but see Riley *et al.*, 2009 and McCormick & Harrison, 2011). Lowland populations of salmon have experienced a decrease in both abundance and body size (Gregory *et al.*, 2017; ICES 2017), and there have been calls to increase production of both quantity and 'quality' of juveniles in order to maximise freshwater output and ensure adult returns (Gregory *et al.*, 2019). Therefore, demonstrating that *Ranunculus* supports greater abundance of juvenile salmon and trout is encouraging, but only one piece of the puzzle. Detailed understanding of the effect of *Ranunculus* on juvenile growth and diet is critically needed for the application of *Ranunculus* as a management tool for improving salmonid populations.

Here I aimed to understand the differences in the influence of *Ranunculus* cover on diet and growth of wild sympatric juvenile salmon and trout in lowland rivers. I tested the effect of *Ranunculus* cover on growth rates, whether this effect was likely to be driven by a change in available prey biomass, body size and community composition, and how salmon and trout responded to these changes in terms of the prey that they select and the extent of dietary niche overlap. Based on the evidence presented previously, I hypothesised that 1) salmon and trout growth rates would be positively affected by *Ranunculus* cover, 2) available prey biomass in the enviroment and, consequently, diet biomass in both species would increase in higher *Ranunculus* cover, 3) mean prey size in both the environment and diets would be larger in higher *Ranunculus* cover, 4) biomass and mean prey size in the diets of juvenile trout would be greater than that of salmon, 5) prey community composition would be strongly influenced by *Ranunculus* cover, and this shift would be reflected in the composition of salmonid diet, 6) terrestrial prey taxa would be found more frequently in the diet of trout compared to salmon, and 7) the interspecific dietary niche overlap would be lower in higher *Ranunculus* cover.

4.3 Methods

4.3.1 Study site and experimental design

This study was conducted as part of a two-year (2016-17) in-field *Ranunculus* manipulation experiment situated on the North Stream of the river Frome, Dorset (Figure 3.1), a southern lowland chalk stream with abundant *Ranunculus* beds and juvenile salmonid populations (Chapter 3). At the beginning of spring (March/April) in each year of the experiment, I imposed three replicates of three *Ranunculus* cover manipulations in nine sites, 20 m in length, situated across three spatial blocks, approximately 100 m in length, on the North Stream (Figure 2.1). Low (<10 %), medium (30-40%) and high (>60%) *Ranunculus* cover was attained by digging out existing plants and re-planting into sites as required, and treatment levels were maintained throughout the summer until natural senescence of the plants in autumn. The manipulation achieved a gradient in *Ranunculus* cover. Peak in *Ranunculus* biomass occurred in early summer between June-August and differences in percentage cover between the treatment levels was the greatest during this period (Figure 3.3).

4.3.2 Sampling and data preparation

To determine the influence of *Ranunculus* cover on the growth rates of salmon and trout and macroinvertebrate prey in the environment and in their diets, sampling was carried out in June and August in each year of the manipulation experiment. As part of determining abundances of juvenile salmon and trout throughout summer and autumn, I electrofished to capture and remove all salmonids in each site, in June and August. Salmonids were identified to species and mildy sedated prior to being weighed (to nearest gram), marked for future identification by clipping the adipose fin, and tagged. A PIT tag (12.5 mm length, 2.12 mm diameter; Biomark, Idaho, USA) was inserted into the body cavity so that recaptured individuals could be identified during the subsequent sampling occasion. Individuals caught that were smaller than 6 cm in length were not tagged to avoid detrimental effects on growth or survival (Richard *et al.,* 2013). During the second sampling occasion in August, I confirmed recaptured individuals by scanning PIT tag codes using a handheld reader (Biomark HPR plus) and reweighed the recaptured individual. Individuals that were recaptured within the same site were assumed to have remained in this site during the period of growth, and therefore been exposed to the *Ranunculus* cover present at that site. Recaptured salmon had a mean weight of 8.3 g (range: 4.6 – 13.0 g), and recaptured trout had a mean weight of 9.3 g (range: 5.0 – 17.0 g).

To collect diet contents of salmon and trout, individuals of both species were randomly sampled across the sites, during all sample occasions. Diet contents were collected by stomach flushing. During stomach flushing, when the fish were mildly sedated, I held the fish ventral surface up, with the head inclined downwards over a collection tray. A small Pasteur pipette connected to a foot pump was inserted into the mouth of the fish, and short pumps of water into the stomach flushed out recently consumed food items (Kamler & Pope, 2001). As well as being non-lethal, this method has shown to be 99% effective in removing stomach contents of salmon (Strange & Kennedy, 1981), and is appropriately sized for juvenile fish (Kamler & Pope, 2001). Diet contents of each individual were transferred to a 60 mL Sterilin pot and preserved in 4% formaldehyde prior to sorting, identification and measuring of diet taxa. All aquatic macroinvertebrate specimens were identified to the lowest taxonomic level (usually species), except Oligochaeta (sub-class), Hydrachnidae (family), Simuliidae (family) and Chironomidae (tribe), and all terrestrial taxa were identified to family, prior to counting to determine taxon abundance. Measures of parasitic Nematoda and Nematomorpha were omitted from diet analyses, as these were not considered to be prey. I measured either the body length, head width or the largest body dimension of up to 30 randomly selected individuals of each taxa and used published length-mass relationships (Table S2.1) to estimate the mean biomass of each taxon. I then multiplied the mean biomass by the abundance of each taxon, which were summed in each sample to generate a measure of the total prey biomass in the diet. The mean biomass per sample was calculated to represent a measure of mean prey size in the diet. Taxa accumulation curves were created using function *specaccum* in R package vegan (Oksanen *et al.*, 2018). The number of individuals used for dietary analyses at these sites was deemed sufficient as the majority of the taxa accumulation curves recorded at least 80% of the taxa estimated by the asymptote (Figures S4.1 - S4.2). Any deviations from the asymptote were likely caused by uncommon prey taxa. Subsequently, analyses incorporated these prey taxa data, while recognising the potential underestimate of taxon richness in a few sites.

To determine prey biomass in the environment, aquatic macroinvertebrates were sampled from representative benthic substrates at three random locations within each site at the two sampling occasions in each year. Samples were collected and processed according to the protocol outlined in Section 3.3.2 *Macroinvertebrate prey biomass.* All macroinvertebrate specimens were identified to the lowest taxonomic level, counted and measured and measures of total prey biomass and mean prey size in the environment were produced as for the prey biomass in the diet (see previous paragraph). Taxa accumulation curves suggested that the number of samples used to represent communities in the environment were sufficient with all taxa curves recording at least 92% of taxa estimated by the asymptote (Figure S4.3).

To determine the influence of *Ranunculus* cover on the salmonid growth and diet responses, we estimated percentage cover of *Ranunculus* at 25 quadrats per site in each sampling occasion. Quadrats (0.5 x 0.5 m) were evenly spaced across five evenly spaced transects spanning the stream channel wetted width. The 25 estimates of *Ranunculus* cover were averaged to create a measure of mean *Ranunculus* cover at each site. To account for any influence of temperature on salmonid growth rates, temperature loggers (HOBO Pendant Temperature/Light, Onset, USA) were placed within each block to record water temperatures at 10-minute time intervals

To calculate the growth in body mass (g) of salmon ($n = 72$) and trout ($n = 47$) caught in June and recaptured in the same site in August, I adapted the standardised mass-specific growth rate estimation (Ostrovsky, 1995) utilised in Jensen *et al.,* (2018), to incorporate thermal-units of degree days. Thermal-unit growth models are more accurate than specific growth rates (Lugert *et al.,* 2016), and better account for the well-established relationship between temperature and fish development (Chezik *et al.*, 2014). Growth rate (Ω, percent per day) was calculated as

$$\Omega = 100 \times \frac{(M_1^b - M_0^b)}{CDD \times b},$$

where M_0 is the mass of fish at first capture, M_1 is the mass of fish at last capture, b is the allometric mass exponent for the specific growth rate and body mass relationship (I used the exponent 0.31 of brown trout (Elliot & Elliot, 1995) for each species), and CDD is the cumulative degree-days from first to last capture. CDD was calculated from Chezik *et al.,* (2014), as

$$CDD_i = \sum_{i=1}^{D}\left(\frac{TMax_i - TMin_i}{2}\right) - T_0,$$

where $TMax_i$ and $TMin_i$ are the maximum and minimum ambient temperatures for day i,… D, and T_0 is the base temperature for a species, below which growth is nonlinear and effectively zero (Chezik *et al.*, 2014). I utilized lower temperature limits reported for Atlantic salmon parr, 6°C (Elliot & Hurley 1997) as the value of T_0 for both species. Absolute degree-day values for each day D were summed over the growth period to give the cumulative degree-days at a given T_0 (CDD; °C·days). Due to poor recruitment of juvenile salmonids in 2016 (ICES, 2017, Chapter 2), there were too few trout data to calculate growth rates in 2016.

4.3.3 Statistical analyses

Growth rates

To test the responses of salmon and trout growth rates to *Ranunculus* cover, and interspecific differences in these responses, two linear mixed-effects models were developed: one for salmon growth rates in 2016 and 2017, and one for salmon and trout growth rates in 2017 only. *Ranunculus* cover was averaged across June and August to represent mean cover during the growth period. The main effects of mean

Ranunculus cover and *block* were included in both models. I also included a main effect of *year* in the salmon model, and a main effect of *fish species* and interaction between *fish species* and *Ranunculus* in the salmon and trout model. Both models included a random effect of *site* to account for measures taken on multiple individuals from the same site.

Prey biomass in the environment and diet

To test whether the biomass and mean size of prey in the environment was influenced by *Ranunculus* cover, the total invertebrate biomass and mean individual invertebrate biomass was calculated for each Surber sample (n = 108). Linear mixed models were used to test the response of these two variables to the main effects of *Ranunculus cover, month, year* and *block*, and an interaction term of *Ranunculus* x *month*. This model structure allowed me to account for variation in the response variable attributed to the experimental design and time of sampling, and to establish whether the influence of *Ranunculus* differed over time. To test whether prey biomass and size of prey in the diet was influenced by *Ranunculus* cover and differed between salmon (n = 204) and trout (n = 94), linear mixed models were used to test the response of these two variables to the same main effects outlined above. Additionally, I included a main effect of *fish species* and interaction between *Ranunculus* and *fish species* to test for interspecific differences in the response, and a main effect of *fork length* because larger fish might consume larger prey based on the established allometric relationship of prey selection. All models included a random effect of *site* to account for the multiple measures (Surber samples and individuals) taken at the same site. Response variables were natural log transformed if necessary, to meet assumptions of normality and homoscedasticity.

Linear mixed model fits were evaluated by calculating marginal and conditional R^2 values using function *rsquared* in R package piecewiseSEM (Lefcheck, 2015), which implements the method of Nakagawa and Schielzeth (2013). Parameter estimates were considered to be statistically significant according to p-values calculated using Satterthwaite's approximations (Satterthwaite, 1946), and if their 95% confidence intervals did not overlap zero. Models were fitted using function *lmer* in R package lmerTest (Kuznetsova, Brockhoff, & Christensen, 2015). Model residuals were inspected to ensure that they did not violate assumptions of homogeneity, normality and independence.

Prey composition

To describe prey taxa present in the environment and diets of salmon and trout, I calculated their frequency of occurrence (F_i) and relative abundance and biomass ($\%A_i/B_i$). Frequency of occurrence of prey taxa was calculated as $F_i = (N_i/N) \times 100$, where N_i is the number of samples containing the ith prey taxa and N is the total number of nonempty samples (Caillet, 1977). Relative abundance and biomass of taxa was calculated as $\%A_i/B_i = (\sum S_i \,/\, \sum S_t) \times 100$, where S_i is the sum of the abundance or biomass of prey i in all samples, and S_t is the sum of the abundance or biomass of all taxa in all samples (Macdonald & Green, 1983).

To examine compositional differences in both the environment and salmonid diet, I used a multivariate extension of a generalised linear model, using the function *manyglm* in the package mvabund (Wang *et al.,* 2012). This model-based approach of analysing multivariate abundance data is more suitable than distance- based analyses, because the latter can misspecify mean-variance relationships and lead to erroneous conclusions (Warton, Wright & Wang, 2011). In the *manyglm* analysis, multiple generalised linear models are fitted to response variables simultaneously, generating output of both community-level test statistics and univariate test statistics calculated for each taxon in the community. This allowed to ascertain both the effect of explanatory variables on the variation in the community and also the contribution of each species to the overall variation in the community. Many invertebrate taxa were encountered only once in the environment and diet contents (Figures S4.4 – S4.5), and therefore assumed to be rare. Subsequently, I omitted rare invertebrate taxa from the multivariate analyses to assess key differences in the communities, removing taxa that were present in less than ten Surber samples, and five diet samples, from the environment and diet analyses respectively. To assess the influence of *Ranunculus* cover at different sample occasions on prey community in the environment, I averaged taxa abundance across the three samples per site. A *manyglm* with negative binomial distribution was applied to account for possible overdispersion, with main effects and an interaction of *month* and *Ranunculus cover*. To assess the influence of *Ranunculus* cover at both different sample occasions, and on interspecific differences in diet composition, a *manyglm* with negative binomial distribution was applied, with main effects of *fish species*, *month*, *Ranunculus cover*, and interactions between *Ranunculus cover* and the other two variables. Where there was a significant community response to an explanatory variable, individual contributions of prey taxa to the *manyglm* analysis were visualised for interpretation.

Prey electivity and dietary niche overlap

To calculate prey electivity by salmon and trout, I used Strauss' prey electivity index (1979): $L = r_i - p_i$, where r_i and p_i represents the relative abundance of prey in the diet and the environment, respectively. Strauss' index is considered to generate less bias measures of prey electivity where sample sizes of the diet and environment are unbalanced, compared to Ivlev's electivity index (Strauss, 1979). The relative abundance of prey in the diets of salmon and trout (r_i) was calculated by dividing the number of each prey taxa found in the diet of each fish in site *i*, by the total number of taxa consumed by each fish (Newkirk & Schoenebeck, 2018). Relative abundance of prey in the environment (p_i) was calculated by dividing the average number of each prey taxa found in site *i* by the average total number of all taxa found in site *i* (averaged across the three Surber samples at each site). The value of Strauss' index can range from -1, representing complete avoidance, to 1, representing complete selection (Strauss, 1979). Cutoff values within this range have been imposed in previous studies to determine selectivity or avoidance of prey taxa. I applied a cutoff value of ±0.15 (Newkirk & Schoenebeck, 2018) and determined values <0.15 to represent prey avoidance, >0.15 to represent prey selection and between -0.15 – 0.15 to represent opportunistic foraging. To test for the influence of *Ranunculus* cover on prey electivity, once electivity values had been calculated for each taxa for each individual fish, I performed bootstrapping to randomly resample rows of individuals that were caught in different levels of *Ranunculus* cover. This method is appropriate for data that can be influenced by non-independence of animals in a group (Llewellyn & Jenkins, 1987; Singer & Norland, 1994). *Ranunculus* cover was grouped as low (<20%), medium (≥20 <50%), and high (≥ 50%) to represent observed measures of *Ranunculus* cover at sites during June and August. This procedure was repeated 1,000 times to generate a distribution of prey electivity values for each prey taxa in each level of *Ranunculus* cover. Empirical bootstrap 95% confidence intervals of the distributions of each taxa in different *Ranunculus* cover were compared to test whether prey electivity was influenced by *Ranunculus* cover.

To represent dietary niches of salmon and trout, the mean of the proportional abundance of prey taxa in gut contents of each individual fish was taken. Dietary niche overlap was calculated using the FT index (Smith & Zaret, 1982):

$$\mathrm{FT} = \sum \sqrt{p_{1i} \times p_{2i}}\,,$$

where p_{1i} and p_{2i} are the mean proportion of the *i*th prey taxa in species 1 and 2, respectively. The value of FT can range between 0 (no overlap) and 1 (complete overlap). In addition to being among the least biased measures of overlap, the FT index is unaffected by unequal sample sizes (Smith and Zaret, 1982), therefore appropriate for this data which has unequal representation of salmon and trout. To test the statistical significance of dietary overlap between salmon and trout in different amounts of *Ranunculus* cover, we employed a bootstrap procedure to estimates distributions and thus, variance of the FT index (Smith, 1985) in different levels of *Ranunculus* cover. Rows of the community matrix of salmon and trout individuals in each level of *Ranunculus* cover (as above) were randomly resampled to calculate the FT index, and this procedure was repeated 1,000 times to generate a distribution of FT index for salmon and trout in different levels of *Ranunculus* cover. This process was repeated to calculate niche overlap in proportional biomass, and to ascertain the influence of *Ranunculus* on both measures of niche overlap, empirical bootstrap 95% confidence intervals were compared between levels of *Ranunculus* cover.

4.4 Results

4.4.1 Growth rates

Juvenile salmon growth rates were positively influenced by *Ranunculus cover* across years (Figures 4.1a and b), and were higher in 2016 relative to 2017 (Figure 4.1a). Model fixed effects explained 43% of the variation in juvenile salmon growth rates (marginal R^2 = 0.43, conditional R^2 = 0.47). In contrast, juvenile trout growth rates were not influenced by *Ranunculus cover* (Figures 4.1a and c). In 2017, growth rates of salmon were higher than those of trout (Figure 4.1c), and the fixed effects in this model explained 37% of the variation in total fish growth rates (marginal R^2 = 0.37, conditional R^2 = 0.40). Block was not an important explanatory variable of growth in either model. Model residuals did not violate any assumptions (Figure S4.6).

4.4.2 Prey biomass in the environment and diet

Total biomass of prey in the environment was influenced by *Ranunculus cover* differently between months (Figure 4.2a), with greater biomass in the environment associated with low *Ranunculus* cover in June, and high *Ranunculus* cover in August (Figure 4.2b). Total biomass of prey in the environment was lower in 2017 and did not differ between blocks (Figure 4.2a). The model explained 11% of the variation in the total prey biomass. Mean prey size in the environment was not significantly influenced by any explanatory variable included in the model (Figure 4.2a), and the model performed poorly (conditional R^2 = 0.05). Total biomass in the diet was greater in higher *Ranunculus* cover (Figure 4.3a), and the influence of *Ranunculus cover* did not differ between fish species (Figure 4.3b), or between months (Figure 4.3c). There was no effect of *fish species*, *month*, *year*, *block*, or *fork length* on total

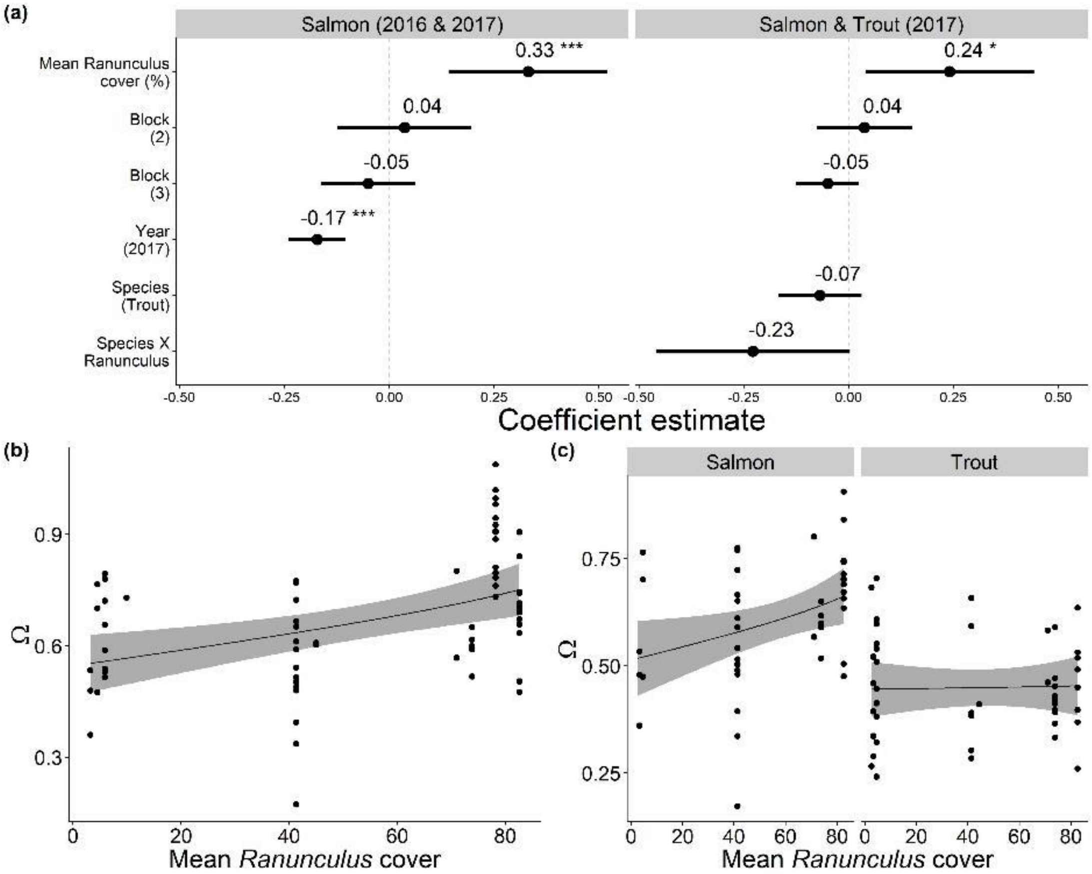


Figure 4.1. Analysis results for the growth rates (Ω, percent per day) of juvenile salmon and trout caught in June and recaptured in August. Plots show results of two linear mixed models: (a) the mean estimate (point), 95% confidence interval (black line) and significance level (* $p < 0.05$, *** $p < 0.001$) of the explanatory variables' effect on growth rate in each model, (b) the marginal effect of mean *Ranunculus* cover on salmon growth rate across both years (2016 and 2017), and (c) the difference in the marginal effect of mean *Ranunculus* cover on salmon and trout growth rate in 2017. In plots (b) and (c), mean effects are shown by a sold black line, with 95 % confidence intervals denoted by grey shading. Raw data is displayed as solid circles.

diet biomass (Figure 4.3a). Mean prey size was greater in the diets of fish caught in high *Ranunculus* cover (Figure 4.4a). Trout fed on average on larger prey than salmon but the relationship between *Ranunculus cover* and prey size did not differ between the fish species (Figure 4.4b). The effect of *Ranunculus cover* did not differ between months (Figure 4.4c), and *year*, *block* and *fork length* had no effect on mean

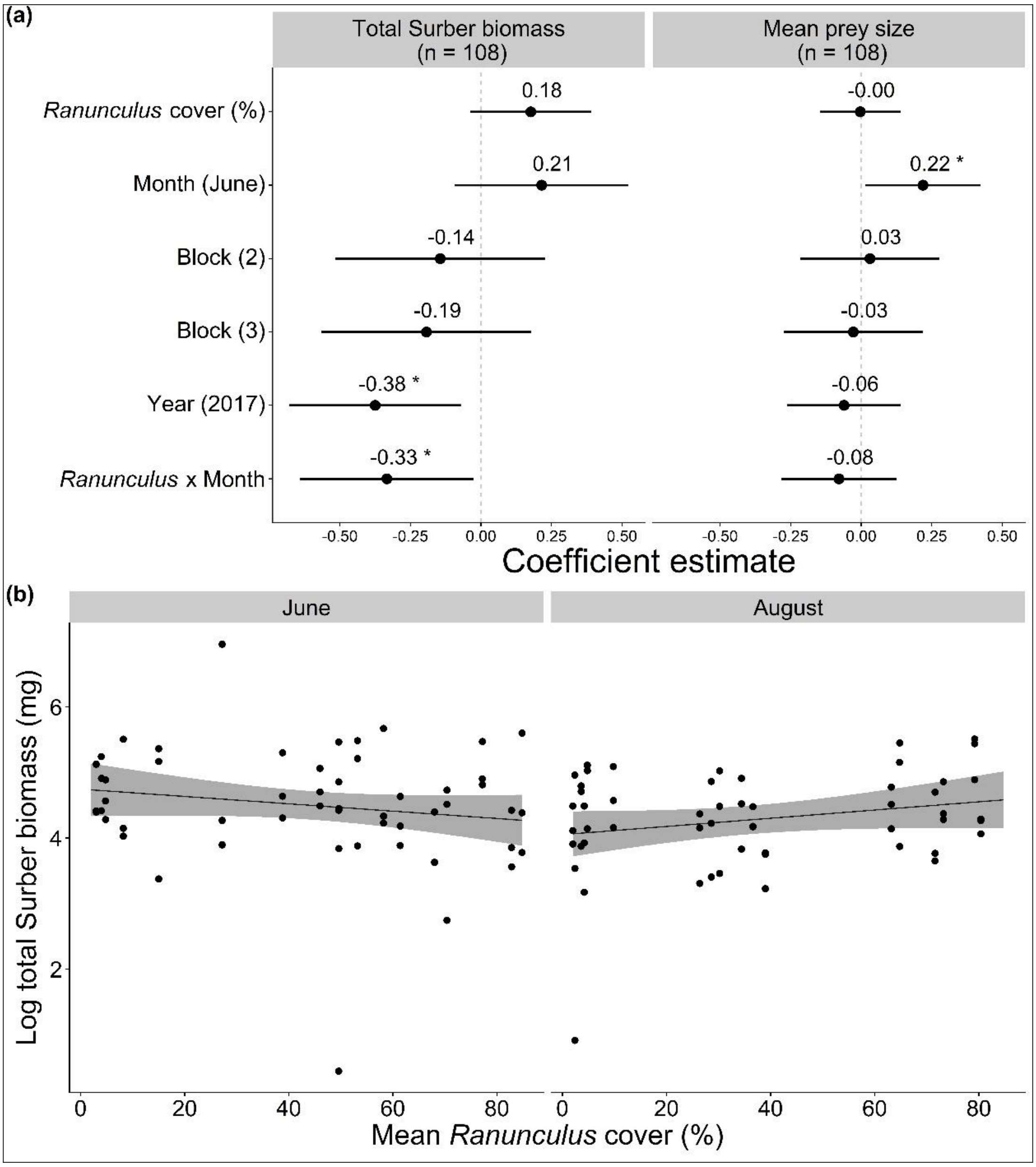


Figure 4.2. The effects of the *Ranunculus* manipulation on the biomass and mean size of invertebrates found in the environment. Plot (a) shows the coefficient estimates of explanatory variables tested to explain the variation in total Surber sample biomass, and the mean prey size per Surber sample. Points and values are the mean estimate, lines are the 95% confidence interval, and significance levels are shown as * $p < 0.05$. Plot (b) depicts the significant interaction between *Ranunculus* cover and month in describing the variation in total Surber sample biomass. The black line is the mean effect estimate, the grey shaded area is the 95% confidence interval, and solid circles show the observed total Surber biomass (log transformed).

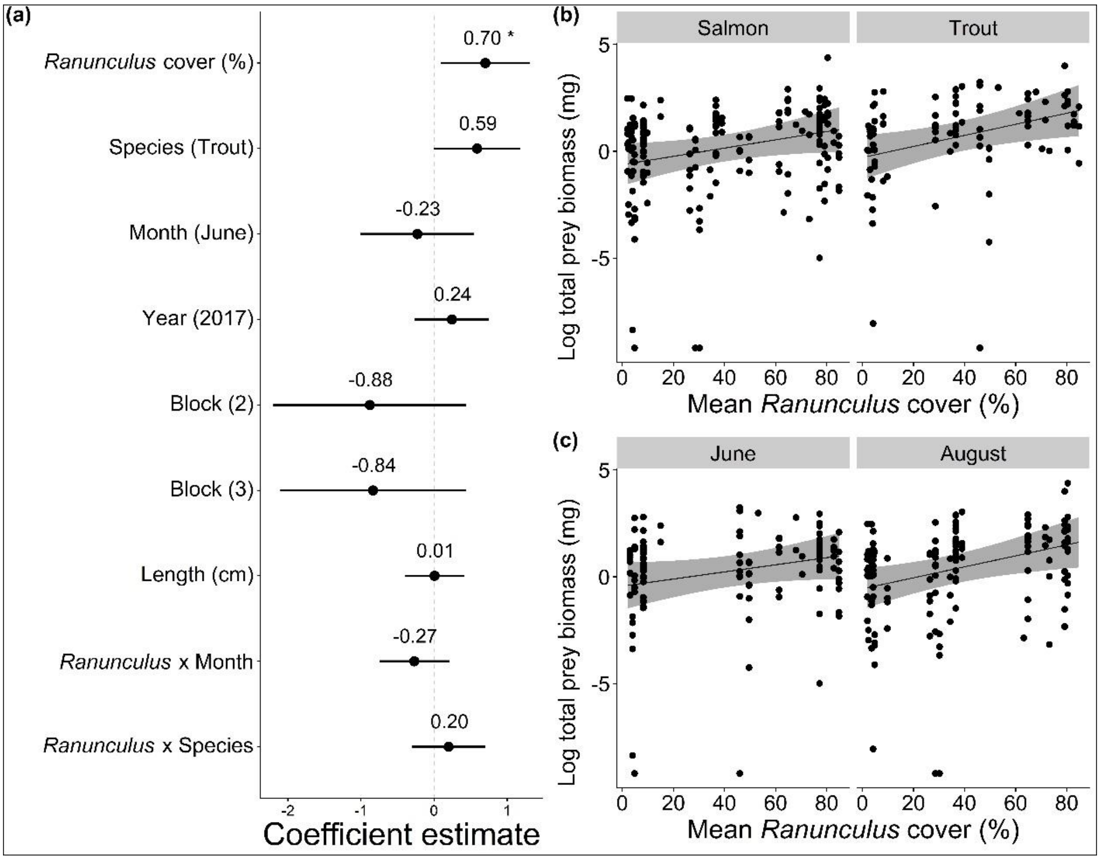


Figure 4.3. Results from the linear mixed model describing variation in total prey biomass in salmon (*n* = 204) and trout (*n* = 94) diet, (a) shows the coefficient estimates of the main effects and interaction tested to explain variation in total prey biomass, mean estimate is the value and point, 95% confidence interval is the line and significance levels are shown as * *p* < 0.05, (b) illustrates the marginal effect of the interaction between *Ranunculus* cover and fish species on total prey biomass, and (c) shows the marginal effect of the interaction between *Ranunculus* and month on total prey biomass. Mean effect size is shown with the black line, 95% confidence intervals are denoted in grey shading, and raw data points are displayed as black circles (log transformed).

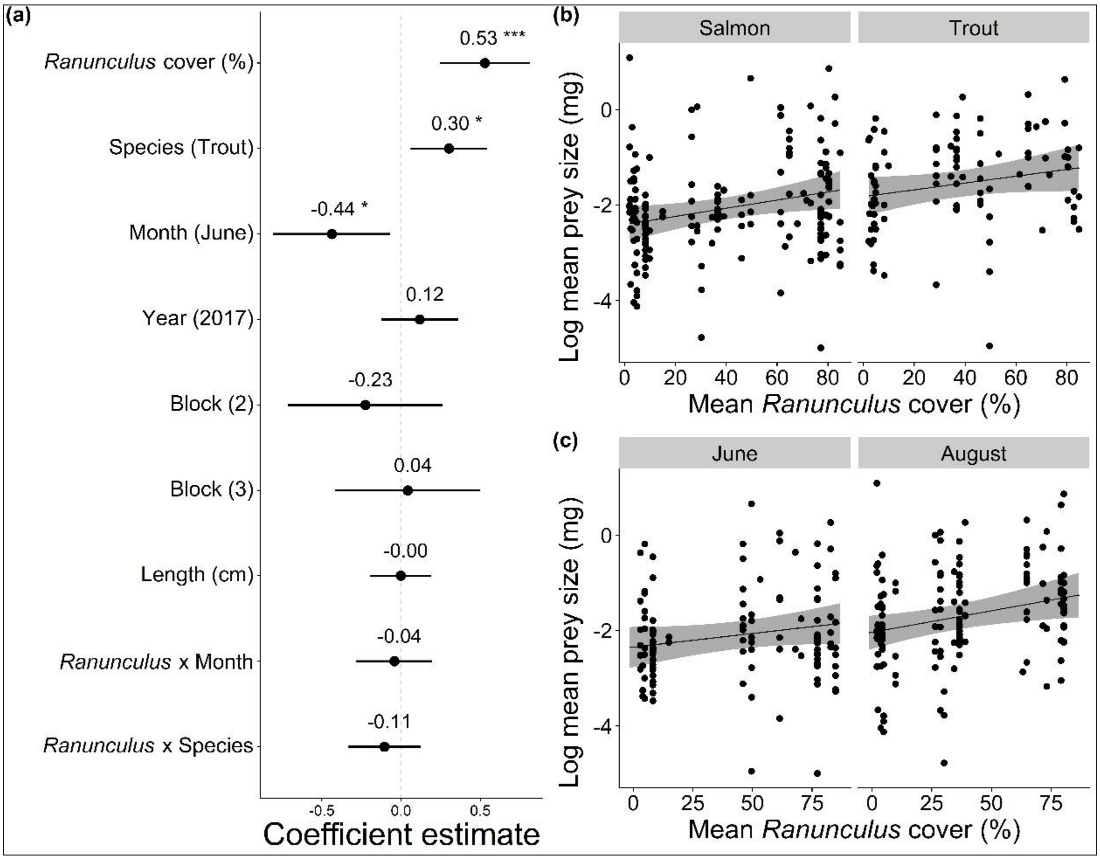


Figure 4.4. Results from the linear mixed model describing variation in mean prey size in salmon ($n = 204$) and trout ($n = 94$) diet. (a) shows the coefficient estimates of the main effects and interaction tested to explain variation in mean prey size, mean estimate is the value and point, 95% confidence interval is the line and significance levels are shown as * $p < 0.05$, *** $p < 0.001$, (b) illustrates the marginal effect of the interaction between *Ranunculus* cover and fish species on mean prey size, and (c) shows the marginal effect of the interaction between *Ranunculus* and month on mean prey size. Mean effect size is shown with the black line, 95% confidence intervals are denoted in grey shading, and raw data points are displayed as black circles (log transformed).

prey body size (Figure 4.4a). The models explained 23% of the variation in both the total diet biomass (marginal $R^2 = 0.13$, conditional $R^2 = 0.23$), and mean prey size (marginal $R^2 = 0.18$, conditional $R^2 = 0.23$). Model residuals did not violate any assumptions (Figures S4.6 - S4.7).

4.4.3 Prey composition

A total of 95 prey taxa were identified in the environment, 65 prey taxa in the salmon diets and 58 taxa in the trout diets. Prey composition in the environment across treatments were consistent, with all ten dominant taxa found in >80% of all Surber samples (Table 4.1). Over 80% of total salmon diet biomass was composed of Simuliidae, *Baetis* sp. and *Serratella ignita,* indicating their particular importance for salmon. Other highly frequent taxa, such as Chironomidae and *Hydroptila* sp., contributed very little to the total biomass (Table 4.1). In contrast, no single prey taxa contributed >20% of the total trout diet content biomass, suggesting they have a more generalist feeding strategy. *S. ignita* was a particularly valuable prey item for salmon and trout, and *Gammarus pulex* group and terrestrial prey taxa for trout, as they contributed highly to total biomass, despite occuring in relatively low abundance in diet contents.

Ranunculus cover had a significant effect on composition of the prey community in the environment, and the influence of *Ranunculus* did not differ significantly between months (Figure 4.5). Greater abundances of Simuliidae, *Rhyacophila dorsalis*, *Radix peregra*, *Hydropsyche* sp, and *Brachycentrus subnubilus* were associated with higher cover of *Ranunculus,* and abundances of *Ylodes conspersus* and *Potamopyrgus antipodarum* were higher in low *Ranunculus* cover (Figure 4.5). Overall, composition of the environment community was highly driven by seasonal changes in taxa abundance between months (Figure 4.5). *Ranunculus cover* also had a significant effect on composition of fish diet, and the influence of *Ranunculus cover* did not differ significantly between months or by fish species (Figure 4.6). Abundances of *S. ignita*, *Hydropsyche* sp. and Chironomidae in the diet were greater in higher *Ranunculus* cover (Figure 4.6). The *fish species* response was mainly driven by significantly lower abundances of prey taxa in salmon diet relative to trout, with the exception of *Baetis* sp. which were found in higher abundance in salmon diet. The composition of the diet contents was also highly driven by seasonal change in taxa abundance between months (Figure 4.6).

Table 4.1. Invertebrate taxa found most frequently and/or in relatively higher abundance/biomass in the environment and fish diet. F_i = percentage occurrence in samples; $\%A_i$ = relative abundance of taxa across all samples, $\%B_i$ = relative biomass of taxa across all samples. The ten most frequently occuring/highest relative abundance and biomass are highlighted in bold.

		Environment (*n* = 108)			Salmon diet (*n* = 204)			Trout diet (*n* = 94)		
Taxa	Common name	F_i	$\%A_i$	$\%B_i$	F_i	$\%A_i$	$\%B_i$	F_i	$\%A_i$	$\%B_i$
Baetis sp.	Mayflies	**100.0**	**9.0**	**3.9**	**86.7**	**23.9**	**28.0**	**85.3**	**13.8**	**6.8**
Chironomidae	Non-biting midges	**100.0**	**21.2**	**3.2**	**67.6**	**8.6**	**1.8**	**68.6**	**9.0**	1.7
Elmis aenea	Riffle beetles	**98.1**	**2.6**	2.1	-	-	-	-	-	-
Simuliidae	Blackflies	**98.1**	**43.8**	2.4	**86.7**	**56.6**	**32.4**	**81.4**	**45.0**	**18.4**
Gammarus pulex group	Freshwater amphipods	**96.3**	**10.1**	**10.7**	**12.2**	**0.6**	**0.8**	**33.3**	**3.5**	**13.1**
Serratella ignita	Mayflies	**96.3**	**3.2**	**10.3**	**51.6**	**4.5**	**21.1**	**50.0**	**5.8**	**17.8**
Hydracarina	Water mites	**94.4**	**1.3**	0.5	-	-	-	-	-	-
Hydropsyche sp.	Netspinning caddisflies	**93.5**	**1.8**	**9.8**	**22.3**	**1.4**	**4.3**	**31.4**	**2.7**	**6.2**
Limnius volckmari	Riffle beetles	**90.7**	**1.2**	**6.6**	-	-	-	-	-	-
Hydroptila sp.	Cased caddisflies	**82.4**	0.5	0.2	**19.1**	**1.4**	0.2	**28.4**	**2.1**	0.2
Oligochaeta	Worms	78.7	**0.9**	0.2	-	-	-	-	-	-
Lumbricidae	Worms	13.0	<0.1	**12.4**	-	-	-	-	-	-
Erpobdella octoculata	Leeches	38.9	<0.1	**11.3**	-	-	-	-	-	-
Radix balthica	Snails	37.0	0.1	**5.6**	-	-	-	-	-	-
Rhyacophila dorsalis	Free-swimming caddisflies	76.9	0.3	**2.5**	**8.5**	**0.4**	**2.8**	**18.6**	**1.0**	**4.8**
Terrestrial Diptera	Adult flies	-	-	-	**6.9**	**0.4**	**1.0**	**11.8**	**2.9**	**3.1**
Terrestrial Thysanoptera	Thrips	-	-	-	**4.3**	**0.2**	0.1	-	-	-
Terrestrial Trichoptera	Adult caddisflies	-	-	-	1.6	0.1	**3.9**	8.8	0.1	**5.7**
Ephemera danica	Mayflies	-	-	-	2.1	0.1	**0.6**	-	-	-
Agapetus sp.	Cased caddisflies	-	-	-	-	-	-	**10.8**	**1.1**	0.3
Terrestrial Lepidoptera	Butterflies & moths	-	-	-	-	-	-	3.9	0.2	**6.9**
Terrestrial Oligochaete	Worms	-	-	-	-	-	-	2.0	0.2	**2.7**

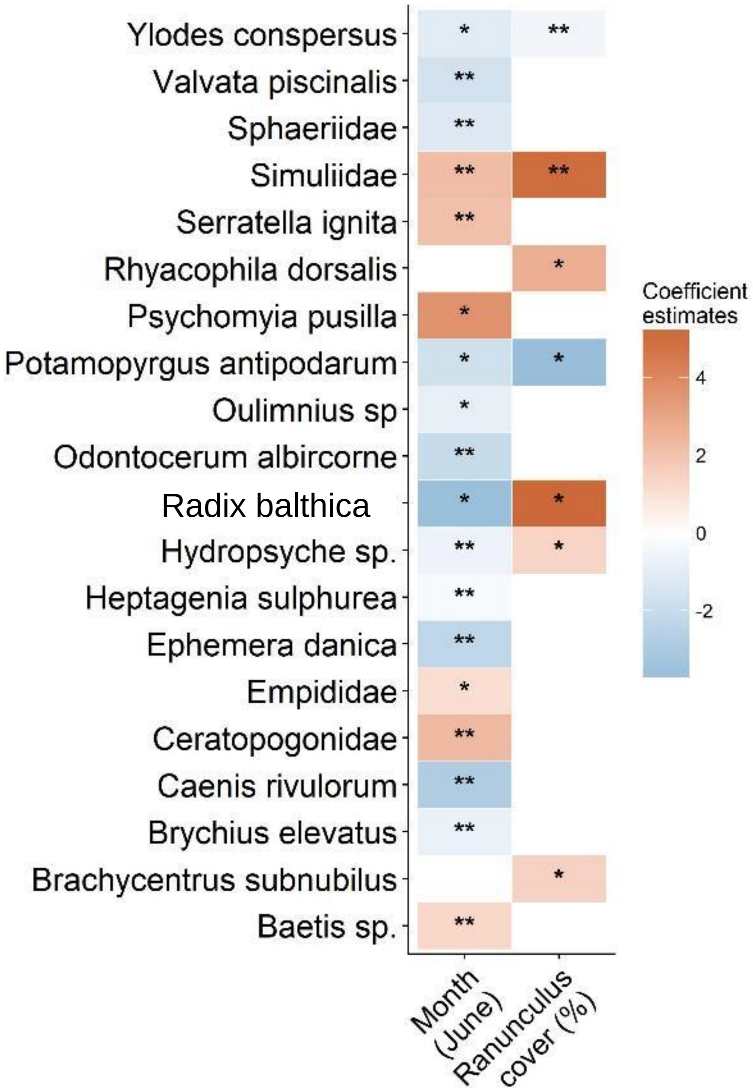


Figure 4.5. Individual invertebrate taxa that significantly contributed to the multivariate community relationship with month and *Ranunculus* cover as determined by the *manyglm* analysis. Black symbols represent *P*-values where ** < 0.1, * < 0.05, and coloured blocks show the coefficient estimate for that association. The stronger the association, the brighter the block. Positive associations are in orange and negative associations are in blue. The invertebrate community composition was significantly influenced by month ($p < 0.01$) and *Ranunculus* cover ($p = 0.02$), and the influence of *Ranunculus* cover did not differ by month ($p = 0.10$).

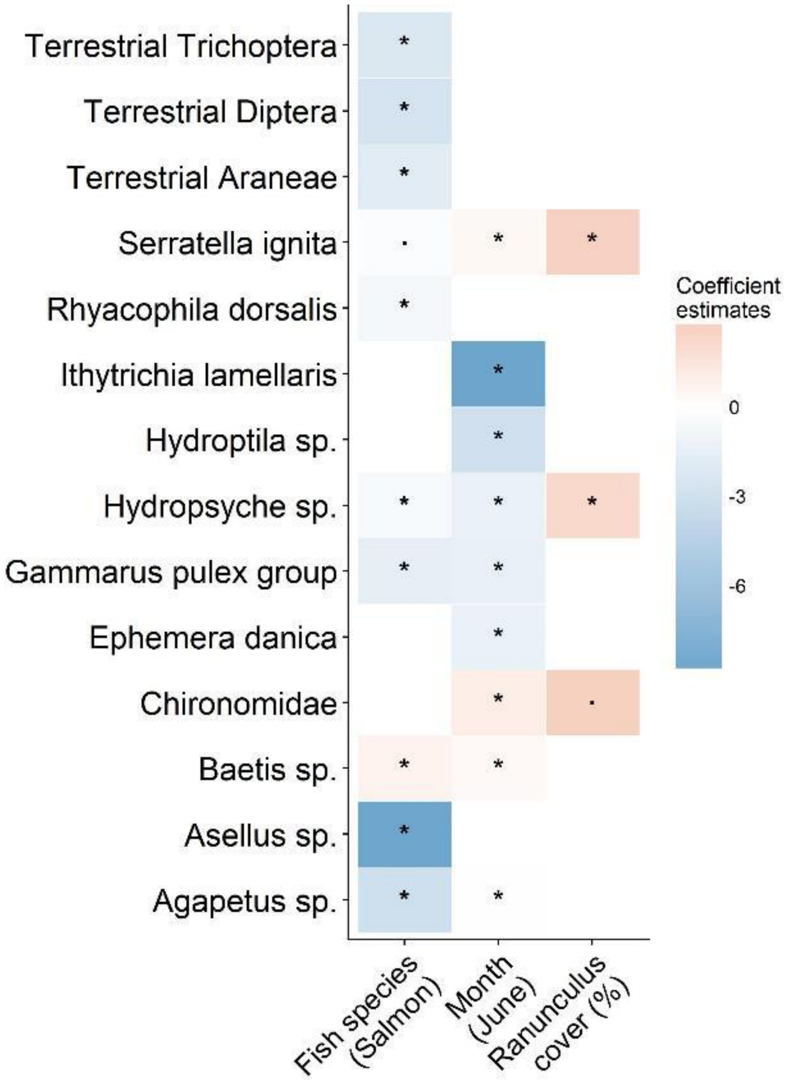


Figure 4.6. Prey taxa that contribution to the relationship between diet composition and fish species, month and *Ranunculus* cover, as determined by the *manyglm* analysis. Significance levels shown for *p*-values where * < 0.05 and · < 0.1, and coloured blocks show the coefficient estimate for that association. The stronger the association, the brighter the block. Positive associations are in orange and negative associations are in blue. The prey composition was significantly influenced by fish species (*p* = 0.01), month (*p* = 0.01) and *Ranunculus* cover (*p* = 0.01), and the influence of *Ranunculus* cover did not significantly differ by fish species (*p* = 0.68) or month (*p* = 0.07).

4.4.4 Prey electivity and dietary niche overlap

The majority of taxa appeared to be foraged opportunistically in relation to their proportional abundance in the environment (Figure 4.7). Salmon selected for *S. ignita* more in high relative to low *Ranunculus* cover, selected for *Baetis* sp. across all levels of cover, and selected for Simuliidae more in low relative to medium and high cover (Figure 4.7). Trout selected for *Baetis* sp. more in medium relative to low and high cover, and selected for Simuliidae in low relative to medium and high cover. Given their abundance in the environment, *G. pulex* was underrepresented more in the diets of both salmon and trout that were caught in low relative to medium and high *Ranunculus* cover (Figure 4.7). Terrestrial taxa were foraged opportunistically, though results suggest that they were more likely to be selected in low or medium cover relative to high *Ranunculus* cover (Figure 4.8). The dietary niche overlap of prey abundance between salmon and trout was moderate, and was significantly higher in low relative to high *Ranunculus* cover (Figure 4.9a). The dietary niche overlap of prey biomass was lower than that of prey abundance. On average biomass overlap was greater in low *Ranunculus* cover relative to medium and high *Ranunculus* cover, which had very similar distributions of prey electivity (Figure 4.9b).

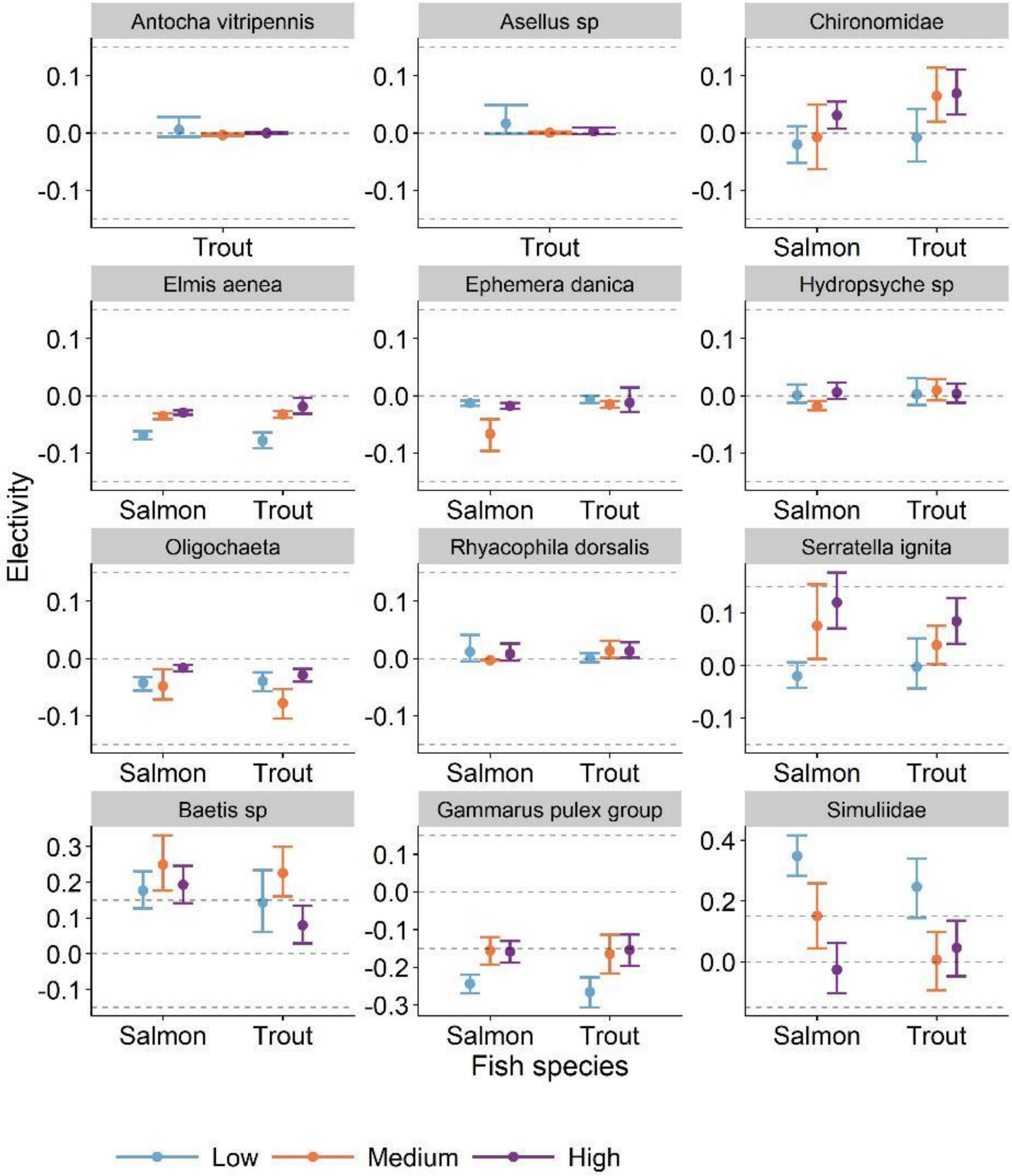


Figure 4.7. Influence of *Ranunculus* cover on prey electivity by each fish species. The bottom row shows taxa that were selected for or under-represented based on relative abundance in the environment calculated by Strauss' index. Note the y-axis differs on the plots on the last row. Points are the mean of the bootstrap distribution, and errorbars show the 95% confidence intervals of the distribution. The top dashed line represents the prey selection threshold (0.15) and bottom dashed line represents the prey avoidance threshold (-0.15).

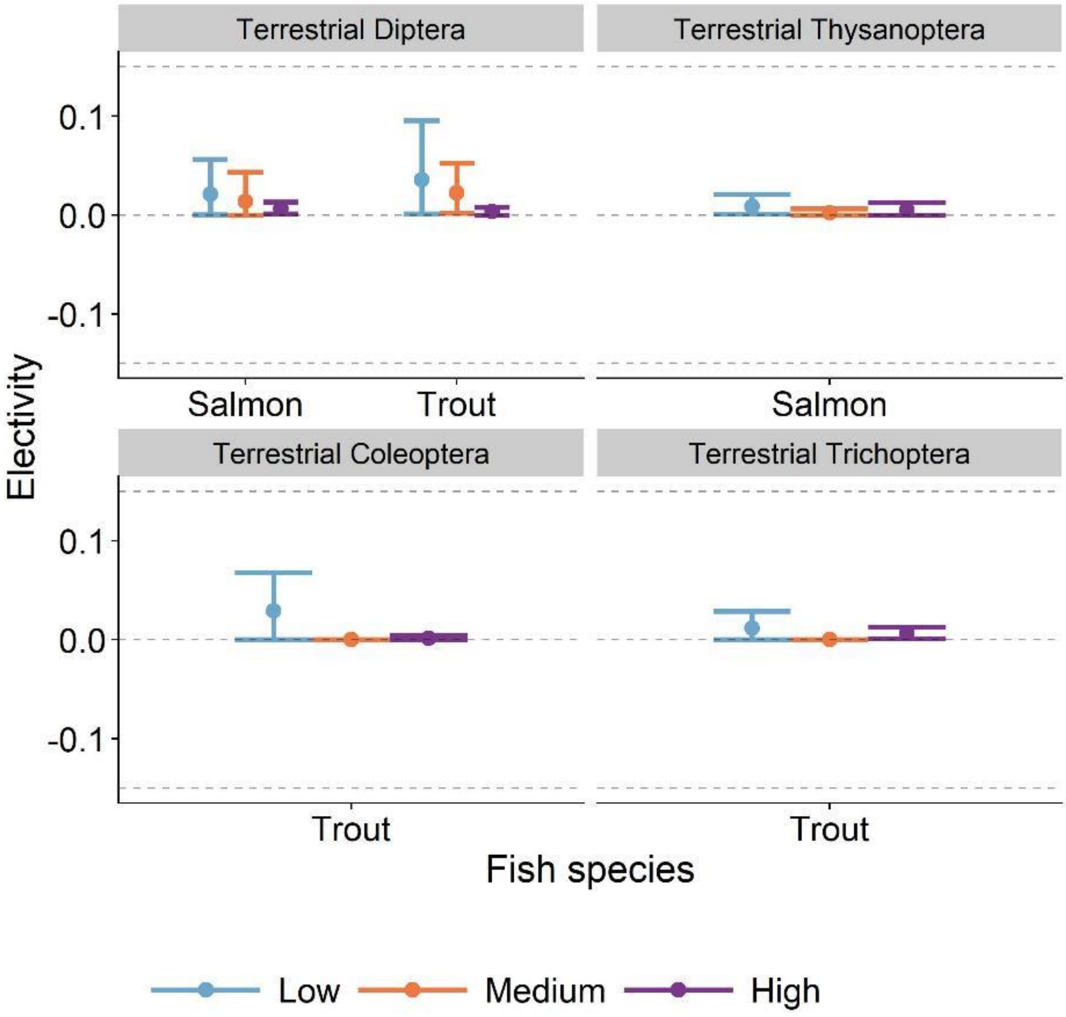


Figure 4.8. Influence of *Ranunculus* cover on electivity of terrestrial prey taxa by salmon and trout. Points are the mean of the bootstrap distribution, and errorbars show the 95% confidence intervals of the distribution. The top dashed line represents the prey selection threshold (0.15) and bottom dashed line represents the prey avoidance threshold (-0.15).

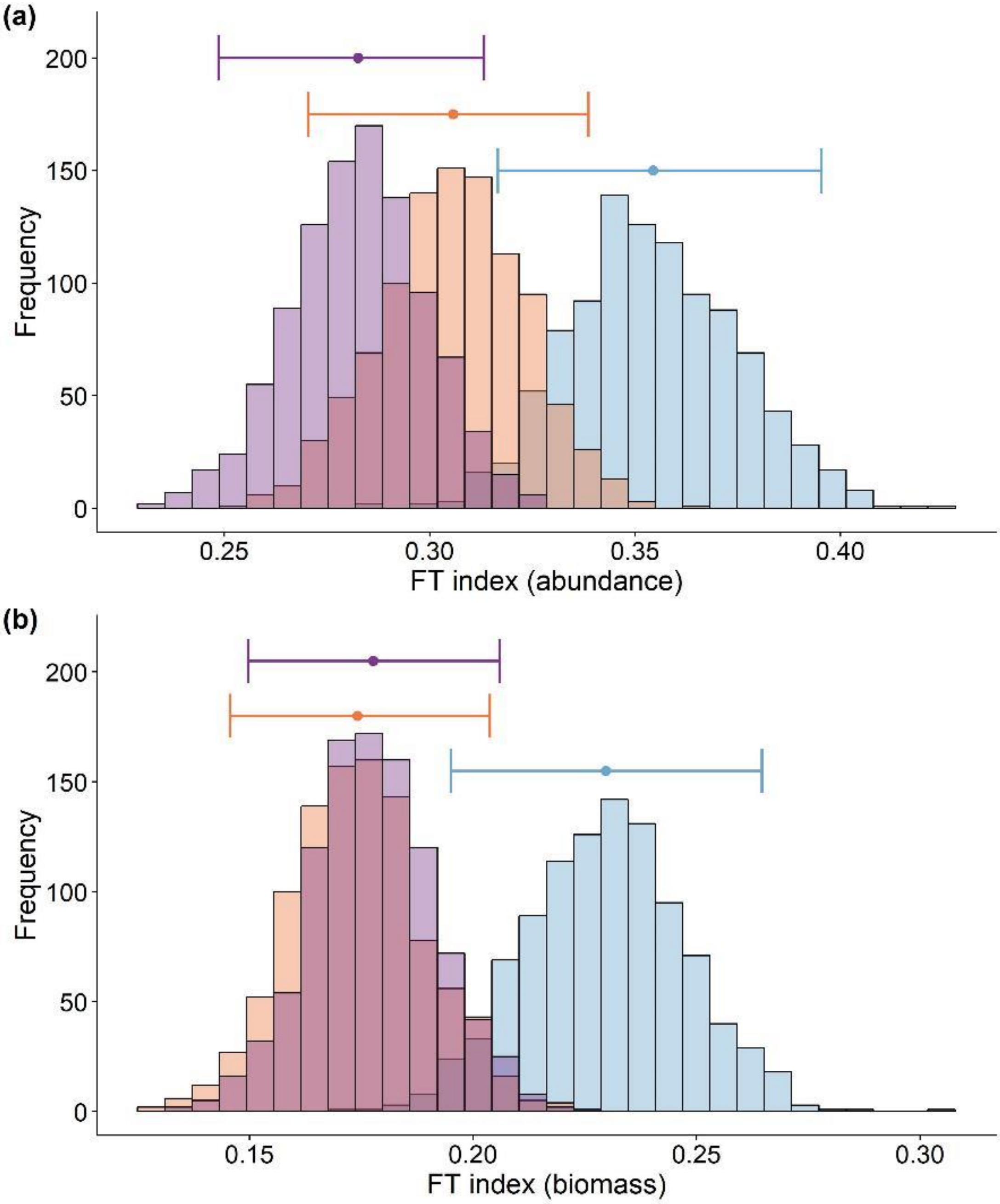


Figure 4.9. Generated distributions of the extent of dietary niche overlap based on (a) proportional abundance, and (b) proportional biomass of prey taxa observed in salmon and trout gut contents. FT index measured the niche overlap between diets of salmon and trout caught in low (blue), medium (orange) and high (purple) *Ranunculus* cover during summer months. At the top of each histogram, the error bar represents the 95% confidence interval of the distribution, and the point shows the mean of the distribution.

4.5 Discussion

Juvenile salmon grew more in high *Ranunculus* cover during summer months, but juvenile trout were not influenced by *Ranunculus* cover. Despite there being few detectable effects on prey biomass in the environment, higher biomass of prey and larger average prey items were found in diets of salmon and trout inhabiting high *Ranunculus* cover. This suggests that *Ranunculus* facilitates foraging and indirectly influences salmon growth. Considering their shared environment and similar size at this life stage, diet choice and niche overlap between salmon and trout was moderate, suggesting different foraging strategies for the two species. An increase in niche overlap and selection for terrestrial taxa in low *Ranunculus* cover suggests that access to aquatic food resources might be lower in the absence of *Ranunculus*, which could explain the negative influences on salmon growth rates. Successful feeding and growth during summer months are essential for surviving the winter period and preparing juvenile salmonids for smoltification (Amundsen & Gabler, 2008). These findings develop our understanding of how wild salmonid populations utilise habitats – and *Ranunculus* specifically - for foraging, and thereby provides essential knowledge that can be applied to habitat management or restoration.

The ability to grow is subject to net energy gain (Heggenes *et al.*, 1993), therefore habitats that offer ample foraging opportunities for low energy demand should encourage fast growth. The potential for higher salmon growth in higher *Ranunculus* cover could mean that the structural complexity of *Ranunculus* creates habitat conditions that allow for energy-efficient behaviours. Water velocities within the canopy of submerged macrophytes are severely reduced due to high waterflow resistence, and are consequently accelerated around macrophyte patches (Sand-Jensen & Mebus, 1996). This effect is most pronounced in macrophytes with complex morphology (Sand-Jensen & Mebus, 1996), such as *Ranunculus* (Cheruvelil, Soranno & Serbin, 2000). These steep velocity gradients created by *Ranunculus* would benefit the sit-and-wait foraging strategy (Keeley & Grant, 1995), where salmon maintain station in low velocity areas to reduce energy expenditure, and wait for prey items to be brought down in the adjacent fast flowing water (Morantz *et al.,* 1987). As well as creating good habitat conditions for foraging, the role of *Ranunculus* as a shelter could influence salmon growth rates. The floating canopy can offer valuable overhead protection from aerial predators, whereas the increased structural complexity within the water column affords visual isolation and refuge from predators and competitors in the river (Johnsson, Rydeborg & Sundstrom, 2004; Venter *et al.,* 2008). This can reduce metabolically-costly vigilance behaviours (Metcalfe, Huntingford & Thorpe, 1987), thus enhancing feeding motivation and foraging success. The presence of a shelter alone is sufficient to reduce metabolic rate in resting salmon, whereas the absence of shelters can substantially increase metabolic costs (Millidine, Armstrong & Metcalfe, 2006; Finstad *et al.,* 2007).

The abundance and availability of suitable food resources is also essential for growth (Amundsen & Gabler, 2008), and *Ranunculus* promotes abundant macroinvertebrate prey (Armitage & Cannan, 2000; Harrison & Harris, 2002).This study however, detected little effect of *Ranunculus* cover on the prey biomass in the environment. Greater prey biomass was associated with high *Ranunculus* cover in August, but not in June. This could coincide with macroinvertebrate life histories, e.g. hatching of larvae that might increase observed abundance, or emergence of adults that might decrease observed abundance. Many families of aquatic macroinvertebrate have short generation times and multiple cohorts per year (Wright & Symes, 1999) and so abundances fluctuate seasonally. Indeed, the macroinvertebrate community composition in the environment differed strongly by month, driven by a greater number of taxa absent in June relative to August. However, only *L. peregra* and *Hydropsyche* sp. were both more abundant in August and in higher *Ranunculus* cover, so this dynamic is unlikely to fully explain the prey biomass relationship observed in August. Spatial patchiness and aggregation is also important in mobile stream invertebrates with varying dispersal abilities (Downes, Lake & Schreiber, 1993). Variation in abundances of stream macroinvertebrates can therefore be high over small spatial scales (Downes, Lake & Schreiber, 1993) and higher spatial resolution in prey sampling could have accounted for this effect.

Although there was little effect of *Ranunculus* cover on the biomass of prey in the environment, both prey biomass and mean size of prey consumed by salmon and trout were greater in high *Ranunculus* cover, suggesting that *Ranunculus* was facilitating greater rates of prey encounter or prey capture success. Predator-prey interactions can be mediated by habitat complexity in aquatic systems but with inconsistent results. Experimental studies report reduced prey capture rates by fish with increasing density of macrophytes and complexity of plant forms, suggesting that structurally complex macrophytes provide more effective prey refuge (Dionne & Folt, 1990; Warfe & Barmuta, 2004). However, increased predation on invertebrate grazers has been demonstrated in pygmy perch, *Nannoperca australis*, in complex plant architectures relative to simple plant structures (Warfe & Barmuta, 2006). Prey evasion in complex structures still relies on prey to modify behaviours to utilise refuges and avoid predators (Savino & Stein, 1989). However, hydrodynamic signals that allow macroinvertebrate prey to detect predators in aquatic systems and adapt their behaviour to avoid predation (Dodson *et al.*, 1994), can be disrupted within complex plant structures, resulting in increased prey encounter (Warfe & Barmuta, 2006). Larger prey were eaten by trout compared with salmon, which might reflect interspecific differences in foraging behaviour. Trout are more active predators, and more likely to feed on the water surface (Dineen, Harrison & Giller, 2007), therefore might encounter large, nutritious terrestrial prey items more often than salmon that are sit-and-wait predators. However, the energy-costs related to this strategy could explain why the benefits of larger prey in the diet has not resulted in higher trout growth rates in these results.

Ranunculus cover had little influence on the abundance of those macroinvertebrate taxa that were exploited by salmon and trout, with the exception of *Hydropsyche* sp. The majority of taxa associated with *Ranunculus* in the environment were not identified as common prey items of salmon or trout, except Simuliidae, which occurred in greater abundances in high *Ranunculus* cover. Abundance of Simuliidae in the diet did not appear to differ between levels of *Ranunculus* cover, and this was likely driven by the high selection of Simuliidae by both salmon and trout in low *Ranunculus* cover, relative to its lower abundance in the environment. Simuliidae are a large component of invertebrate drift in streams (Waters, 1972), and therefore the increased production in high *Ranunculus* cover has the potential to increase food resources both within the plant structure and further downstream. *Ranunculus* cover did not influence the diet composition as widely as month or fish species, though greater abundances of the valuable taxa, *S. ignita*, were positively associated with *Ranunculus* cover.

Juvenile salmon are described as opportunistic feeders (Keeley & Grant, 1997; McCormick & Harrison, 2011), though they appeared to be selective in this study compared to the more generalist trout. The majority of prey taxa that were recorded in both the diet contents and in the environment were relatively uncommon, and salmon and trout displayed a preference for very few taxa. *Baetis* sp. were selected for by salmon across all levels of *Ranunculus* cover highlighting it as a valuable prey item. Strauss (1979) suggests that prey selection and avoidance can also be interpreted as prey accessibility and inaccessibility, respectively. This view could explain the avoidance of *G. pulex* in low cover, particularly by trout for which it was a valuable resource in the diet. *G. pulex* behaviourally respond to predator activity (Dodson *et al.*, 1994). Lack of cover and habitat structure might allow for more effective predation detection, reducing encounter rates or success of capture, and thus accessibility to fish. Terrestrial prey appeared to be selected for more in low *Ranunculus* cover relative to high cover, which could represent a lack of available aquatic food resources in low cover. Alternatively, high cover could obstruct access by fish to terrestrial inputs on the water surface.

Dietary niche overlap between salmon and trout were unexpectedly moderate, suggesting that these sympatric species have defined niches in the environment and can coexist without negative impacts on each other. Dietary niche overlap of prey abundance and biomass were on average higher in low *Ranunculus* cover. Where the intensity of inteference competition increases, i.e. with increased numbers of competitors, a reduced niche overlap is expected (Llewellyn & Jenkins, 1987). This has been observed in the habitat selection of three sympatric trout species; at low densities the trout species occupied highly similar habitats, but at high brown trout densities, the habitat niche overlap greatly reduced (Blanchet, 2007). In a previous study testing the impact of *Ranunculus* cover on salmon and trout abundances in the same experimental sites as this study, higher abundances of both species were found in the high cover throughout the summer months (Chapter 3). Perhaps these higher abundances resulted in the reduced niche overlap observed here. Alternatively, the structural complexity of *Ranunculus* can create more numerous and varied habitats to support more diverse and abundant macroinvertebrate communities (Diehl, 1992), and consequently more varied prey for salmonids to exploit in high *Ranunculus* cover compared to low cover. Conversely, salmonids in low cover environment might compete for limited and similar resources and thus overlap greater in their dietary niche.

Interestingly, trout growth rates were neither positively, nor negatively affected by *Ranunculus* cover. Studies linking reduced riparian canopy with increased macrophyte production have found inconsistent associations between less canopy cover and trout growth (Riley *et al.,* 2009; McCormick & Harrison, 2011), and therefore drivers regulating trout growth appear to be more complex than considered in this study. Although drivers of trout growth rates remain elusive, prey biomass and prey size in their diets were greater in high *Ranunculus* cover, suggesting that *Ranunculus* may benefit trout by facilitating better prey capture opportunities.

The increase in salmon growth rates in high *Ranunculus* cover at the beginning of summer improves feeding opportunities, allows for predator evasion, and increases the chance of surviving the winter period and subsequent life stages (Werner & Gilliam, 1984; Finstad *et al.,* 2004; Zabel & Achord, 2004; Armstrong *et al.,* 2018). Enhancing growth prior to winter is particularly crucial for salmon populations in lowland rivers at the southern part of their geographical range, as higher winter temperatures might deplete energy reserves quicker (McGinnity *et al.,* 2009). Previous studies have suggested an association between macrophyte cover and macroinvertebrate production and salmonid diets in lowland rivers by comparing these responses between sites with and without riparian canopy cover, which impedes macrophyte growth (Riley *et al.*, 2009; McCormick & Harrison, 2011). This study directly quantified the presence and abundance of *Ranunculus* cover with macroinvertebrate communities, salmonid diet responses and individual growth rates, providing valuable evidence on the role of *Ranunculus* in lowland rivers. These findings augment those of a previous study demonstrating higher abundances of salmon and trout in high *Ranunculus* cover throughout the summer months (Chapter 3). Together, this suggests that summer *Ranunculus* cover is able to support higher quantities and quality of juvenile salmonids in lowland rivers. The exact mechanisms driving these relationships warrant further investigation, to better understand the potential of macrophytes to enhance salmonid populations in lowland rivers.

Chapter 5: The direct and indirect effects of *Ranunculus* on abundance and growth rates of Atlantic salmon in a lowland river

5.1 Abstract

Existing literature suggests that the relationships between macrophytes and the physical and biological characteristics of the environments they inhabit are complex. Previous studies show that *Ranunculus* might influence salmon abundance and growth to a greater degree than other physical and biological habitat characteristics. However, these previous studies did not consider the whole complexity of direct and indirect relationships among all of these variables. I explore whether the direct relationships between *Ranunculus* and salmon abundance and growth manifest through interactions with other physical and biological characteristics of the environment. Specifically, I applied structural equation modelling to explore the importance and magnitude of the direct and indirect influences of physical variables, such as water velocity, and biological variables, such as prey biomass and abundance of con- and hetero-specifics, on abundance and growth rate of salmon. I showed that *Ranunculus* cover had the strongest positive effect on salmon abundance, but that it also affected velocity heterogeneity and water depth, which had indirect positive and direct negative effects on salmon abundance, respectively. In contrast, there was no direct effect of *Ranunculus* cover on salmon growth. Rather, *Ranunculus* cover increased velocity heterogeneity, prey biomass and mean prey size, of which mean prey size and velocity heterogeneity were positively associated with growth rates. These findings highlight the key role of *Ranunculus* as a structural feature of lowland rivers to enhance abundance and improve condition for multiple trophic levels. Restoration of salmonid ecosystems should focus on understanding and fostering good *Ranunculus* management.

5.2 Introduction

Terrestrial and aquatic vegetation forms key ecosystem structures that modify physical conditions, and provide shelter and other resources that benefit multiple taxonomic groups (Tews *et al.,* 2004). Density and morphology of plants often drive habitat heterogeneity (Diehl, 1992; Tews *et al.,* 2004; Warfe & Barmuta, 2004, 2006), which is essential for resilient, abundant and diverse animal communities (Kovalenko, Thomaz & Warfe, 2012). Macrophytes can be considered key structures in freshwater ecosystems and their influence on specific dynamics are well researched, for example predator-prey interactions (e.g. Dionne & Folt, 1991; Warfe & Barmuta, 2004), or influences on water velocities and sediment retention (e.g. Sand-Jensen & Mebus, 1996; Sand-Jensen, 1998; Wharton *et al.,* 2006). However, previous research has focused on responses of animal abundances to macrophyte structures with less consideration of how habitat heterogeneity created by macrophytes can influence animal responses together with other ecosystem characteristics (Kovalenko, Thomaz & Warfe, 2002).

In lowland rivers, which are typically more stable and less dynamic than upland river systems (Berrie, 1992), macrophytes are particularly important for juvenile salmonids as they are a key source of habitat heterogeneity in the absence of large substrate structures (Berrie, 1992; Riley *et al.,* 2009). Studies have shown greater abundances of salmon and trout, and faster growth rates of salmon occupying habitats with high *Ranunculus* cover (Chapters 2-4), though the mechanisms driving these relationships remain unclear. Additionally, there is a paucity of evidence where direct or indirect effects of macrophytes on juvenile salmonid populations have been quantified, and given the potential interacting influences discussed above, it could be expected that these effects are indirect and complex.

The impact of *Ranunculus* cover on salmon populations or individuals might be mediated through physical habitat characteristics, food resources or competition from con- and heterospecifics. As such, teasing apart key habitat components to inform fisheries management can be challenging because of the interdependence among habitat factors (Armstrong *et al.,* 2003). The structural complexity of submerged macrophytes, particularly those with dense canopies such as *Ranunculus* (Cotton *et al.*, 2006), dramatically increases the resistance to water flow. This creates refuges of low water velocity and increased water depths (Dawson, 1979), the latter of which might not be preferred by juvenile salmon avoiding predators (Gibson, 1993; Wharton *et al.,* 2006, O'Briain *et al.,* 2017). As water velocities slow within the plant stands, water flow is accelerated around the plant beds, creating adjacent areas of fast velocities (Sand-Jensen & Mebus, 1996). This results in heterogeneous water velocities, a desirable habitat characteristic for juvenile salmonids to exploit for energy-efficient foraging opportunities (Morantz *et al.,* 1987). Diversity in water velocities and depths can drive more abundant and diverse macroinvertebrate communities, which salmonids feed upon (Keeley & Grant, 1997; Riley *et al.,* 2009; McCormick & Harrison, 2011, Chapter 3). Fast water velocities provide sites with valuable drifting prey, though these might be energetically demanding environments to forage in (Wankowski & Thorpe, 1979).

As a consequence of reduced water velocities within plant stands, the dense canopies result in increased retention of fine sediment and organic material (Gregg & Rose 1982; Cotton *et al.,* 2006), providing food for macroinvertebrate communities, and fostering potentially larger individuals. The complexity provided by plant stands can offer macroinvertebrates protection from predators (Dionne & Folt, 1991, but see Warfe & Barmuta, 2006). As such, *Ranunculus* communities are often associated with productive and abundant macroinvertebrate communities (Armitage & Cannan, 2000; Riley *et al.,* 2009; McCormick & Harrison, 2011). Cover is important for juvenile salmonids (Milner, 1982). The vertical structure of *Ranunculus* throughout the water column, coupled with the floating canopy on the water surface, affords protection from both aerial and aquatic predators (Diehl & Kornijow, 1998; Johnsson, Rydeborg & Sundstrom, 2004), harsh environmental conditions (Gries & Juanes, 1998), and potential competitors (Venter *et al.,* 2008).

Detailed understanding of the complex relationships between *Ranunculus* and juvenile salmonid populations is essential if we are to effectively apply management strategies. Atlantic salmon populations have suffered unprecedented declines in the last few decades and have yet to return to pre-decline numbers (Parrish *et al.,* 1998; Russell *et al.,* 2012; ICES 2018). Natural recovery of salmonid populations is hindered by a decline in both the numbers of juvenile salmon migrating to sea, and, in some regions, the condition of the individuals prior to migrating. Recent works have quantified the relationship between size of salmon pre-migration and the likelihood of individuals returning to freshwater to reproduce (Armstrong *et al.,* 2018; Gregory *et al.,* 2019). Individual condition is strongly influenced by habitat conditions experienced during the first summer for juvenile salmonids (Zabel & Achord, 2004), prompting calls to for better understanding of habitat conditions that maximise numbers and quality of juveniles to inform fisheries management (Armstrong *et al.,* 2018; Gregory *et al.,* 2019). Macrophytes, such as *Ranunculus,* are also under threat and have suffered population crashes in lowland rivers within the last three decades (Cranston, 2004). Lowland rivers have been subjected to considerable anthropogenic impacts including flow modifications, impoundments, bank erosion, increased agricultural inputs, and over abstraction (Cranston, 2004;

Cotton *et al.*, 2006). The confounding influence of many of these factors on each other means that it is challenging to identify important ecological mechanisms that can be used by management to mitigate against another crash. There is, therefore, an urgency to understanding the role of *Ranunculus* in promoting healthy juvenile salmon populations, to be able to better manage habitats to benefit salmon and anticipate the implications of poor macrophyte growth on salmon productivity.

Structural equation modelling (SEM) is a quantitative framework that is increasing in popularity in ecological studies owing to its ability to explore direct and indirect effects among key variables measured to describe a system (Grace, 2006; Fan *et al.,* 2016). This approach has been applied in studies of complex systems and scenarios. For example, it has been used to assess the response of marine food webs to storm frequencies (Byrnes *et al.,* 2011), to identify the direct and indirect role of anthropogenic impacts on trophic cascades (Dorresteijn *et al.,* 2015), and to evaluate direct and indirect causes of forest degradation (Santibáñez-Andrade *et al.,* 2015). I considered the application of SEM suitable for these data which might represent a complex system.

Using data collected during an in-field *Ranunculus* manipulation experiement, I investigated the observed relationships between *Ranunculus* cover and salmon abundances and growth rates. I aimed to determine whether these relationships are direct, through a source of cover, or indirect, through influences to the wider ecosystem dynamics, and the magnitude of these relationships. I expected *Ranunculus* to positively influence variables representing the physical habitat (water depths and velocity heterogeneity), basal resources and prey (organic material and macroinvertebrate prey biomass and size), and competitors (abundances of juvenile salmon and trout). I postulated a postive influence of velocity heterogeneity, fast velocities and prey biomass, and a negative influence of water depths on salmon abundance, representing habitat characteristics considered to be preferred by this species. I expected velocity heterogeneity, prey biomass and size to promote higher salmon growth rates, but fast velocities and abundances of salmon and trout competitors to negatively impact growth rates.

5.3 Methods

5.3.1 Ranunculus manipulation experiment and data

The in-field *Ranunculus* manipulation experiment took place over two years (2016-2017) on the North stream, a carrier of the river Frome, a lowland river situated in Dorset, UK (Figure 3.1). Three blocks, approximately 100 m in length, were selected on the North Stream in locations with similar physical habitat, existing *Ranunculus* beds and no riparian canopy. At each block, three sites, 20 m in length, were designated and each assigned a different *Ranunculus* treatment. Following manipulation of the existing *Ranunculus* plant cover in spring (March/April) of each year, the treatments of low (<10%), medium (30-40%) and high (>60%) cover were maintained throughout the year, producing a gradient of *Ranunculus* cover until the plants began natural senescence in autumn. On four sample occasions between June and October of each year, juvenile salmonid populations, aquatic macroinvertebrates and basal resources were sampled, and *Ranunculus* cover, water velocity and depths were recorded. Previous findings from this experiment showed that both salmon abundance and salmon growth rates were enhanced by *Ranunculus* during summer months (Chapters 3 and 4). I used these data to investigate whether these positive influences were driven by direct or indirect effects of *Ranunculus* cover.

Salmon abundance and growth rates

Salmon abundance and biometric data were collected between June and October of each year at each of the nine sites (see Section 3.3.2 *Fish abundance, body size and retention rates* for full fish sampling procedure). Growth rates of individual salmon were calculated using weight measurements of individuals that were recaptured in the same site, with the assumption that the individuals had been exposed to the site-specific *Ranunculus* cover for the duration of the growing period measured. Growth in body mass was calculated using the standardised mass-specific growth rate estimation (Ostrovsky, 1995), adapted to incorporate thermal units of degree days (see Section 4.3.2 for growth rate calculation procedure).

Physical habitat variables

Physical habitat variables were recorded at 25 evenly spaced quadrats (0.5 x 0.5 m) per site, at each sample occasion. *Ranunculus* cover was estimated as the percentage quadrat cover, water depth was measured (cm), and water surface velocity was visually estimated as one of five categories [1 = 0-25 cm s^{-1}; 2 = 25-50 cm s^{-1}; 3 = 50-75 cm s^{-1}; 4 = 75-100 cm s^{-1}; 5 >100 cm s^{-1}]. I calculated the site-level proportion of fast velocities as the proportion of velocity categories 3, 4 and 5 recorded in quadrats at a site. Measures of *Ranunculus* cover, water depth and proportion of fast velocities were averaged to create a site-level measure of each variable. The steepness in velocity gradients between a quadrat and its neighbouring quadrats was calculated using the Terrain Ruggedness Index (TRI, Wilson *et al.,* 2007, see Section 2.3.2 for TRI equation). Absolute values of TRI were averaged to represent site-level velocity heterogeneity.

Prey and basal resources

To determine biomass and size of prey, and the resources potentially used by the prey (basal resources), I sampled the benthos at three randomly selected locations per site, at each sample occasion. Using a Surber sample (0.25 m x 0.25 m, mesh aperture 250 µm), I disturbed the substrate by hand for 30 seconds to collect macroinvertebrates and organic material. Samples were preserved in 70 % ethanol solution for sorting, identification and measuring individual macroinvertebrates, and processing of the organic material. All macroinvertebrate specimens were identified to the lowest taxonomic level, counted and measured. These data were subset to include only frequently consumed prey, as determined by observed diet contents of juvenile salmon (see Section 2.3.2 for full details on identifying frequently consumed prey). I used macroinvertebrate measurements to estimate biomass of each taxon, and multiplied the mean biomass by the abundance of each taxon to generate a measure of biomass of preferred prey. I averaged the biomass of each taxon to produce a measure of average size of preferred prey (see Section 3.3.2 *Macroinvertebrate prey biomass* for full procedure). After macroinvertebrate specimens had been picked from the sample, the remaining organic material was dried to constant mass (70°C, 72 h) and weighed, prior to being combusted (550°C, 4 h) and re-weighed. The ash-free dry mass of organic material was calculated by subtracting the combusted weight from the dried weight, producing a measure of *basal resources*. Measures of *biomass of preferred prey*, *average size of preferred prey*, and *basal resources* were averaged across the three Surber samples to create a site-level variable of each.

Using data from the summer months in which *Ranunculus* had a positive effect on both salmon abundance and growth rate, included August and September data to investigate salmon abundance (*n* = 36), and June and August data to investigate salmon growth rates (*n* = 97). Explanatory variables used in the growth rate analysis were averaged across June and August to represent average conditions during the growth period. Although trout abundance and growth rates were recorded during the experiment, I did not consider them in this analysis due to the low number of fish caught in 2016. Additionally, no influence of *Ranunculus* cover on trout growth rates was identified (Chapter 4) for which to explore in this analysis.

5.3.2 Statistical analyses

To investigate whether and how the effects of *Ranunculus* cover on salmon abundance and growth rates were mediated by changes in the physical habitat, food resources and/or competition, I applied confirmatory path analysis (Grace, 2006) in a piecewise SEM framework (Lefcheck, 2016). Piecewise SEM fits multiple component models within a global model to allow for testing of direct and indirect effects within a single causal network (Shipley, 2009; Lefcheck, 2016). The component models are solved separately and are therefore appropriate for smaller sample sizes and different assumed error distributions (Shipley, 2000; Shipley, 2009). I constructed the global path model for each main response variable (abundance and growth rate) based on previously determined relationships (Chapters 3 & 4), and other hypothesised drivers of salmonid abundance and growth rates (Table 5.1).

First, I explored whether the observed positive influence of *Ranunculus* cover on salmon abundance was best represented as a direct effect of cover, or an indirect effect operating through changes to the physical environment and prey resources associated with *Ranunculus* cover (Figure 5.1a). The path model consisted of a set of linear regressions (identity-link function), describing the variation in variables representing physical environment or prey resources, and a negative binomial regression (log-link function), describing the variation in salmon abundance. A negative binomial distribution was used to account for potential overdispersion in the abundance data and log site area (m^2) was included in the model as an offset to account for variation in abundance that might be due to differences in habitat size (O'Hara & Kotze, 2010). I also down-weighted occasions when no salmon were captured (n = 2/36) because zero captures do not contribute to estimating the effect of the explanatory variables on abundance (see Section 3.3.3. *Effect of Ranunculus cover on salmonids* for weighting procedure). Model residuals were inspected to ensure assumptions of homogeneity, normality and independence were not violated.

Table 5.1. Summary of the variables used in path analysis of salmon abundance (*n* = 36) and growth rates (*n* = 97) with mean and standard error (prior to transformation/standardising).

Variable (unit)	**Type**	**Error**	**Model**	**Mean (± SE)**
Salmon abundance (N)	Response	Negative binomial	Abundance	14.47 (2.07)
Proportion of fast velocities (%)	Response/Explanatory	Gaussian	Abundance	0.62 (0.04)
Velocity heterogeneity (Index)	Response/Explanatory	Gaussian	Abundance	0.80 (0.06)
Water depth (cm)	Response/Explanatory	Gaussian	Abundance	31.58 (1.82)
Total biomass of preferred prey (mg)	Response/Explanatory	Gaussian	Abundance	51.54 (10.6)
Basal resources (mg)	Response/Explanatory	Gaussian	Abundance	0.83 (0.07)
Ranunculus cover (%)	Explanatory	-	Abundance	34.00 (4.28)
Salmon growth rates (Ω)	Response	Gaussian	Growth rate	0.68 (0.02)
Average salmon abundance (N)	Response/Explanatory	Negative binomial	Growth rate	33.97 (1.45)
Average trout abundance (N)	Response/Explanatory	Negative binomial	Growth rate	13.38 (1.05)
Average proportion of fast velocities (%)	Response/Explanatory	Gaussian	Growth rate	0.72 (0.01)
Average velocity heterogeneity (Index)	Response/Explanatory	Gaussian	Growth rate	0.96 (0.05)
Average total biomass of preferred prey (mg)	Response/Explanatory	Gaussian	Growth rate	164.61 (10.93)
Average size of preferred prey (mg)	Response/Explanatory	Gaussian	Growth rate	0.86 (0.10)
Average *Ranunculus* cover (%)	Explanatory	-	Growth rate	53.91 (3.54)

Second, I investigated whether the observed positive effect of *Ranunculus* cover on salmon growth rates was best represented as a direct effect of cover, or an indirect effect operating through changes to the physical environment, prey sources and/or abundance of competitors (Figure 5.2a). This path model consisted of a set of linear and negative binomial regressions to describe physical habitat, prey resource and salmonid abundance variables as described above, and a linear mixed effect model (identity link function) to describe variation in salmon growth rates with a random intercept of site to account for multiple measures (individuals) at each site.

Path models for both salmon abundance and growth rate were fitted and model performance was evaluated using R package piecewiseSEM (Leftcheck, 2016), which applies Shipley's (2000) directed-separation test to determine if all variables are conditionally independent and identify any important missing links in the path model. Any missing links that were ecologically important were incorporated into the model, and non-significant links were dropped to ensure they did not have an undue influence on the remaining paths in the system before refitting the model (Tables S5.1 – S5.2 outline the specific process of removal/addition of links). The goodness-of-fit of models fitted to individual response variables were measured using marginal R^2 and overall SEM adequacy was evaluated with the approximately distributed Chi-squared Fisher's C-statistic (Shipley, 2009). Prior to model fitting: (1) percentage explanatory variables were arcsine transformed according to $(asin(x/100) \times 2/\pi)$, where x is the explanatory variable; (2) collinearity of explanatory variables was assessed using Pearson's correlation, none of which were highly correlated ($r \geq |0.6|$, Dormann *et al.,* 2013, Figures. S5.1 – S5.2); and (3) all numerical explanatory variables were standardised prior to analyses by subtracting their mean and dividing by their standard deviation. All statistical analyses were performed in R version 3.4.4 (R Development Core Team, 2018), utilising R packages lmerTest (Kuznetsova, Brockhoff & Christensen, 2017) and MASS (Venables & Ripley, 2002), in addition to those previously mentioned.

5.4 Results

5.4.1 Salmon abundance

There was a strong and positive direct effect of *Ranunculus cover* on salmon abundances ($\gamma = 0.58$, $p < 0.001$) and an overall positive effect of *Ranunculus* (Table 5.2a), which was mediated through water velocities and depths (Figure 5.1b). *Ranunculus cover* was positively associated with increased *velocity heterogeneity* ($\gamma = 0.45$, $p = 0.005$), which had a negative association with the *proportion of fast velocities* ($\beta = -0.30$, $p = 0.07$). *Proportion of fast velocities* in turn had a positive effect on salmon abundances ($\beta = 0.28$, $p = 0.01$). *Ranunculus cover* was also positively associated with increased water depths ($\gamma = 0.38$, $p = 0.02$), which was negatively related to salmon abundance ($\beta = -0.38$, $p = 0.001$). There was no significant effect of *velocity heterogeneity* or *biomass of preferred prey* on salmon abundance, and *Ranunculus cover* was not related to *basal resources* or *biomass of preferred prey*. Consequently, these pathways were not retained in the final model, though there was a positive relationship between *basal resources* and *biomass of preferred prey* ($\beta = 0.36$, $p = 0.06$). The model was an adequate representation of the data (i.e. all paths were judged to be independent: Fisher's $C_8 = 10.8$, p value = 0.22), and explained a high amount of variation in salmon abundance ($R^2 = 0.54$). Model residuals did not violate assumptions of homogeneity, normality or independence.

Table 5.2. Standardised effects of the paths retained in the best fitting model between *Ranunculus* cover (R) and salmon abundance (A) and growth rates (GR), shown in section (a) and (b), respectively. Variables represented as VH – velocity heterogeneity, FV – fast velocity, WD – water depth, PS – average size of preferred prey, P – total biomass of preferred prey. Indirect effects are calculated by multiplying the partial path coefficients and represent the effect of *Ranunculus* on salmon abundance/growth rates directly and mediated by the physical habitat/food resource variables. The overall effect of *Ranunculus* on salmon abundance/growth rate is calculated by summing all indirect effects.

Response variable	**Pathways**	**Indirect effects**	**Overall effect**
(a)			
Salmon abundance	R > A	0.58	0.40
	R > VH > FV > A	-0.04	
	R > WD > A	-0.14	
(b)			
Salmon growth rates	R > VH > GR	0.14	0.37
	R > PS > GR	0.67	
	R > P > PS > GR	-0.06	
	R > VH > PS > GR	-0.29	
	R > VH > FV > PS > GR	-0.09	

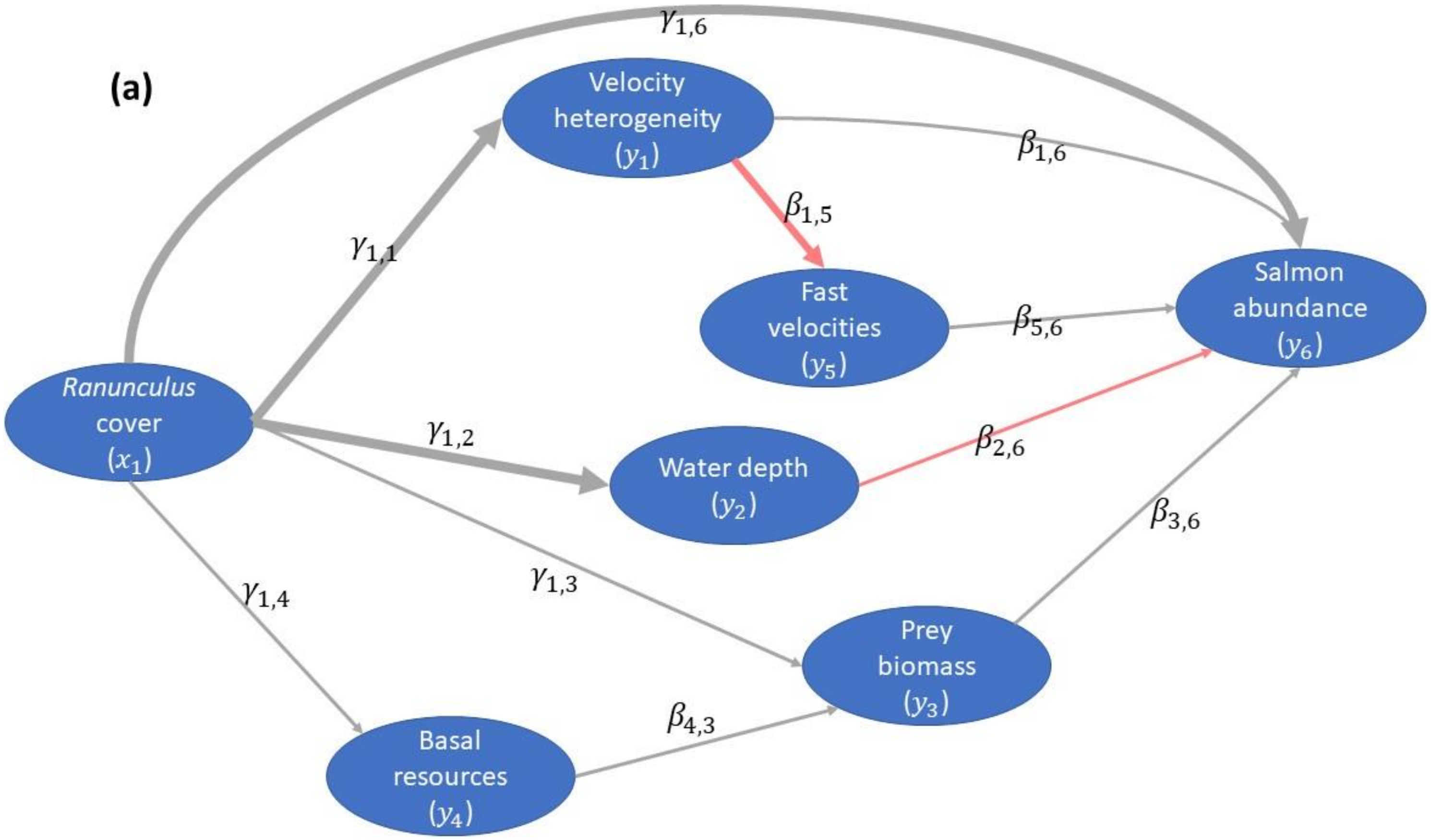


Figure 5.1. Hypothesised relationships and results of the piecewise SEM to describe variation in salmon abundance. (a) path diagram representing hypothesis of direct and indirect effects of *Ranunculus* cover on salmon abundance, γ represents links between an exogenous and endogenous variable, and β represents links between two endogenous variables, numbers correspond to the variable number, e.g. x_1, y_2, that are linked, [continued]

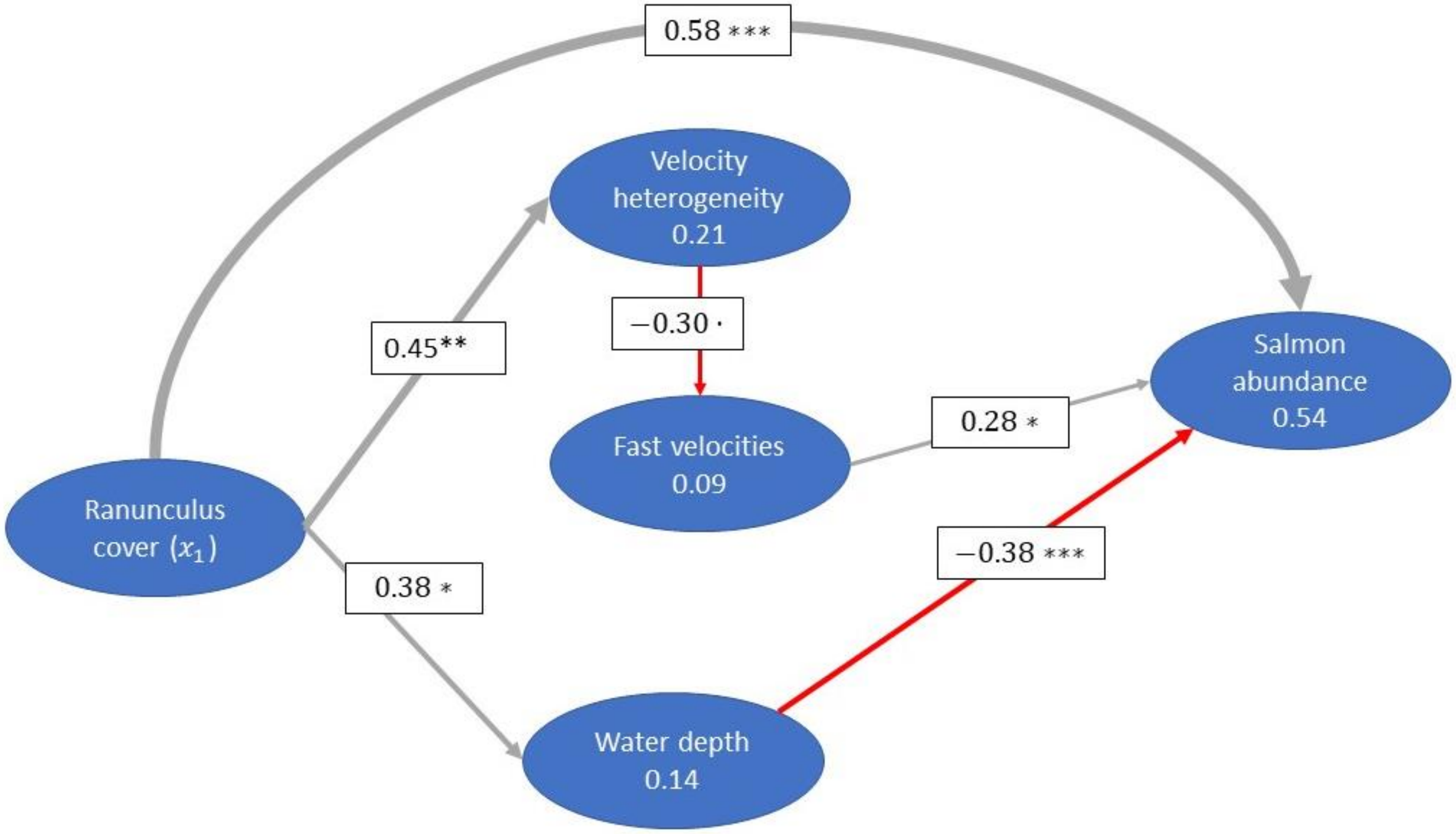


Figure 5.1. [continued] (b) results of the final piecewise SEM testing direct and indirect effects of *Ranunculus* cover on salmon abundance. Non-significant pathways were omitted from the final model. Standardised coefficient estimates are shown for each pathway in boxes, significance levels are denoted as *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, · $p < 0.1$, R^2 values for each component response variable are shown under the response variable name, strength of effect is shown by the weight of the line, with stronger effects in thicker lines, positive effects are in grey, negative effects are in red.

5.4.2 Salmon growth rates

The direct positive influence of *Ranunculus* cover on salmon growth rates was not retained in the path model. Instead, there were multiple indirect influences of *Ranunculus* cover on growth rates via physical habitat and prey resource variables (Figure 5.2b). The strongest effect of *Ranunculus cover* was a positive relationship with *mean size of preferred prey* ($\gamma = 0.98$, $p < 0.001$), which was positively related to salmon growth rates ($\beta = 0.68$, $p < 0.001$). *Velocity heterogeneity* was positively related to *Ranunculus cover* ($\gamma = 0.55$, $p < 0.001$), which, in turn, was positively related to salmon growth rates directly ($\beta = 0.25$, $p = 0.03$) and indirectly through a negative relationship with *mean size of preferred prey* ($\beta = -0.77$, $p < 0.001$) and *proportion of fast velocities* ($\beta = -0.59$, $p < 0.001$). *Proportion of fast velocities* had a positive effect on *mean size of preferred prey* ($\beta = 0.41$, $p < 0.001$), and thus indirectly influenced salmon growth rates. *Ranunculus cover* was positively related to *biomass of preferred prey* ($\gamma = 0.39$, $p < 0.001$), which in turn was negatively related to *mean size of preferred prey* ($\beta = -0.24$, $p < 0.001$). The influence of both *salmon* and *trout abundance* on salmon growth rates were not significant, and so these variables were not retained in the best model. *Biomass of preferred prey* and *proportion of fast velocities* did not directly affect salmon growth rates, so these pathways were also removed. The overall effect of *Ranunculus cover* on growth rates was positive (Table 5.2b), and the model was judged to be an adequate representation of the data (Fisher’s $C = 4.95_{12}$, $p = 0.96$). The model explained a high proportion of the variation in salmon growth rates (marginal $R^2 = 0.49$), moderate levels of variation in the *velocity heterogeneity* ($R^2 = 0.31$) and *proportion of fast velocities* ($R^2 = 0.36$), and most variation in *mean size of prey* ($R^2 = 0.94$). Model residuals did not violate assumptions of homogeneity, normality or independence.

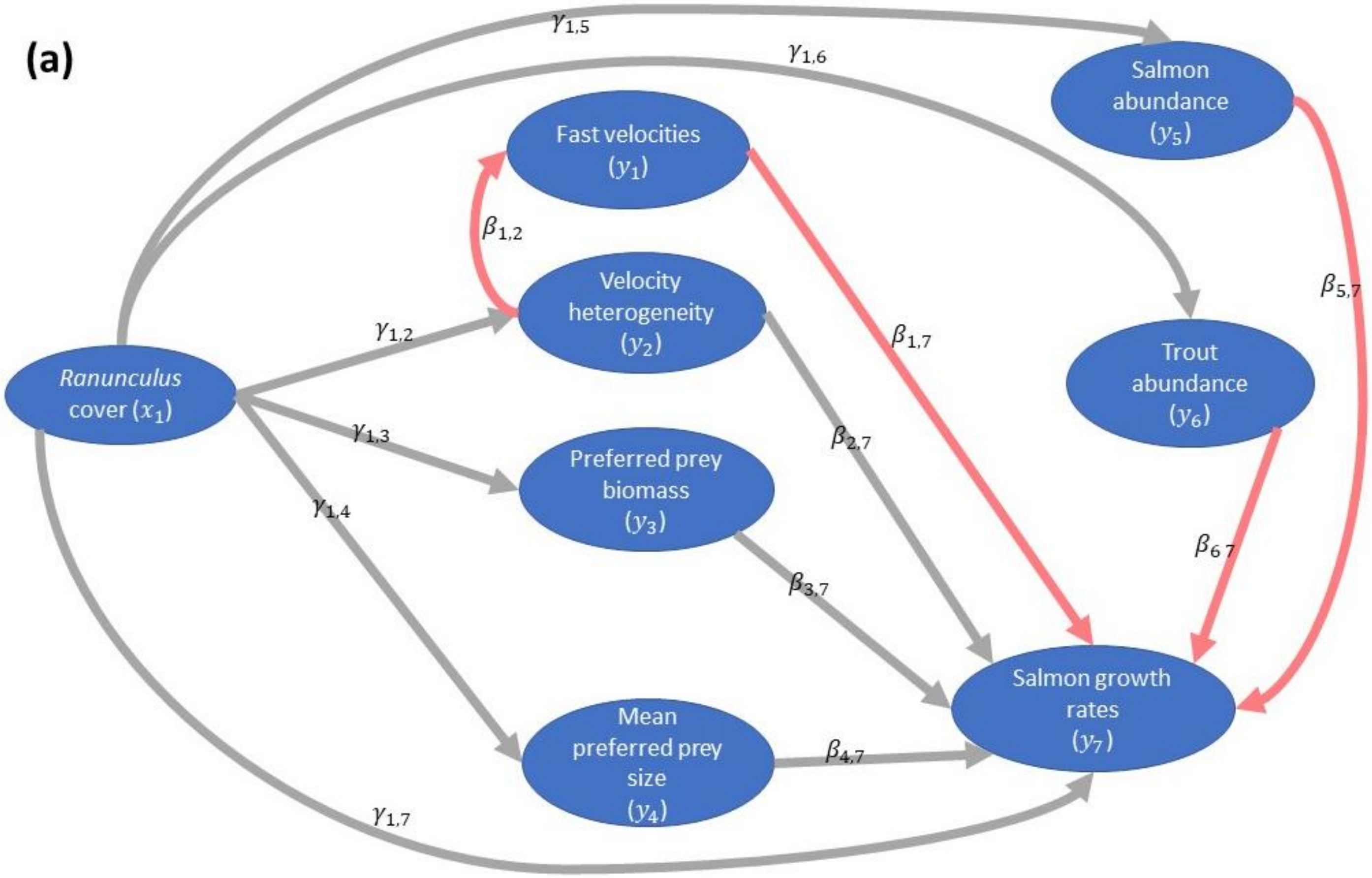


Figure 5.2. Hypothesised relationships and results of the piecewise SEM to describe variation in salmon growth rates. (a) path diagram representing hypothesis of direct and indirect effects of *Ranunculus* cover on salmon growth rates, γ represents links between an exogenous and endogenous variable, and β represents links between two endogenous variables, numbers correspond to the variable number, e.g. x_1, y_2, that are linked, [continued]

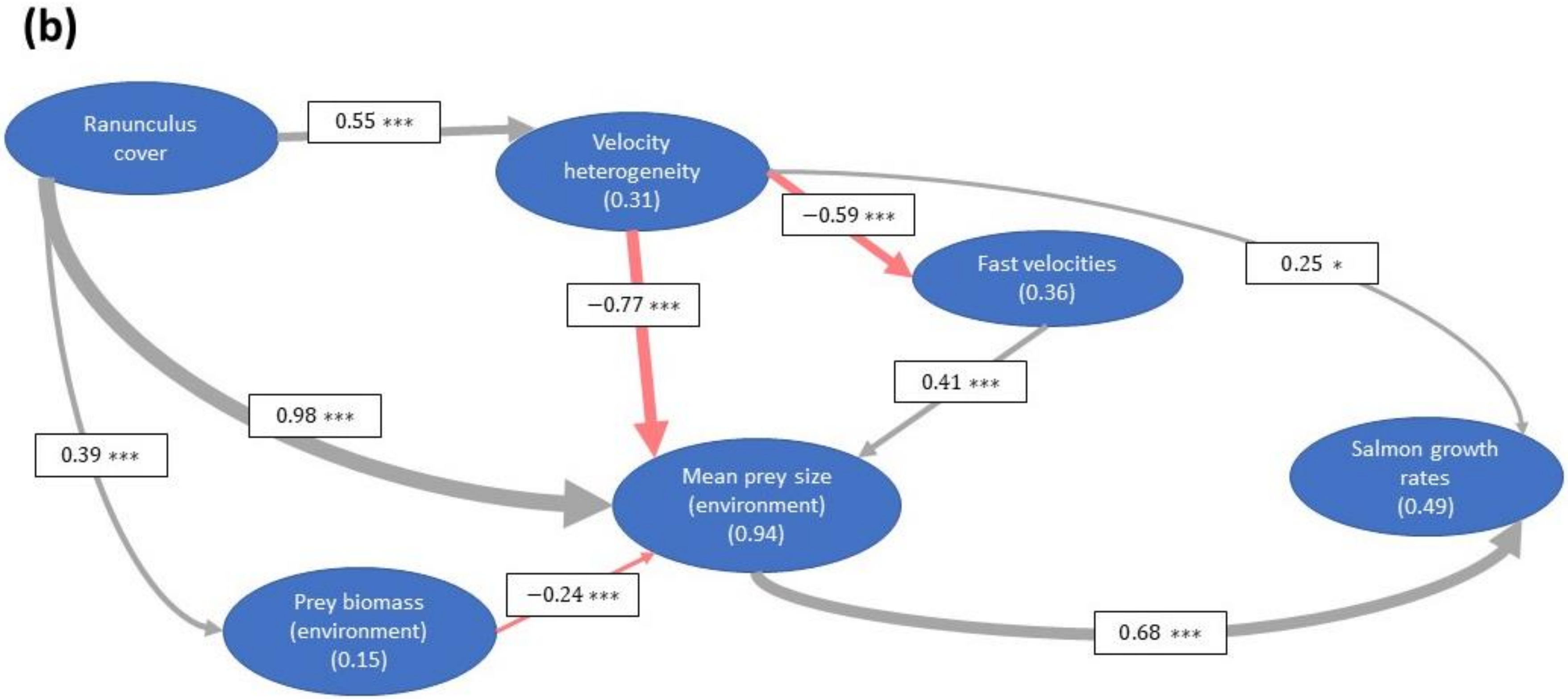


Figure 5.2. [continued] (b) results of the final piecewise SEM testing direct and indirect effects of *Ranunculus* cover on salmon growth rates. Non-significant pathways were omitted from the final model, and missing paths were identified using d-separation tests and incorporated. Standardised coefficient estimates are shown for each pathway, significance levels are denoted as *** $p < 0.001$, * $p < 0.05$, R^2 values for each component response variable are shown under the response variable name, strength of effect is shown by the weight of the line, with stronger effects in thicker lines, positive effects are in grey, negative effects are in red.

5.5 Discussion

The positive effect of *Ranunculus* cover on salmon abundance and growth rates observed during summer months (Chapters 3 and 4), was driven by a direct effect of cover and indirect effects operating through multiple pathways, respectively. These findings highlight the key influence of macrophytes on salmonid communities inhabiting lowland rivers. Salmon abundance was strongly influenced by a direct effect of *Ranunculus* and indirectly, through influences on water depths and velocities. In contrast, salmon growth rates were not substantially affected by a direct effect of *Ranunculus,* but instead were influenced indirectly via impacts on water velocities and prey resources. Several indirect pathways were identified in each analysis, via physical habitat and food resource variables, highlighting the potential of *Ranunculus* to influence many ecosystem components in lowland rivers.

Higher *Ranunculus* cover was directly associated with higher abundances of salmon, supporting a theory proposed by Riley *et al.* (2009) that densities of juvenile salmonids were determined by availability of shelter, rather than food resources. Greater plant cover increases the area of shelter afforded by both the floating canopy on the water surface, to protect salmon from aerial predators (Johnsson, Rydeborg & Sundstrom, 2004), and a complex vertical structure throughout the water column to shield or aid evasion from aquatic predators (Dionne & Folt, 1991; Diehl & Kornijow, 1998). Such structural complexity could result in plant cover being preferable habitat, attracting more individuals and resulting in reduced mortality rates through increased predator evasion. Higher abundance of salmon may also result from reduced vision of salmon occupying patches with high *Ranunculus* cover. Visual isolation from competitors can reduce aggressive behaviours, and consequently the territory size defended by an individual (Fraser, Metcalfe &

Thorpe, 1993; Imre *et al.,* 2002; Venter *et al.,* 2008), such that the structural complexity of *Ranunculus* might support more numerous, smaller territories, increasing the effective carrying capacity of a site (Venter *et al.,* 2008). The presence and use of shelters by salmon (e.g. boulders, tree roots, aquatic vegetation) can also lead to lower resting metabolic rates (Millidine, Armstrong & Metcalfe, 2006), sheltering from extreme daytime summer temperatures (Gries & Juanes, 1998) and resting out of fast water flows during night (Riley *et al.*, 2006), and therefore be preferred habitat by greater numbers of salmon.

There was a strong, positive effect of fast velocities on salmon abundance, which is consistent with studies that suggest water velocity is a key determinant of juvenile salmon habitat selection (Morantz *et al.,* 1987; Cunjak, 1988; Girard, Grant & Steingrimsson, 2004). Body morphology can influence habitat choice by fish (Riddell & Leggett, 1981; Armstrong *et al.,* 2003), and the large pectoral fins and streamlined body assist juvenile salmon to maintain position near the riverbed in fast flowing water (Arnold, Webb & Holford, 1991). Fast velocities might be preferred by salmon individuals due to the continuous supply of food resources in the water flow. Salmon prey heavily on three taxonomic groups, *Baetis* sp and *Serratella ignita* (Ephemeroptera), and Simuliidae (Diptera), which are characteristic of drift taxa (Waters, 1972; Chapter 4). Faster water velocity might therefore support a greater number of salmon by providing an adequate supply of drifting invertebrates, to ensure sufficient resources for greater number of individuals. *Ranunculus* cover mediates this effect by its strong influence on velocity heterogeneity, i.e. the steepness of adjacent velocity gradients in and around plant stands (Sand-Jensen, 1998; Wharton *et al.,* 2006). The presence of *Ranunculus* cover in fast water velocities can be particularly beneficial as it offers a nearby low velocity refuge.

The negative effect of water depth on salmon abundance suggests that shallow habitats are preferred during the summer feeding period. Ontogenetic shifts in habitat selection occur in salmonid species, and older and larger fish tend to shift to deeper habitats (Morantz *et al.*, 1987; Maki-Petays *et al.*, 1997). Subsequently, increased water depths are associated with greater abundance of older (and potentially more successful) competitors and predators (Gregory, 1993; Keeley & Grant, 1995). Therefore, salmon individuals may either not select for, or suffer higher mortality rates in deeper water, and so are recorded in fewer numbers in these habitats. Conversely, juvenile salmonid populations in upland rivers avoid shallow water in favour for intermediate depths (Morantz *et al.*, 1987; Girard, Grant & Steingrimsson, 2004), as depth benefits include increased prey encounter rates for drift-feeding salmonids and protection from aerial predators and high flows (Gregory, 1993; Piccolo *et al.*, 2007). *Ranunculus* can provide comparable habitat conditions in lowland rivers, which might diminish the advantages of occupying deeper water over shallow habitats.

Velocity heterogeneity and prey biomass in the environment were not identified as important drivers of salmon abundance, suggesting that shelter has a greater influence than access to prey resources. The strong relationships between *Ranunculus* and velocity heterogeneity and water depth illustrate how macrophytes may shape and influence the physical environment, predominately through altering water flow dynamics. *Ranunculus* was not identified as an important influence on basal resources. This result contrasts with existing knowledge on the ability of *Ranunculus* plant stands to retain substantial amounts of organic material (Gregg & Rose, 1982; Cotton *et al.*, 2006). This could demonstrate a limitation of the benthic sampling procedure, i.e. not enough samples were collected to capture accurate average levels of organic matter associated with site-level *Ranunculus* cover, due to patchy distributions (Downes, Lake & Schreiber, 1993).

Salmon growth rates were not directly affected by *Ranunculus* cover, suggesting that the previously observed positive influence of cover on salmon growth rates (Chapters 3 & 4) was mediated by the physical habitat and food resources associated with *Ranunculus* cover. It was apparent that the effect of *Ranunculus* operated through positive impacts on velocity heterogeneity and average size of preferred prey, which in turn promoted greater growth rates. Both velocity heterogeneity and average size of preferred prey influences foraging gains: benefits will be gained through access to large, nutritionally valuable prey items (Wankowski & Thorpe, 1979; Keeley & Grant, 1997), whilst minimising energy expenditure (Morantz *et al.*, 1987). The biomass of preferred prey did not directly influence growth rates as hypothesised. This suggests either that the availability of quality resources had more influence on salmon growth than the quantity of resources available, or that average size of preferred prey was a less variable characteristic of the macroinvertebrate community than biomass. High velocities were expected to be detrimental to salmon growth rates due to the increased energetic demands of inhabiting fast flowing water (Wankowski & Thorpe, 1979), but a direct influence of fast velocities was not found to be important. Although drift feeding in salmonids is considered to be energetically expensive (Puckett & Dill, 1984, 1985), behaviour responses to foraging in increased velocities, such as reducing attack distances can negate any additional energy costs (Godin & Rangeley, 1989).

For the data used in the growth rate analysis, which was collected during June and August, biomass of preferred prey and average size of preferred prey were directly and positively affected by *Ranunculus* cover. This finding supports the expectation that higher *Ranunculus* cover produces greater abundance and biomass of macroinvertebrates. The relationship between *Ranunculus* cover and preferred prey is likely seasonal, due to the rapid turn-over and multiple annual life cycles of some macroinvertebrate taxa (Wright & Symes, 1999), which could also explain why it wasn't identified in the abundance model that included data later in the year (September). Macrophytes provide new microhabitats that invertebrates can occupy (Hutchens *et al.*, 2004), and plants with complex architectures are purported to support greater macroinvertebrate biomass as surface area for colonisation and protection from predators increases (Heck & Crowder, 1991; Diehl, 1992). Structural complexity from highly dissected *Ranunculus* leaves enhances ability to trap detritus and epiphytic biomass (Gregg & Rose, 1982), therefore provides higher food supply for macroinvertebrates. These increased resources might boost growth of macroinvertebrates and explain why average size of prey was greater in higher *Ranunculus* cover. As larvae of certain macroinvertebrate species, including *S. ignita*, increase in size, individuals shift to low velocity conditions to maintain stability in physical factors such as gas diffusion (Sagnes, Merigoux & Peru, 2008). Low velocity refuges in and around *Ranunculus* plant stands could therefore provide requirements of larger larvae.

The negative influence of biomass of preferred prey and velocity heterogeneity, and positive influence of fast velocities on average size of prey were not originally hypothesised but identified in the model fitting process. This could represent limited availability of food resources under increased competition and the varied habitat preferences of taxa, which are strongly affected by water flow (Barmuta, 1990; Degani *et al.*, 1993; Sagnes, Merigoux & Peru, 2008). Different developmental stages of taxa can have contrasting habitat preferences to suit ontogenetic shifts in habitat and resource requirements; for example, adult Elmidae (Coleoptera) prefer higher water velocities compared to their smaller larvae (Degani *et al.,* 1993). Larger individuals of Ephemeroptera and Trichoptera larvae also utilise high velocity conditions probably to meet increased oxygen requirements and to aid predator evasion (Sagnes, Merigoux & Peru, 2008).

There was no significant influence of salmon or trout abundance on salmon growth rates. This supports previous findings (Chapters 3 & 4), where growth rates of salmon were higher in high *Ranunculus* cover and suggests that growth was not negatively impacted by the abundance of conspecifics. Greater abundances of trout were also found in high *Ranunculus* cover, and dietary niche overlap between the two species was moderate to low, suggesting that they may not be competing intensively for the same resources, and thus numbers of trout might have little influence on salmon growth. This demonstrates the potential of *Ranunculus* cover to produce resilience populations containing greater numbers of salmonid individuals, which can also be of higher condition, and so likely to survive winter and seaward migration periods (Armstrong *et al.,* 2003; Gregory *et al.*, 2019).

Direct and indirect influences of *Ranunculus* underlie greater numbers of higher quality salmon at a reach-scale. Even in these relatively simple path analyses, the important links retained for the two salmon responses demonstrate complex interactions, which govern the impact of *Ranunculus* cover on many variables. This highlights the role of *Ranunculus* as a key aquatic structure that can promote diversity, abundance and quality in individuals of species at various trophic levels by creating suitable physical habitat with adequate food resources. Restoration and enhancement of salmonid ecosystems often utilise artificial structures to create suitable habitat conditions to benefit juvenile salmonids. Recreating the role of

Ranunculus with an artificial structure would be challenging, given its ability to impact many factors. Instead, more research should be directed to understand current and future threats to *Ranunculus* plants in lowland rivers to ensure their resilience and resurgence in anthropogenically impacted ecosystems.

Chapter 6: General discussion

6.1 Discussion

The main aim of this thesis was to produce empirical evidence of the influence of the macrophyte *Ranunculus* in shaping habitats in lowland rivers, to the benefit of juvenile salmonids. Using a combination of field survey and correlation together with a manipulation experiment, I have demonstrated the importance of *Ranunculus* through its potential to support greater numbers, growth opportunities and diet biomass of juvenile salmonids.

Two important references that are frequently cited in this thesis are Riley *et al.*, 2009 and McCormick and Harrison, 2011 because they provide assumed relationships between abundance of macrophytes, and the densities, growth rates and diets of juvenile salmon and trout in lowland rivers. Although they visually estimated macrophyte cover, Riley *et al.* did not attempt to relate macrophyte cover to the salmonid response variables, but rather, tested the influence of closed (dense riparian canopy cover) vs open (removed canopy) sites to assess the impact of riparian canopy on salmonid densities, body length and macroinvertebrate communities. They also did not measure any other physical habitat variables that might influence these responses, but concluded responses of salmonids to be driven by changes in macrophyte cover between the closed and open sites. Similarly, McCormick and Harrison measured cover of instream macrophytes and collected macroinvertebrate samples from macrophyte beds, but only related responses in salmonid densities and body size comparisons between open sites and sites shaded by riparian canopy. McCormick and Harrison did however correlate macrophyte densities to mean total gut contents of juvenile salmon to show a positive influence of macrophytes during August. The work of this thesis builds on these studies by directly (and indirectly) quantifying effects of macrophyte cover on salmonid populations in a lowland river.

It also increases our understanding of how this macrophyte can influence macroinvertebrate salmonid prey and physical habitat conditions. Both of these habitat characteristics could be important for juvenile salmonids and confound effects observed in the salmonid responses. By comparing the performance of other habitat variables, such as water depth, velocities and prey biomass, alongside that of *Ranunculus* cover (Chapters 2, 3 & 5), I have been able to demonstrate the importance of *Ranunculus* in promoting higher abundances and diet biomass of salmon and trout, as well as greater growth rates of salmon in a lowland river (Chapters 2-5).

This thesis complements extensive literature detailing the impact of macrophytes in structuring standing freshwater ecosystems by advancing our knowledge of the holistic role of macrophytes in rivers. By investigating indirect effects of *Ranunculus* on the abundance and growth rates of salmon operating through physical variables, I identified large positive influences of *Ranunculus* cover on water depths and velocity heterogeneity (Chapter 5). These findings suggest that *Ranunculus* cover can encourage habitat complexity at a wider scale, beyond its own intricate structure. This effect of *Ranunculus* is therefore somewhat comparable to large substrates, such as boulders and woody debris, that are found in upland rivers and frequently employed in habitat complexity studies and successful restoration schemes (Binns, 2004; Venter *et al.*, 2008). Using macrophytes in lowland rivers could yield similar habitat complexity to regulate salmonid populations in good quality rivers, and restore habitat function to degraded rivers.

Other habitat variables were considered throughout this thesis to either contrast the effects of *Ranunculus* on salmonid response variables with (Chapters 2 & 3), or to identify whether the habitat variables mediated the effect of *Ranunculus* cover on salmon abundance and growth rates (Chapter 5). Water depth and proportion of fast velocities were used owing to their association with determining the densities of juvenile salmonids (Heggenes, 1990). The negative influence of water depth on salmon abundance during summer and autumn was consistent across two chapters using different analytical techniques (Chapters 3 & 5). These results suggest that shallow water depths are preferred by salmon, which is consistent with studies on salmon habitat use in upland rivers (Wankowski & Thorpe, 1979; Rimmer, Paim & Saunders, 1984). Whereas the finding that trout were more likely to be recaptured in sites with greater water depths, suggest a preference for this habitat. These results contrast with a study on habitat use of individual salmonids in a lowland river (Riley *et al.*, 2006), which observed juvenile trout to occupy shallow (<10 cm) depths, and salmon to occupy both shallow and deeper water (<10 – 55 cm). The study did however base these conclusions on few trout individuals (*n* = 12), and the results could have been influenced by individual habitat preferences, which might not represent larger population requirements. Similar differences in the selection of depths by salmon have been reported in upland rivers (Morantz *et al.*, 1987), which emphasises the importance of monitoring populations locally and not generalising habitat requirements, especially when considering conservation of salmonid populations. Salmon are purported to occupy fast-flowing riffle habitats (e.g. Heggenes, 1990; Heggenes, Saltveit & Lingaas, 1996; Riley *et al.*, 2006) but few studies have quantified an effect of fast water velocities on the abundance or growth rates of salmon (but see Everest & Chapman, 1972). I found a positive relationship between the proportion of fast velocities and salmon abundance (Chapter 5) and change in salmon body size (Chapter 3). Furthermore, I demonstrated that a higher proportion of fast velocities was related to larger average size of preferred prey taxa in the environment (Chapter 5), which could explain why more individuals inhabited sites with faster velocities, and how higher velocities might have influenced change in body length, i.e. through provision of larger, more nutritiously valuable prey items. By testing the effects of fast velocities on multiple response variables pertaining to abundance and growth of salmon, I have produced results that advance our understanding of habitat requirements of salmon beyond observations of habitat use alone.

The sit-and-wait feeding strategy of juvenile salmonids is well described (Morantz *et al.*, 1987; Keeley & Grant, 1997), and studies of habitat use by salmonids incorporating measurements of nose velocities (i.e. the velocity experienced by a fish on its snout (Morantz *et al.*, 1987), and water velocities at observed feeding stations (Rimmer, Paim & Saunders, 1984)), have contributed important knowledge to the microhabitat use of salmonids. In this thesis I aimed to expand this concept to assess how site-level differences in water velocities can support abundances and growth rates of salmonids. By creating a measure of differences in velocities at the larger, reach scale, I was able to quantify the effect of velocity heterogeneity on abundances and growth of juvenile salmonids. A positive effect of velocity heterogeneity at the site-level was ubiquitous in studies on densities (Chapter 2) and abundances (Chapter 3) of trout, which sampled populations over multiple years both throughout the river catchment and locally on a small stream. This is an important finding that can contribute to knowledge bases informing habitat restoration schemes aiming to increase production of juvenile trout. Another exciting finding from this thesis was the strong, positive relationship between *Ranunculus* cover and velocity heterogeneity, and a positive effect of *Ranunculus* on salmon growth rates that was mediated by velocity heterogeneity (Chapter 5). Due to the lack of large substrates in lowland rivers, I hypothesised that *Ranunculus* would provide essential structure to influence physical habitat variables, such as creating varied velocities that might benefit salmonids. Together these findings illustrate the importance of *Ranunculus* in providing suitable physical habitat conditions for salmonids in lowland rivers.

The impacts of *Ranunculus* cover on macroinvertebrate standing stock, measured in biomass and average taxa size, were less clear, perhaps a consequence of the spatial variation in macroinvertebrate assemblages in streams (Downes, Lake & Schreiber, 1993). I identified a positive effect of *Ranunculus* cover on the total biomass of macroinvertebrates in the environment during August, but this relationship was reversed during June. Additionally, there was no influence of *Ranunculus* on average size of invertebrates in the environment (Chapter 4). A positive effect of *Ranunculus* cover on macroinvertebrate biomass or size could be expected through provision of resources and protection from predators (Gregg & Rose 1982; Warfe & Barmuta, 2004), but the work in this thesis showed higher abundances of salmon and trout associated with higher *Ranunculus* cover (Chapters 2, 3 & 5). There could therefore be fewer salmonids to predate upon macroinvertebrates in low cover sites resulting in abundant and fast-growing macroinvertebrate communities in both low and high *Ranunculus* cover. When I subset the macroinvertebrate data to only include preferred prey taxa, identified as the most frequently consumed prey taxa (Chapter 4), I found a strong positive relationship between *Ranunculus* cover and both the biomass of preferred prey and the average size of preferred prey (Chapter 5). *Ranunculus* could be producing abundant taxa that are favoured by salmon, or alternatively, these taxa were frequently observed in diets of salmon because the salmon are foraging opportunistically in or nearby *Ranunculus* cover, and so more likely to encounter them. While salmon are often described as opportunistic predators (Gibson, 1993), the selection for three of the preferred taxa in high cover (*S. ignita*), low cover (Simuliidae) and across all levels of *Ranunculus* cover (*Baetis* sp.) (Chapter 4) suggests that the prey taxa were particularly desired by, or accessible to, salmon. Therefore, habitats that produce abundant communities of these preferred prey taxa appear to be particularly beneficial to juvenile salmonids for feeding and growth opportunities.

Responses of juvenile trout to *Ranunculus* cover were more challenging to detect, which could be an artefact of their complex life history, i.e. juveniles may remain in the river as resident brown trout or become anadromous sea trout. Due to the involved physiological process of undergoing smoltification (McCormick & Saunders, 1987), juveniles of different morphotypes might diverge in their habitat requirements. It is encouraging however to see that high *Ranunculus* cover also supported greater trout abundance, and prey biomass in the diets, which suggest that the species is not being negatively impacted by the presence of *Ranunculus* cover.

By sampling during summer and autumn months, the work in this thesis identified that the biomass and average size of prey preferred by salmon, growth rates, site fidelity and abundance of salmon (Chapters 3, 4 & 5), as well as abundance of trout (Chapter 3) were most positively influenced by *Ranunculus* cover in June and August. These findings highlight a peak influence of *Ranunculus* at the beginning of summer, which corresponds to its peak biomass in the river Frome (Wood *et al.*, 2012). This knowledge should direct efforts to maintaining suitable macrophyte cover during this important time period to ensure the greatest positive impact on salmonids, both directly, and indirectly through influences on their prey resource.

In conclusion, this thesis has advanced our knowledge on the holistic role of macrophytes in lowland rivers through testing the influence of *Ranunculus* on physical habitat variables and macroinvertebrate communities and characteristics. Additionally, this work contributes critical knowledge of the influence of a dominant macrophyte on juvenile salmonid populations in lowland rivers. The influence of *Ranunculus* cover on diet content, composition and selection of salmon and trout and their dietary niche overlap, provides knowledge alongside very few studies of salmonid diet in lowland rivers (Riley *et al.*, 2009), and evidence for coexistence between these sympatric species, which are often considered to outcompete one another in similar habitats (Bardonnet & Bagliniere, 2000). The demonstrated positive effects of *Ranunculus* on juvenile salmonid reach-scale population sizes and growth rates (Figure 6.1) are encouraging findings amid a period of decline in both number and size of salmon in some regions (Gregory *et al.,* 2017; ICES 2018). Ensuring natural macrophyte growth in lowland rivers, therefore, could improve the population viability of at-risk salmonid populations, and contribute to a diverse and productive river ecosystem.

6.2 Management recommendations and future directions

- The findings of this thesis have possible implications for management of both riparian and aquatic vegetation. Restoration of riparian vegetation might mitigate against rising temperatures and create a buffer to protect the river from agricultural runoffs and nutrient enrichment, but dense canopy cover tends to reduce macrophyte growth (Riley *et al.*, 2009; McCormick &

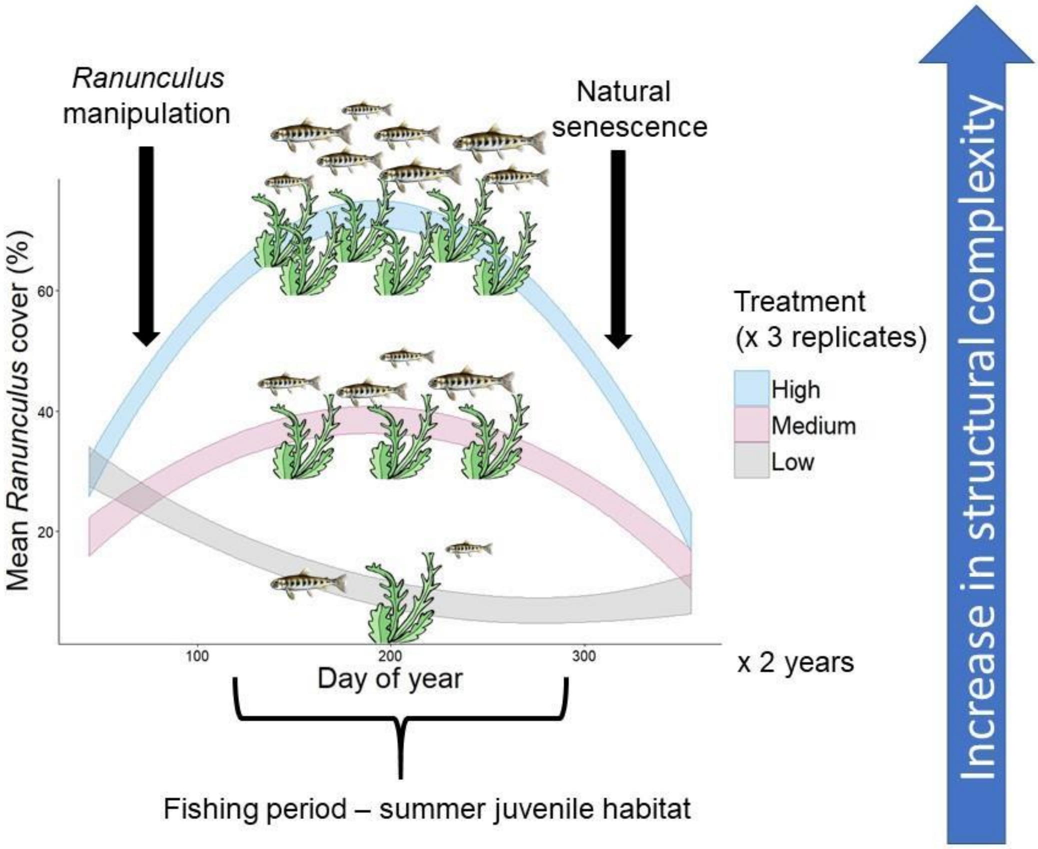


Figure 6.1. Graphical representation of the experimental design and findings from the *Ranunculus* manipulation experiment (Chapters 3 & 4).

- Harrison, 2011). Macrophyte cutting in lowland rivers is undertaken to promote suitable recreational fisheries and prevent flooding of adjacent farmland, but these practices can disrupt macrophyte communities and potentially negatively influence densities of juvenile salmon. We recommend that land managers consider maintaining a heterogenous river ecosystem, and avoid full canopy closure or excessive macrophyte cutting, particularly in areas downstream of habitual salmonid spawning sites.
- In this project, I have identified short-term influences of *Ranunculus* cover and the habitat it creates for juvenile salmonid populations. It would be

exciting to see whether this influence manifests in population viability in the long term, (e.g. increased overwinter survival, higher smoltification rates or marine survival). The set-up for long-term monitoring of salmonid populations on the river Frome allows for the identification of tagged salmonids at various life stages, from smolts leaving the river and adults returning from the sea, thus investigating this long-term influence is possible, if sufficient data are available.

- Additionally, attempting to tease apart the pattern of declining number of juveniles and the declining amount of *Ranunculus* in late summer/early autumn could be fruitful to understanding whether the loss of habitat (i.e. *Ranunculus* cover) encourages migration of juveniles out of feeding territories. This could be of importance to salmonid populations if summer populations of *Ranunculus* cover were compromised, and certainly warrants further investigation. It would be fascinating to establish the plasticity of juvenile salmonid life histories in lowland rivers to respond to changes in macrophyte communities, which, as natural organisms themselves, can fluctuate in presence and abundance. As lowland rivers such as the river Frome are relatively productive, the majority of anadromous salmonids migrate to sea after their first year in the river. It would be interesting to see whether changes in macrophyte communities during the summer could influence this proportion of migrants in the following spring.
- Extending the manipulation study to other lowland rivers with salmonid populations across the UK and Europe would be beneficial, to increase the generality of the findings for a greater potential application. There is a growing body of literature concerning how the importance of macrophytes

as structural engineers is influenced by their morphology and architecture as well as density and biomass (e.g. Kovalenko, Thomaz & Warfe, 2012). It would be interesting to compare influences of macrophytes with simpler morphologies to *Ranunculus* which is relatively complex in structure. It would also be advantageous to monitor responses of populations of other aquatic organisms inhabiting lowland rivers to assess their response to *Ranunculus* cover.

- Having demonstrated the importance of *Ranunculus* for juvenile salmonids, it is essential to understand the possible future status of this native macrophyte. In southern lowland rivers, populations of *Ranunculus* suffered a crash during the early 1990's, which could not be attributed to one key factor, but likely a synergy of effects (Cranston, 2004). Possible drivers of this crash included low flows, which might increase in frequency and severity under global climatic change (Marx *et al.*, 2018). Management of channels, e.g. deepening and widening, and over abstraction were also cited to have had a detrimental impact of *Ranunculus*, through consequent reductions in velocity (Cranston, 2004). Finally, increased siltation, nutrient enrichment and vegetation management were thought to have created conditions that allowed other macrophytes, such as algae, to outcompete *Ranunculus* and negatively impacted its growth. Further research is encouraged to establish current threats that we may be able to currently control for, as this could mitigate any future impacts associated with climatic changes to water flows and temperatures.

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Appendices

Supplementary tables

Table S2.1. Sites sampled in 2015 (*n* = 18), 2016 (*n* = 19), and 2017 (*n* = 22). Sites are ordered in ascending distance from the tidal limit. Position in Frome catchment determined by Environment Agency operational catchment (http://environment.data.gov.uk/catchment-planning/OperationalCatchment/1120)

Site	Length (m)			Average width (m)			Average Ranunculus cover (%)			Position in river catchment	Missing data
	2015	*2016*	*2017*	*2015*	*2016*	*2017*	*2015*	*2016*	*2017*		
1	100	100	100	14.8	16.5	19.8	7	10	51	Lower	
2	NA	91	91	NA	10.6	11.7	NA	58	71	Lower	
3	100	100	100	17.1	15.6	20.0	4	32	42	Lower	
4	60	60	60	14.0	12.5	14.1	0	2	6	Lower	2015: No macroinvertebrate data
5	NA	60	60	NA	7.1	7.6	NA	1	20	Lower	
6	NA	90	85	NA	8.8	7.5	NA	32	16	Lower	
7	60	60	60	11.6	9.6	11.5	39	15	10	Lower	2015: No macroinvertebrate data
8	100	NA	100	8.3	NA	8.3	49	NA	65	Lower	
9	114	114	85	7.5	14.6	11.4	7	12	23	Lower	
10	100	100	100	5.7	7.3	7.2	19	33	50	Lower	
11	100	100	100	12.0	12.2	12.7	17	18	61	Lower	
12	74	74	55	9.2	11.3	10.5	6	27	59	Lower	
13	50	50	50	5.5	5.6	5.6	34	8	23	Lower	
14	100	100	100	14.5	14.5	14.2	8	4	8	Lower	
15	100	NA	100	8.8	NA	9.9	36	NA	62	Upper	
16	100	100	100	10.7	11.3	11.8	41	77	67	Upper	
17	95	95	95	11.3	10.9	12.0	9	55	54	Upper	
18	110	110	110	5.6	5.4	5.1	5	31	10	Upper	
19	NA	90	90	NA	10.2	10.3	NA	25	12	Upper	
20	90	NA	90	7.8	NA	7.9	2	NA	7	Upper	
21	80	80	75	11.7	10.0	10.2	21	11	17	Upper	2016: No macroinvertebrate data
22	85	85	85	8.0	8.1	8.8	38	50	52	Upper	

Table S2.2. Abundance of macroinvertebrates in kick samples per site (1 – 22) and year (2015 – 2017): total macroinvertebrate abundance; abundance of frequently consumed prey (FCP) for salmon and trout, and percentage contribution of FCP taxa to total abundance.

	2015					2016					2017				
Site	Total	FCP		% contribution		Total	FCP Abundance		% contribution of		Total	FCP		% contribution	
		Salmon	*Trout*	*Salmon*	*Trout*		*Salmon*	*Trout*	*Salmon*	*Trout*		*Salmon*	*Trout*	*Salmon*	*Trout*
1	7201	3614	4100	50.1	56.9	2481	1428	1553	57.6	62.6	3364	2335	2391	69.4	71.1
2	NA	NA	NA	NA	NA	2014	1297	1371	64.4	68.1	3299	2351	2380	71.3	72.1
3	7322	5224	5306	71.3	72.5	2472	1656	1707	67.0	69.1	199	21	25	10.6	12.6
4	NA	NA	NA	NA	NA	1695	1072	1109	63.2	65.4	4026	2198	2322	54.6	57.7
5	NA	NA	NA	NA	NA	1872	821	1007	43.9	53.8	2435	1229	1376	50.5	56.5
6	NA	NA	NA	NA	NA	3315	2303	2379	69.5	71.8	4495	2399	2549	53.4	56.7
7	NA	NA	NA	NA	NA	3215	1722	1823	53.6	56.7	7125	3854	4350	54.1	61.1
8	6366	2274	2607	35.7	41.0	NA	NA	NA	NA	NA	4226	2934	3021	69.4	71.5
9	4776	2085	2311	43.7	48.4	4325	2990	3115	69.1	72.0	4033	1684	2401	41.8	59.5
10	915	111	168	12.1	18.3	4565	3279	3464	71.8	75.9	5688	3135	3705	55.1	65.1
11	4162	2582	2757	62.0	66.2	2644	1825	1863	69.0	70.5	4367	3337	3450	76.4	79.0
12	7571	4292	4376	56.7	57.8	2209	1157	1224	52.4	55.4	2333	1727	1793	74.0	76.9
13	3219	1837	1976	57.1	61.4	4804	3265	3482	68.0	72.5	7540	5140	5850	68.2	77.6
14	5783	4823	4885	83.4	84.5	4294	2931	3013	68.3	70.2	2505	1783	1948	71.2	77.8
15	2451	816	940	33.3	38.4	NA	NA	NA	NA	NA	584	292	320	50.0	54.8
16	3714	2202	2278	59.3	61.3	3116	2261	2339	72.6	75.1	5495	4553	4695	82.9	85.4
17	4404	3387	3433	76.9	78.0	2473	1066	1102	43.1	44.6	4132	2634	2718	63.7	65.8
18	4142	2337	2362	56.4	57.0	4716	2518	2589	53.4	54.9	2306	1079	1138	46.8	49.3
19	NA	NA	NA	NA	NA	3036	2109	2201	69.5	72.5	6557	3762	3933	57.4	60.0
20	5531	3295	3386	59.6	61.2	NA	NA	NA	NA	NA	2139	1027	1147	48.0	53.6
21	5595	3868	4056	69.1	72.5	NA	NA	NA	NA	NA	8255	5909	6316	71.6	76.5
22	1802	990	1082	54.9	60.0	3244	2664	2737	82.1	84.4	596	292	316	49.0	53.0

Table S2.3. Linear models were used to test for differences in the explanatory variables between years. We report the *p*-values to show statistical significance.

	Comparison years		
Variable	2015:2016	2015:2017	2016:2017
Ranunculus cover	0.31	0.02*	0.17
Depth	0.45	0.11	0.40
Velocity Heterogeneity	0.68	0.51	0.81
Fast velocities	0.35	0.83	0.43
Distance from tidal limit	0.27	0.48	0.63
Salmon prey abundance	0.12	0.50	0.32
Trout prey abundance	0.72	0.72	0.24
Salmon redds	-	0.18	-

Table S2.4. Full candidate model selection process for 3-year analysis. AIC statistics are supplied for initial Stage 1 to determine which variables should be retained for further analyses.

Stages of model development	Hypothesis tested	Candidate models		Salmon		Trout	
		Model no.	Model Terms	AICc	ΔAICc	AICc	ΔAICc
Stage 1: Identify most important (ΔAICc >1) and least important (ΔAICc <1) variable/s for both species.	Global model	Global	Year, Ranunc, Depth, FastVelocity, VelocityHet, Abundance, Distance	-140.4	2.79	-268.6	2.46
	Distance is not important	1	Year, Ranunc, Depth, FastVelocity, VelocityHet, Abundance	-138.9	4.28	-267.7	3.28
	Prey abundance is not important	2	Year, Ranunc, Depth, FastVelocity, VelocityHet, Distance	-141.5	1.74	-270.1	0.92
	Velocity heterogeneity is not important	3	Year, Ranunc, Depth, FastVelocity, Abundance, Distance	-143.2	0.00	-258.8	12.17
	Fast velocity is not important	4	Year, Ranunc, Depth, VelocityHet, Abundance, Distance	-143.1	0.06	-270.5	0.51
	Depth is not important	5	Year, Ranunc, FastVelocity, VelocityHet, Abundance, Distance	-142.3	0.88	-271.0	0.00
	Ranunculus is not important	6	Year, Depth, FastVelocity, VelocityHet, Abundance, Distance	-142.2	1.02	-269.7	1.30
	Year is not important	7	Ranunc, Depth, FastVelocity,	-130.9	12.29	-258.4	12.65

			VelocityHet, Abundance, Distance				
Keep Year, Distance & Ranunc in all subsequent models as important for both species and omit Depth and Fast Velocity from all subsequent candidate models because not important for either species. Test combinations of remaining variables, i.e. Abundance and Velocity heterogeneity, which are considered to be important for one of the species.							
Stage 2: Test different combinations of most important variables	Velocity heterogeneity and abundance both important	6	Year, Ranunc, Distance, VelocityHet, Abundance				
	Velocity heterogeneity not as important as abundance	7	Year, Ranunc, Distance, Abundance				
	Abundance not as important as velocity heterogeneity	8	Year, Ranunc, Distance, VelocityHet				
	Velocity heterogeneity and abundance not important	9	Year, Ranunc, Distance				
Test all variables individually alongside Year to test for importance of Ranunculus vs other variables.							
Stage 3: Test all variables individually alongside Year to test for important of Ranunculus vs other variables	Ranunculus most important	10	Year, Ranunc				
	Depth most important	11	Year, Depth				
	Fast velocity most important	12	Year, FastVelocity				
	Distance most important	13	Year, Distance				
	Prey abundance most important	14	Year, Abundance				
	Velocity heterogeneity most important	15	Year, VelocityHet				
If Ranunculus included in the best performing model, test model with quadratic effect & test without Year for all best performing model							
Stage 4: Post model selection test	e.g. Quadratic ranunc performs better than linear	P1_s	e.g. Year, Ranunc^2, Distance				

Table S2.5. Full candidate model selection process for 3-year analysis. AIC statistics are supplied for initial Stage 1 to determine which variables should be retained for further analyses.

Stages of model development	Hypothesis tested	Candidate models		Salmon		Trout	
		Model no.	Model Terms	AICc	ΔAICc	AICc	ΔAICc
Stage 1: Identify most important (ΔAICc >1) and least important (ΔAICc <1) variable/s for both species	Global model	Global	Year, Ranunc, FastVelocity, VelocityHet, Abundance, Distance	-81.1	3.19	-173.9	2.37
	Distance is not important	1	Year, Ranunc, FastVelocity, VelocityHet, Abundance	-80.7	3.61	-173.5	2.78
	Prey abundance is not important	2	Year, Ranunc, FastVelocity, VelocityHet, Distance	-84.1	0.25	-174.3	1.95
	Velocity heterogeneity is not important	3	Year, Ranunc, FastVelocity, Abundance, Distance	-84.1	0.22	-167.9	8.32
	Fast velocity is not important	4	Year, Ranunc, VelocityHet, Abundance, Distance	-84.3	0.00	-175.0	1.25
	Year is not important	5	Ranunc, FastVelocity, VelocityHet, Abundance, Distance	-83.9	0.47	-176.2	0.00
	Ranunculus is not important	6	Year, FastVelocity, VelocityHet, Abundance, Distance	-80.6	3.74	-175.2	1.00
Keep Ranunc & Distance in all subsequent models as important for both species and omit Year from all subsequent candidate models because not important for either species. Test combinations of remaining variables, i.e. Abundance, Fast Velocity & Velocity heterogeneity, as variables are considered to be important for one of the species.							

Stage 2: Test different combinations of most important variables	Velocity heterogeneity and abundance most important	6	Ranunc, Distance, VelocityHet, Abundance				
	Fast velocity and abundance most important	7	Ranunc, Distance, FastVelocity, Abundance				
	Velocity heterogeneity and fast velocity most important	8	Ranunc, Distance, VelocityHet, FastVelocity				
	Velocity heterogeneity most important	9	Ranunc, Distance, VelocityHet				
	Abundance most important	10	Ranunc, Distance, Abundance				
	Fast velocity most important	11	Ranunc, Distance, FastVelocity				
	Distance most important	12	Ranunc, Distance				
Test all variables individually test for importance of Ranunculus vs other variables.							
Stage 3: Test all variables individually to test for important of Ranunculus vs other variables	Ranunculus most important	13	Ranunc				
	Fast velocity most important	14	FastVelocity				
	Distance most important	15	Distance				
	Prey abundance most important	16	Abundance				
	Velocity heterogeneity most important	17	VelocityHet				
If Ranunculus included in the top performing model, test quadratic effect of Ranunc							
Stage 4: Post model selection test	As above						

Table S3.1. Mass-length relationships used for calculating macroinvertebrate biomass.

Taxa (Class/Sub-Class)	Reference
Hydrozoa, Insecta, Turbellaria	Benke, A.C., Huryn, A.D., Smock, L.A. & Wallace, J.B. (1999). Length-mass relationships for freshwater macroinvertebrates in North America with particular reference to the southeastern United States. *Journal of the North American Benthological Society*, 18, 308-343.
Insecta	Burgherr, P. & Meyer, E.I. (1997). Regression analysis of linear body dimensions vs. dry mass in stream macroinvertebrates. *Archiv für Hydrobiologie*, 139, 101-112.
Copepoda	Dumont, H.J., Van de Velde, I. & Dumont, S. (1975). The dry weight estimate of biomass in a selection of Cladocera, Copepoda and Rotifera from the plankton, periphyton and benthos of continental waters. *Oecologia*, 19, 75-97.
Hirudinea	Edwards, F.K., Lauridsen, R.B., Armand, L., Vincent, H.M. & Jones, J.I. (2009). The relationship between length, mass and preservation time for three species of freshwater leeches (Hirudinea). *Fundamental and Applied Limnology*, 173, 321-327.
Gastropoda	Hawkins, J.W., Lankester, M.W., Lautenschlager, R.A. & Bell, F.W. (1997). Length-biomass and energy relationships of terrestrial gastopods in northern forest ecosystems. *Canadian Journal of Zoology*, 75, 501-505.
Branchiopods	Herzig, A. (1974). Some population characteristics of planktonic crustaceans in Neusiedlersee. *Oecologia*, 15, 127-141.
Insecta	Hildrew, A.G. & Townsend, C.R. (1982). Predators and prey in a patchy environment: A freshwater study. *Journal of Animal Ecology*, 51, 797-815.
Insecta	Johnston, T.A. & Cunjak, R.A. (2001). Dry mass-length relationships for benthic insects: a review with new data from Catamaran Brook, New Brunswick, Canada. *Freshwater Biology*, 41, 653-674.
Malacostraca, Hirudinea, Gastropoda, Oligochaeta	Mason, C.F. 1977. Populations and production of benthic animals in two contrasting shallow lakes in Norfolk. *Journal of Animal Ecology*, 46, 147-172.
Gastropoda, Insecta, Turbellaria	Meyer, E. (1989). The relationship between body length parameters and dry mass in running water invertebrates. *Archiv für Hydrobiologie*, 117, 191-203.
Arachnida, Insecta	Sabo, J.L., Bastow, J.L. & Power, M.E. (2002). Length-mass relationships for adult aquatic and terrestrial invertebrates in a California watershed. *Journal of the North American Benthological Society*, 21, 336-343.
Nematoda (Order)	Andrassy I. (1956) Die Rauminhalts- und Gewichtsbestimmung der Fadenwu¨rmer (Nematoden). *Acta Zoologica Hungarica*, 2, 1-15.
Insecta	Smock, L.A. (1980). Relationships between body size and biomass of aquatic insects. *Freshwater Biology*, 10, 375-383.
Gastropoda	Vincent, H.M. (2010). Algal resource depression by macro-invertebrate herbivory in a chalk stream: An empirical approach. *Unpublished PhD thesis*. Available online at http://etheses.bham.ac.uk/550/.

Table S3.2. Complete maximum-likelihood model comparison statistics for fits of all salmon models comparing *Ranunculus* cover main effects and interactions to alternative habitat variable main effects. Part (a) displays negative binomial regression models developed to best explain variation in juvenile salmon abundance. θ = dispersion parameter, R^2_{ML} = maximum-likelihood pseudo-R^2. Part (b) displays binomial regression models developed to best explain variation in site retention rate of juvenile salmon. D^2 = percentage of deviance explained. Part (c) displays linear mixed effect regression models developed to best explain variation in the salmon growth rates between initial capture and first recapture. All models also include a random effect of *site*. Table is ordered by difference in ΔAIC, from the best performing model (model with the lowest AIC) from each analysis.

Mod	Model terms	Model fit		Comparison			Performance	
(a) Abundance (n = 54)		*θ*	logLik	*K*	AIC	ΔAIC	R^2_{ML}	
SA5	Ranunc, Month, Block, PreyBiom	19.3	-135.5	6	290.1	0.0	.77	
SA4	Ranunc, Month, Block, VelHet	20.2	-135.7	6	290.6	0.5	.76	
SA1	Ranunc, Month, Block	15.5	-137.3	5	291.1	0.9	.75	
SA3	Ranunc, Month, Block, FastVel	15.7	-136.9	6	293.1	2.9	.75	
SA2	Ranunc, Month, Block, Depth	15.8	-137.2	6	293.7	3.6	.75	
SA9	Block, Month, PreyBiom	9.3	-142.3	5	301.0	10.9	.70	
SA6	Block, Month, Depth	8.4	-143.2	5	302.9	12.8	.69	
SA8	Block, Month, VelHet	7.9	-144.4	5	305.3	15.2	.67	
SA7	Block, Month, FastVel	7.8	-144.5	5	305.4	15.3	.67	
(b) Site retention rate (n = 54)		Dev	logLik	*K*	AIC	ΔAIC	D^2	
SR3	Ranunc, Period, Block, Year, Ranunc x Period, VelHet	780.0	-1400.1	9	2825.4	0.0	62.2	
SR2	Ranunc, Period, Block, Year, Ranunc x Period, Depth	785.6	-1403.0	9	2831.0	5.6	61.9	
SR5	Ranunc, Period, Block, Year, Ranunc x Period, PreyBiom	791.1	-1405.7	9	2836.5	11.1	61.6	
SR1	Ranunc, Period, Block, Year, Ranunc x Period	797.5	-1408.9	8	2839.8	14.5	61.3	
SR4	Ranunc, Period, Block, Year, Ranunc x Period, FastVel	797.4	-1408.8	9	2842.8	17.4	61.3	
SR9	Period, Block, Year, PreyBiom	1235.3	-1627.8	6	3272.0	446.6	40.1	
SR6	Period, Block, Year, Depth	1316.9	-1668.6	6	3353.6	528.2	36.2	
SR8	Period, Block, Year, FastVel	1329.2	-1674.7	6	3365.9	540.5	35.6	
SR7	Period, Block, Year, VelHet	1332.5	-1676.4	6	3369.2	543.9	35.4	
(c) Growth rates (n = 173)		*σ*	logLik	*K*	AIC	ΔAIC	R^2_M	R^2_C
SG3	Ranunc, Period, Ranunc x Period, FastVel	7.4	-573.5	6	1166.1	0.0	.64	.68
SG5	Ranunc, Period, Ranunc x Period, VelHet	7.6	-585.3	6	1189.7	23.5	.58	.67
SG2	Ranunc, Period, Ranunc x Period, Depth	7.5	-585.9	6	1190.8	24.7	.52	.72
SG4	Ranunc, Period, Ranunc x Period, PreyBiom	7.7	-586.9	6	1192.9	26.8	.58	.67

SG1	Ranunc, Period, Ranunc x Period	7.7	-589.5	5	1195.9	29.8	.58	.65
SG7	Period, FastVel	7.8	-592.8	3	1198.0	31.9	.59	.65
SG6	Period, Depth	7.7	-601.8	3	1216.0	49.9	.50	.76
SG8	Period, PreyBiom	7.9	-602.3	3	1217.2	51.0	.56	.66
SG9	Period, VelHet	7.9	-602.6	3	1217.8	51.6	.55	.65

Table S3.3. Complete maximum-likelihood model comparison statistics for fits of all trout models comparing *Ranunculus* cover main effects and interactions to alternative habitat variable main effects. Part (a) displays negative binomial regression models developed to best explain variation in juvenile trout abundance. θ = dispersion parameter, R^2_{ML} = maximum-likelihood pseudo-R^2. Part (b) displays binomial regression models developed to best explain variation in site retention rate of juvenile trout. D^2 = percentage of deviance explained. Table is ordered by difference in ΔAIC, from the best performing model (model with the lowest AIC) from each analysis.

Mod	Model terms	Model fit		Comparison			Performance
	(a) Abundance (n = 54)	θ	logLik	K	AIC	ΔAIC	R^2_{ML}
TA6	Block, Month, Year, Depth	11.1	-89.5	6	198.2	0.0	0.52
TA1	Ranunc, Block, Month, Year	10.8	-89.9	6	198.9	0.8	0.52
TA8	Block, Month, Year, VelHet	11.0	-89.9	6	199.0	0.8	0.51
TA3	Ranunc, Block, Month, Year, FastVel	11.4	-89.1	7	200.3	2.1	0.53
TA2	Ranunc, Block, Month, Year, Depth	11.7	-89.2	7	200.5	2.3	0.53
TA7	Block, Month, Year, FastVel	9.4	-90.7	6	200.6	2.4	0.50
TA4	Ranunc, Block, Month, Year, VelHet	11.3	-89.3	7	200.7	2.5	0.53
TA5	Ranunc, Block, Month, Year, PreyBiom	10.9	-89.8	7	201.7	3.6	0.52
TA9	Block, Month, Year, PreyBiom	9.2	-91.4	6	202.1	3.9	0.49
	(b) Site retention rate (n = 54)	Dev	logLik	K	AIC	ΔAIC	D^2
TR5	Ranunc, Period, Block, Ranunc x Period, PreyBiom	229.8	-561.0	8	1144.0	0.0	47.3
TR1	Ranunc, Period, Block, Ranunc x Period	245.2	-568.7	7	1156.5	12.5	43.8
TR3	Ranunc, Period, Block, Ranunc x Period, VelHet	243.3	-567.7	8	1157.5	13.5	44.2
TR4	Ranunc, Period, Block, Ranunc x Period, FastVel	245.0	-568.6	8	1159.2	15.2	43.8
TR2	Ranunc, Period, Block, Ranunc x Period, Depth	245.2	-568.7	8	1159.4	15.4	43.8
TR9	Period, Block, PreyBiom	272.2	-582.2	5	1178.1	34.1	37.6
TR7	Period, Block, VelHet	287.8	-590.0	5	1193.7	49.7	34.0
TR6	Period, Block, Depth	291.3	-591.7	5	1193.2	53.2	33.2
TR8	Period, Block, FastVel	291.6	-591.9	5	1193.5	53.5	33.1

Table S5.1. Model fitting procedure undertaken to identify the final model fit to describe salmon abundance. Non-significant pathways were removed iteratively, and model adequacy is assessed after each removal by calculating Fisher's C test. A – Abundance, R – Ranunculus, FV – Fast velocities, D – water depth, VH – velocity heterogeneity, P – biomass of prey, BR – basal resources

Model	Model terms	Model term change	Fisher's C	df	*P* value
1	A ~ R + FV + D + VH +P D ~ R FV ~ R + VH VH ~ R P ~ R + BR BR ~ R	Full model	23.67	20	0.257
2	A ~ R + FV + D + VH +P D ~ R FV ~ R + VH VH ~ R P ~ R + BR	Removed basal resources (BR) model	23.66	20	0.257
3	A ~ R + FV + D +P D ~ R FV ~ R + VH VH ~ R P ~ R + BR	Removed velocity heterogeneity (VH) from abundance (A) model	26.24	22	0.241
4	A ~ R + FV + D +P D ~ R FV ~ R + VH VH ~ R P ~ BR	Removed Ranunculus (R) from prey (P) model	29.5	24	0.202
5	A ~ R + FV + D D ~ R FV ~ R + VH VH ~ R	Removed prey (P) model	10.76	8	0.216

Table S5.2. Model fitting procedure undertaken to identify the final model fit to describe salmon growth rates. Non-significant pathways, and important missing pathways identified using Shipley's d-sep test and were removed/added iteratively. Model adequacy is assessed after each removal/addition by calculating Fisher's C test.

Model	Model terms	Model term change	Fisher's C	df	*P* value
1	G ~ R + VH + FV + PS + P + SA +TA PS ~ R + P P ~ R FV ~ VH VH ~ R SA ~ R TA ~ R	Full model	403.12	28	0
2	G ~ R + VH + FV + PS + P +TA PS ~ R + P P ~ R FV ~ VH VH ~ R TA ~ R	Removed salmon abundance (SA) model, and SA term in growth (G) model	316.07	18	0
3	G ~ VH + FV + PS + P +TA PS ~ R + P P ~ R FV ~ VH VH ~ R TA ~ R	Removed Ranunculus (R) from growth (G) model	316.15	20	0
4	G ~ VH + FV + PS + P +TA PS ~ R + P + FV P ~ R FV ~ VH VH ~ R TA ~ R	Included fast velocities FV in prey size (PS) model after identifying as a missing link	205.4	18	0
5	G ~ VH + FV + PS + P +TA PS ~ R + P + FV + VH P ~ R FV ~ VH VH ~ R TA ~ R	Included velocity heterogeneity (VH) in prey size (PS) model after identifying as a missing link	80.78	16	0
6	G ~ VH + PS + P +TA PS ~ R + P + FV + VH P ~ R FV ~ VH VH ~ R TA ~ R	Removed fast velocities (FV) from growth (G) model	81.03	18	0
7	G ~ VH + PS +TA PS ~ R + P + FV + VH P ~ R FV ~ VH VH ~ R TA ~ R	Removed prey biomass (P) from growth (G) model	83.67	20	0
8	G ~ VH + PS PS ~ R + P + FV + VH P ~ R FV ~ VH VH ~ R	Removed trout abundance model, and TA from growth (G) model	4.95	12	0.96

Supplementary figures

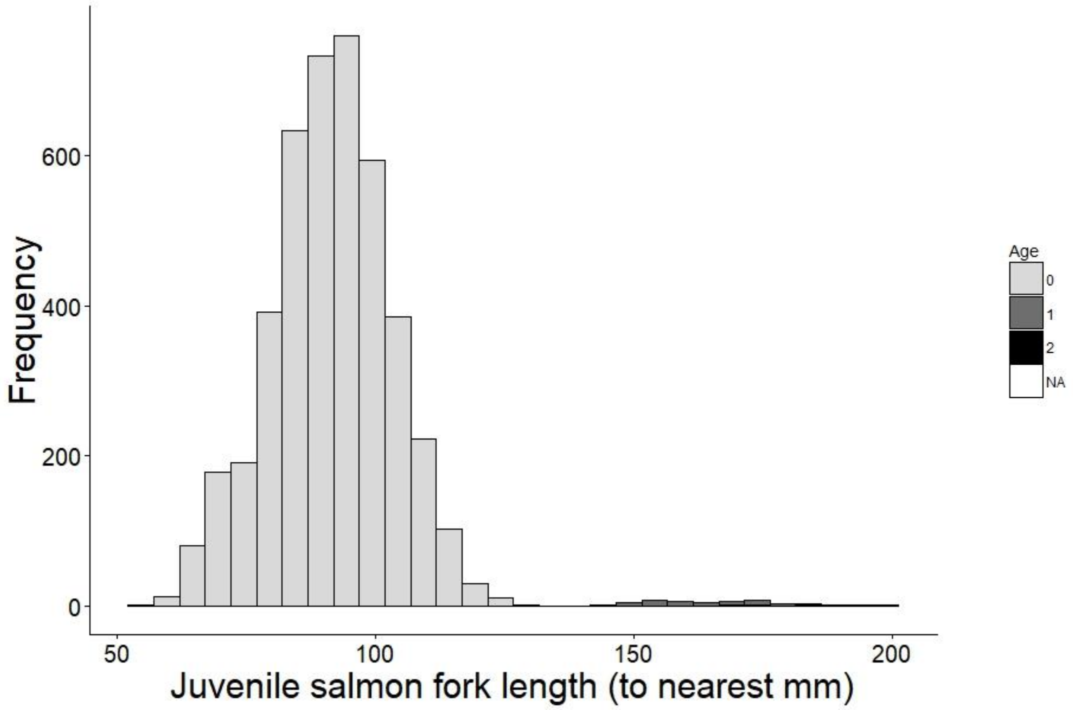


Figure S2.1. Fork length-frequency histogram for juvenile salmon. Maximum length of juvenile salmon (Age 0+) is 129 mm, classified by fork length and verified using scale samples. NA values represent older salmon of which age could not be verified using scale samples.

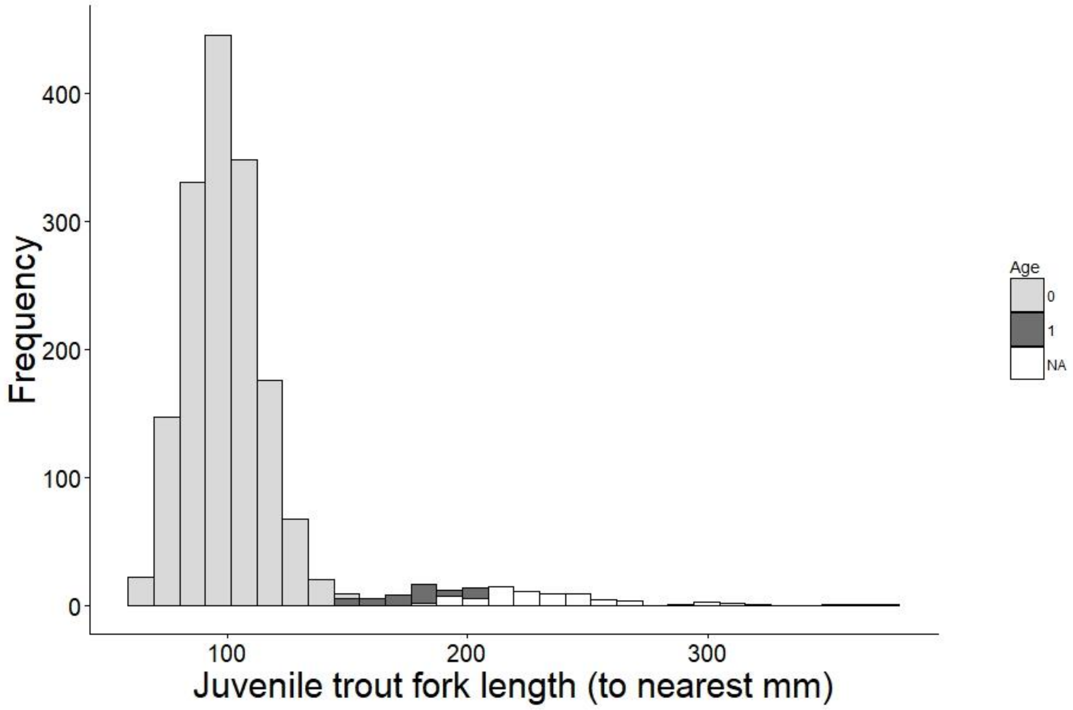


Figure S2.2. Fork length-frequency histogram for juvenile trout. Maximum length of juvenile trout (Age 0+) is 150 mm, classified by fork length and verified using scale samples. NA values represent older trout of which age could not be verified using scale samples.

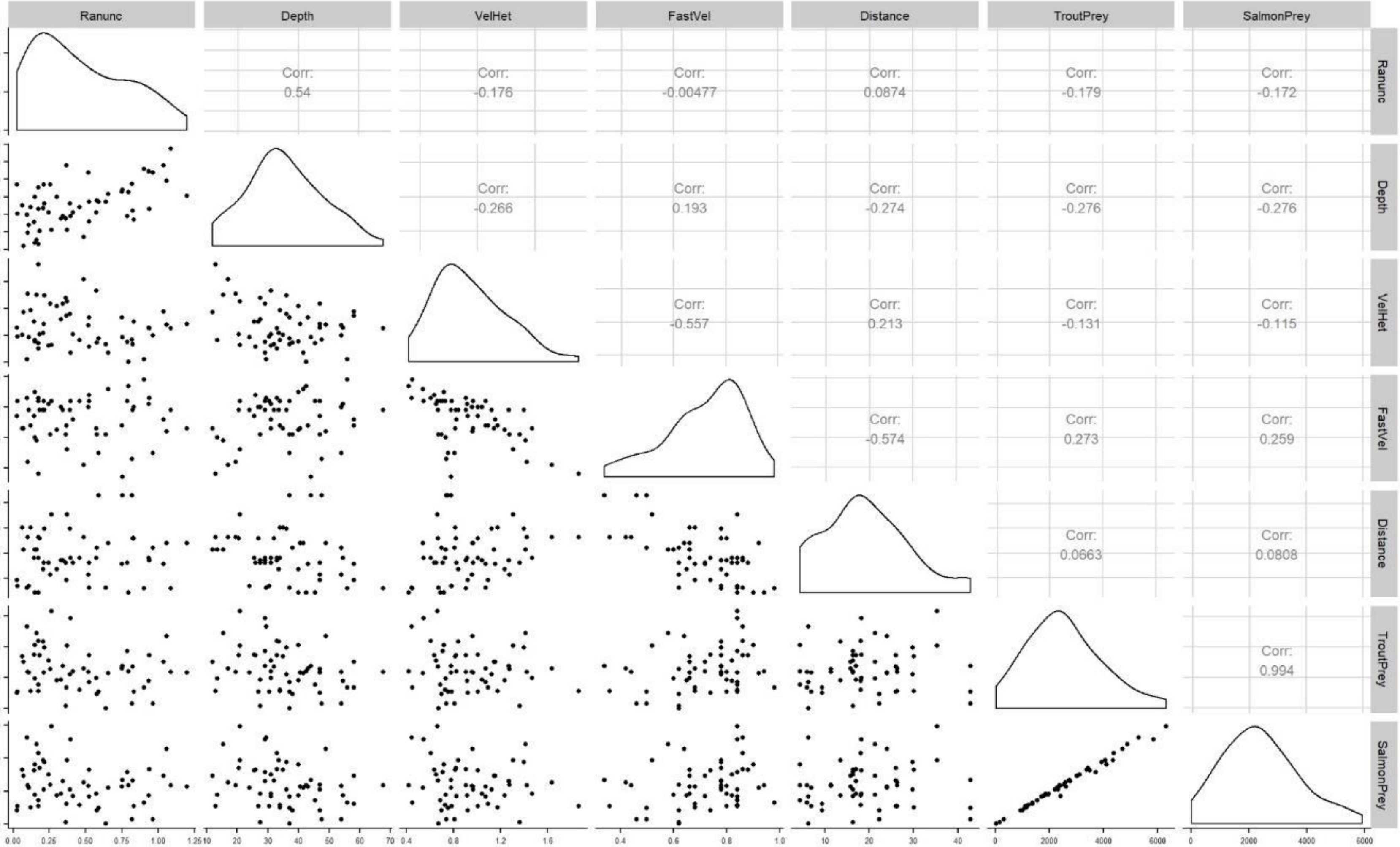


Figure S2.3. Pearson's pairwise correlation of all explanatory variables considered in the 3-year analysis; Ranunc = *Ranunculus* cover; Depth = water depth; VelHet = velocity heterogeneity; FastVel = proportion of fast velocities; Distance = distance from tidal limit; TroutPrey = Abundance of preferred prey of trout; SalmonPrey = Abundance of preferred prey of salmon.

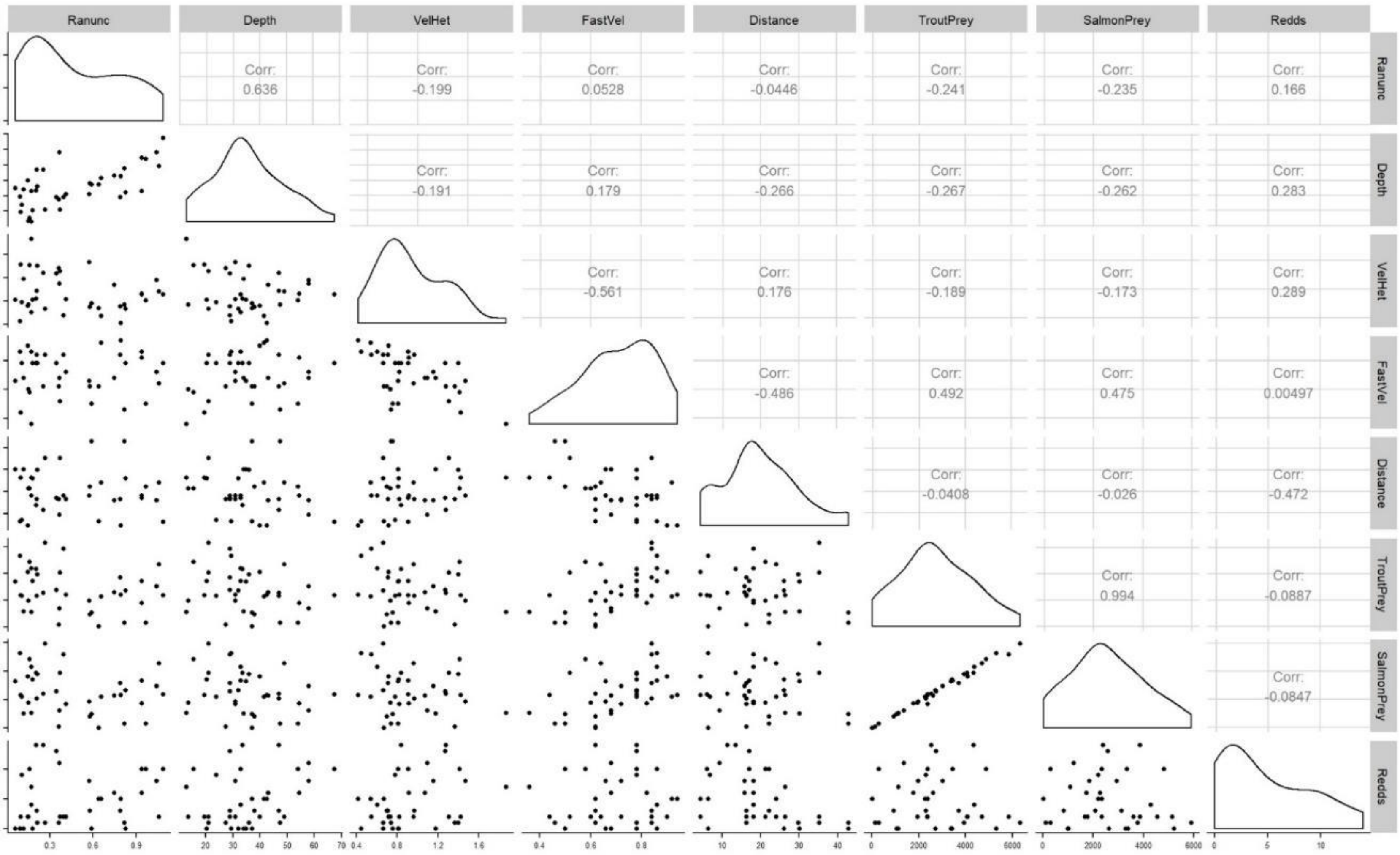
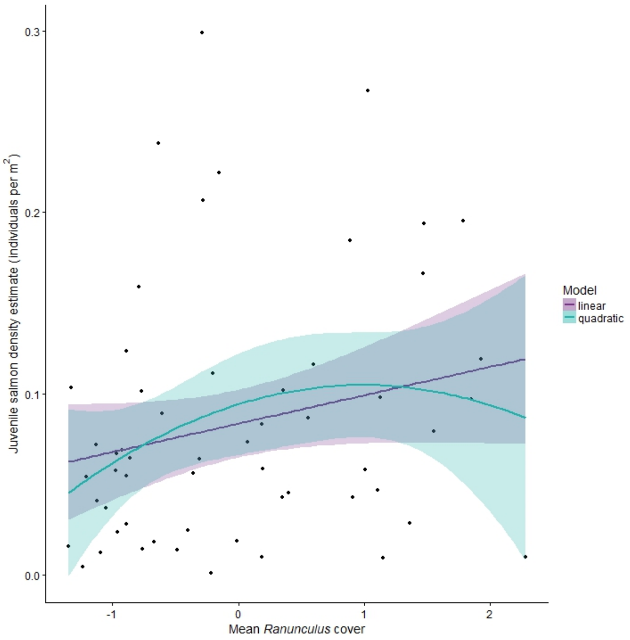


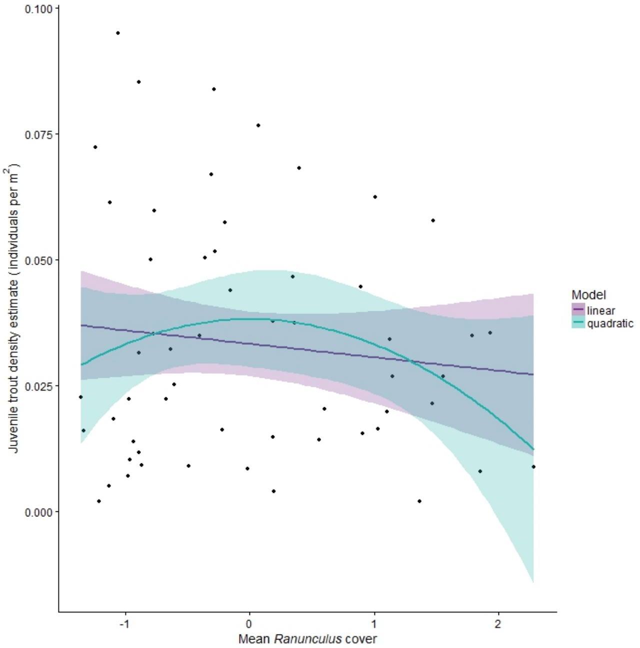
Figure S2.4 Pearson’s pairwise correlation of all explanatory variables considered in the 2-year analysis and 2-year salmon redd analysis; Ranunc = Ranunculus cover; Depth = Water depth; VelHet = Velocity Heterogeneity; FastVel = Proportion of fast velocities; Distance = distance from tidal limit; TroutPrey = Abundance of preferred prey of trout; SalmonPrey = Abundance of preferred prey of salmon; Redds = Number of nearby upstream redds (only in 2-year salmon redd analysis).

a)



(Salmon: Linear model ΔAICc = 0.00. Quadratic model - ΔAICc = 1.21)

b)



(Trout: Linear model - ΔAICc = 0.00. Quadratic model - ΔAICc = 0.29)

Figure S2.5. Scatter plots of a) salmon, and b) trout density as a function of *Ranunculus* cover. Lines are fitted linear regression (purple) and quadratic regression (green) predictions.

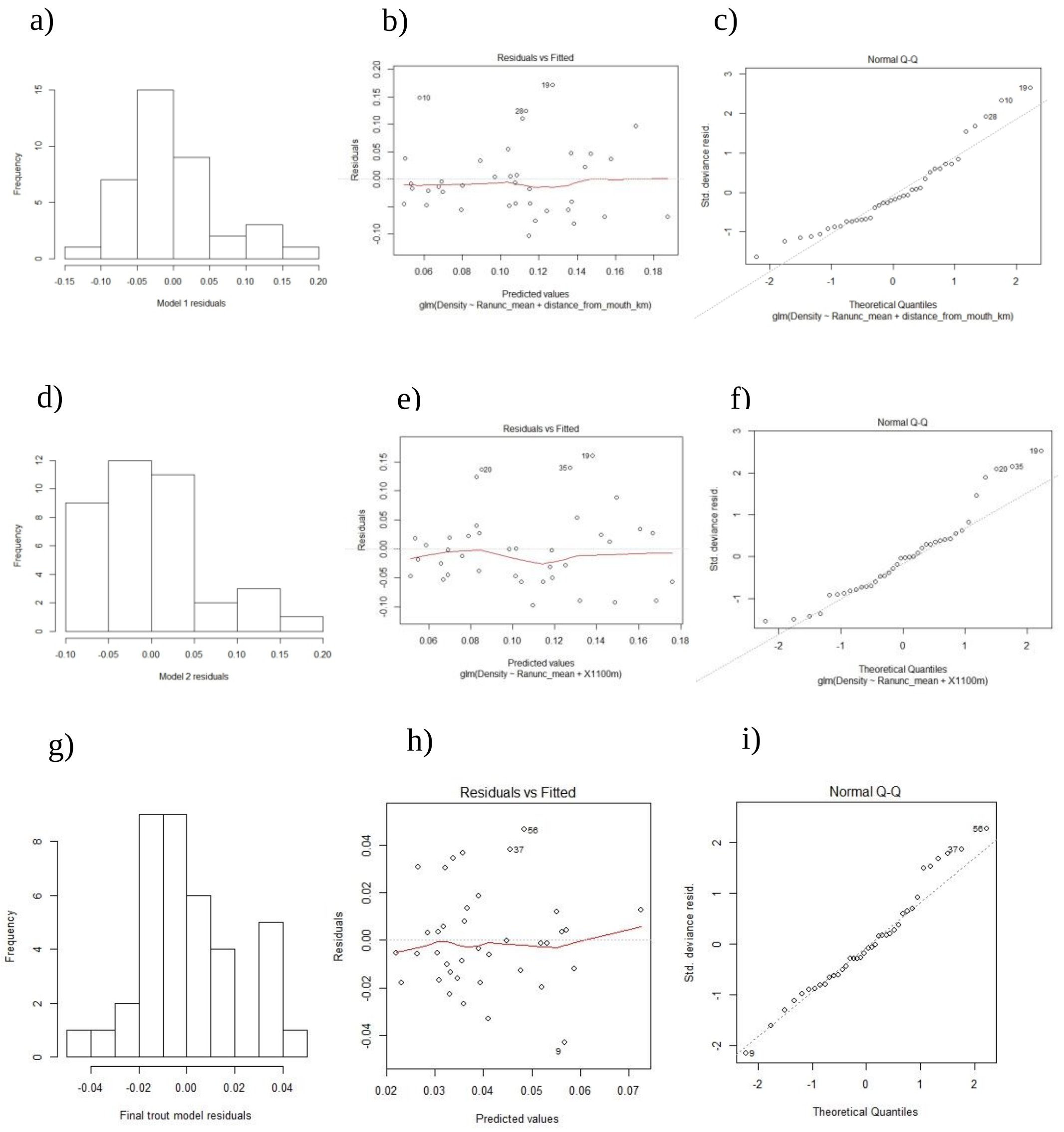


Figure S2.6. Model diagnostic plots for the best performing 2-year salmon and trout models: (a-c) salmon 2-year redd model (Model 1), (d-f) salmon 2-year redd model (Model 2), (g-i) trout 2-year model (Model 18).

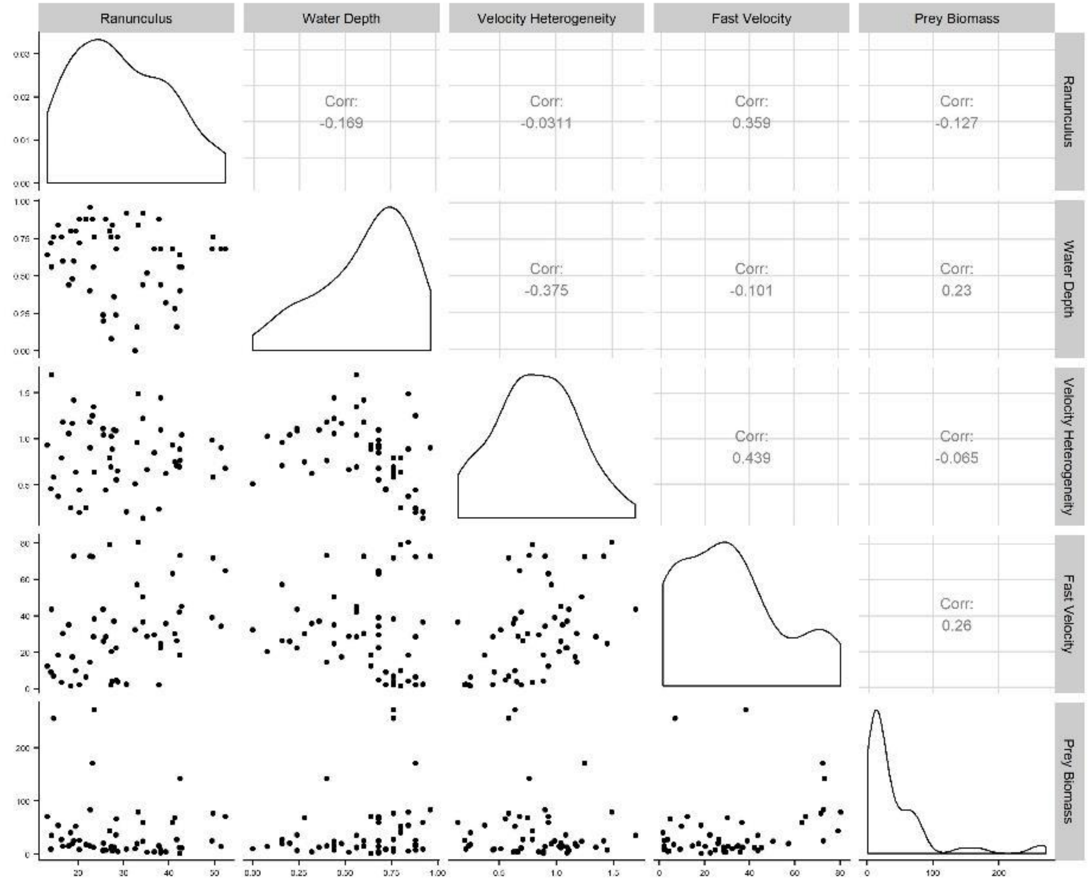


Figure S3.1. Pearson pairwise correlation tested between all explanatory variables included in analyses for salmon responses to test for highly correlated ($r \geq |0.6|$) variables.

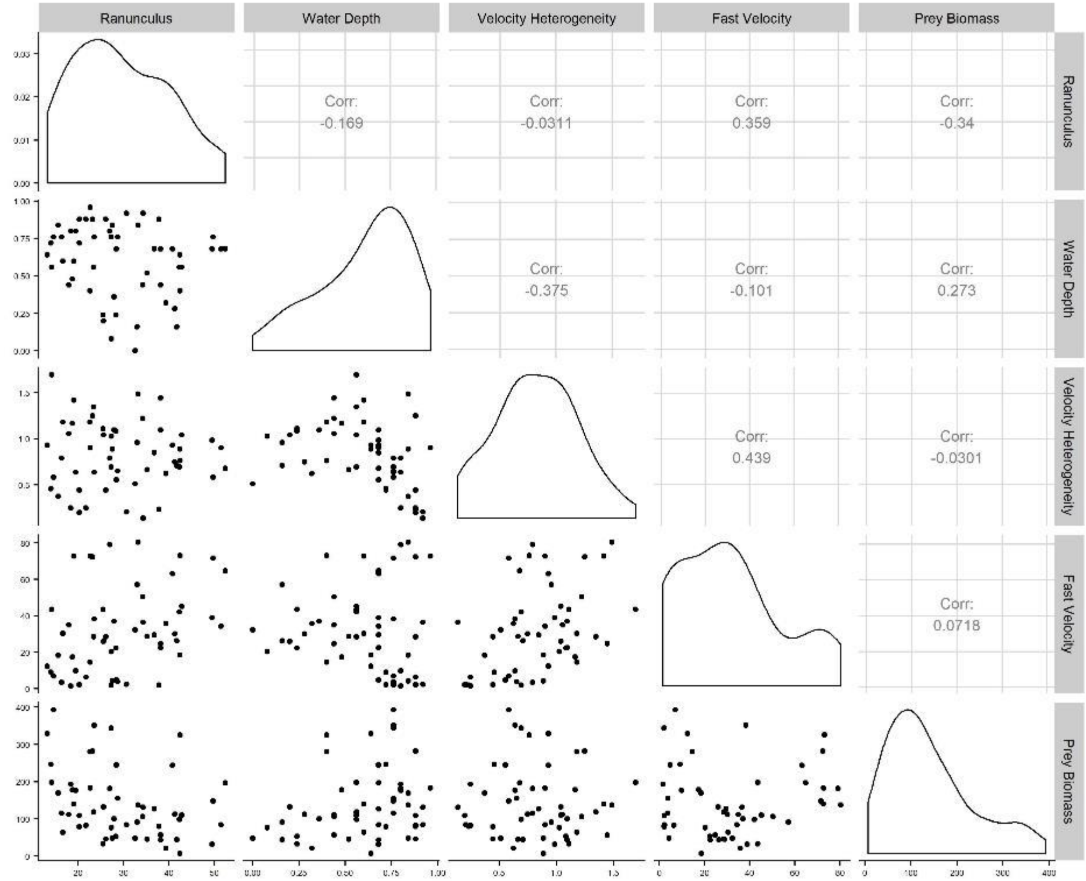


Figure S3.2. Pearson pairwise correlation tested between all explanatory variables included in analyses for trout responses to test for highly correlated ($r \geq |0.6|$) variables.

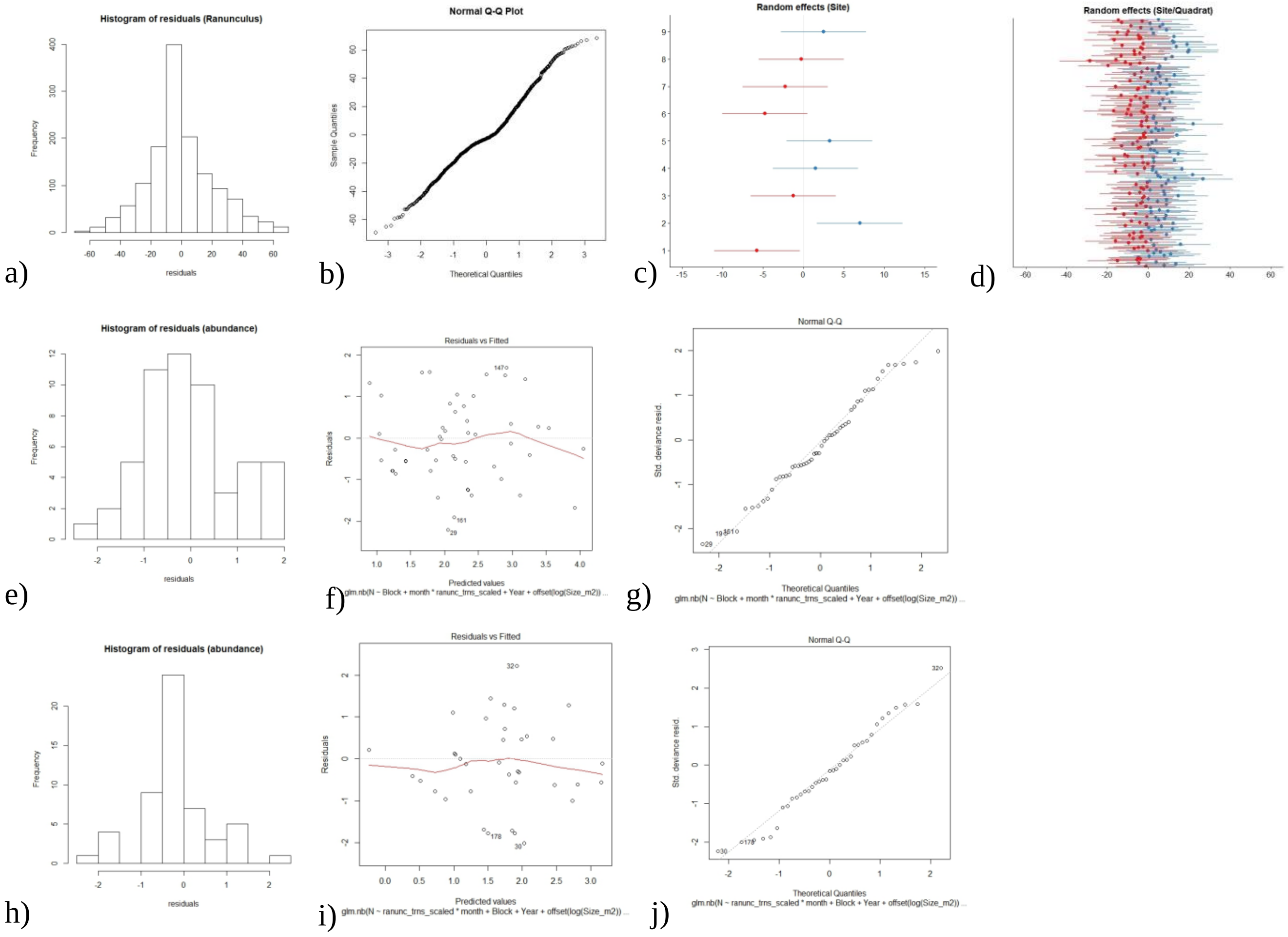


Figure S3.3. Model diagnostic plots for: (a-d) linear mixed effects model for *Ranunculus* cover, (e-g) negative binomial regression for salmon abundance (Model SA1), (h-j) negative binomial regression for trout abundance (Model TA1).

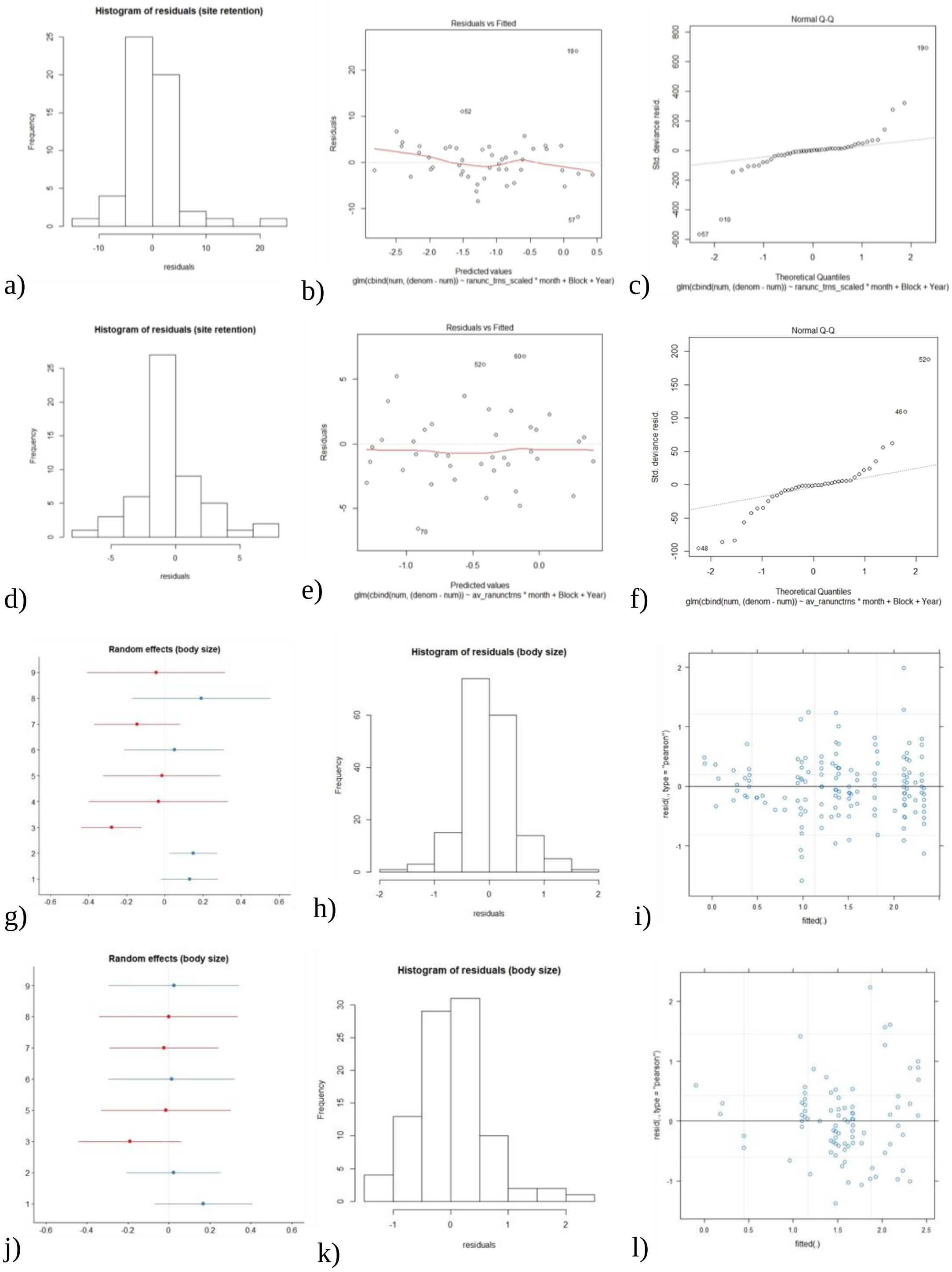


Figure S3.4. Model diagnostic plots for: (a-c) binomial regression for salmon site retention rate (Model SR1), (d-f) binomial regression for trout site retention rate (Model TR1), (g-i) linear mixed effects model for change in body size of salmon (Model SB1), (j-l) linear mixed effects model for change in body size of trout (Model TB1)

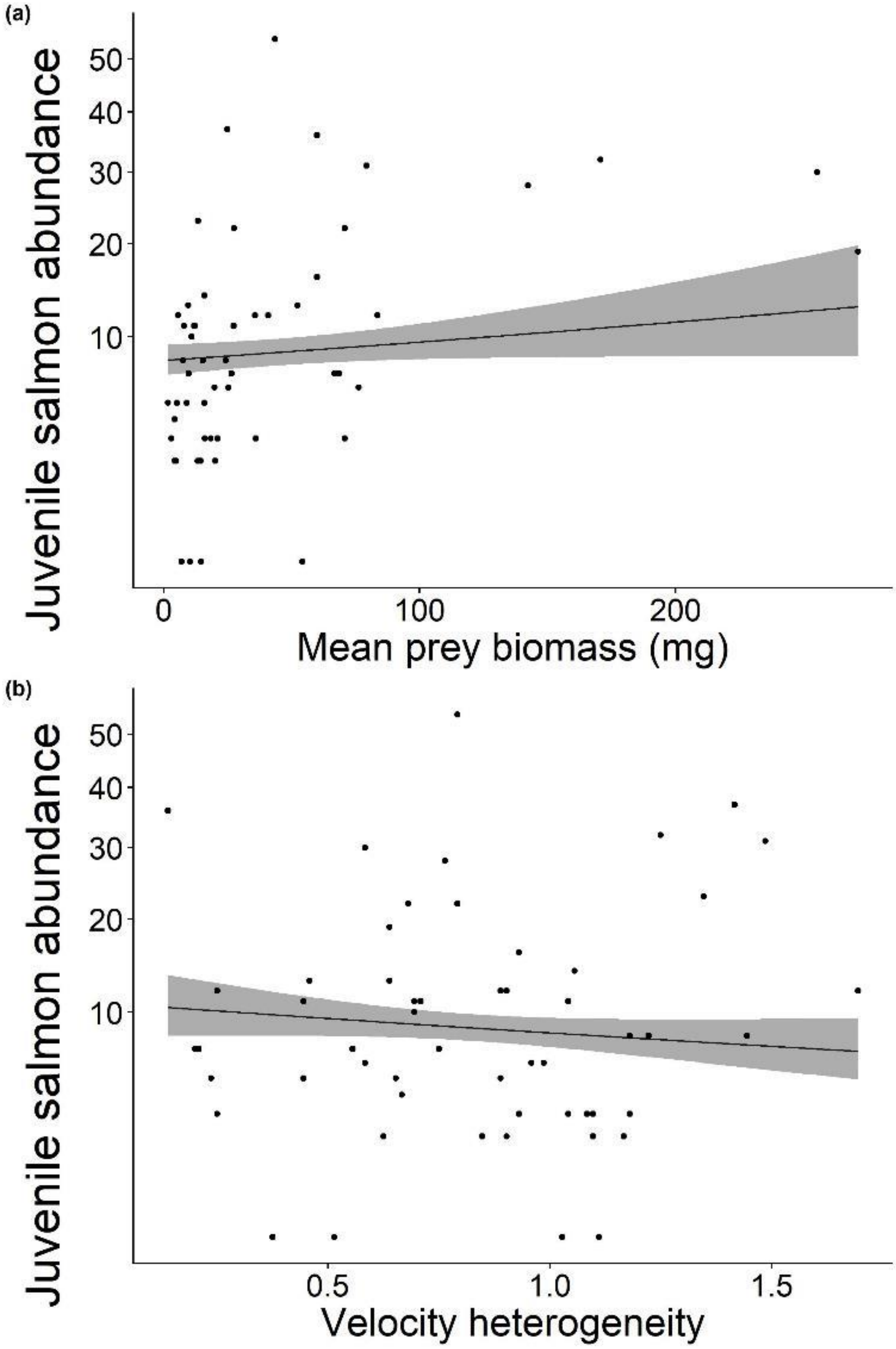


Figure S3.5. Marginal effects of (a) mean salmon prey biomass, taken from Model SA5, and (b) velocity heterogeneity, taken from Model SA4, on juvenile salmon abundance. Both models were among the top performing models to describe variation in salmon abundance. The solid line is the mean estimate, the grey shaded area denotes the 95% confidence interval, and the black circles are the observed salmon abundance. Y axis is on a square-root scale for visual clarity.

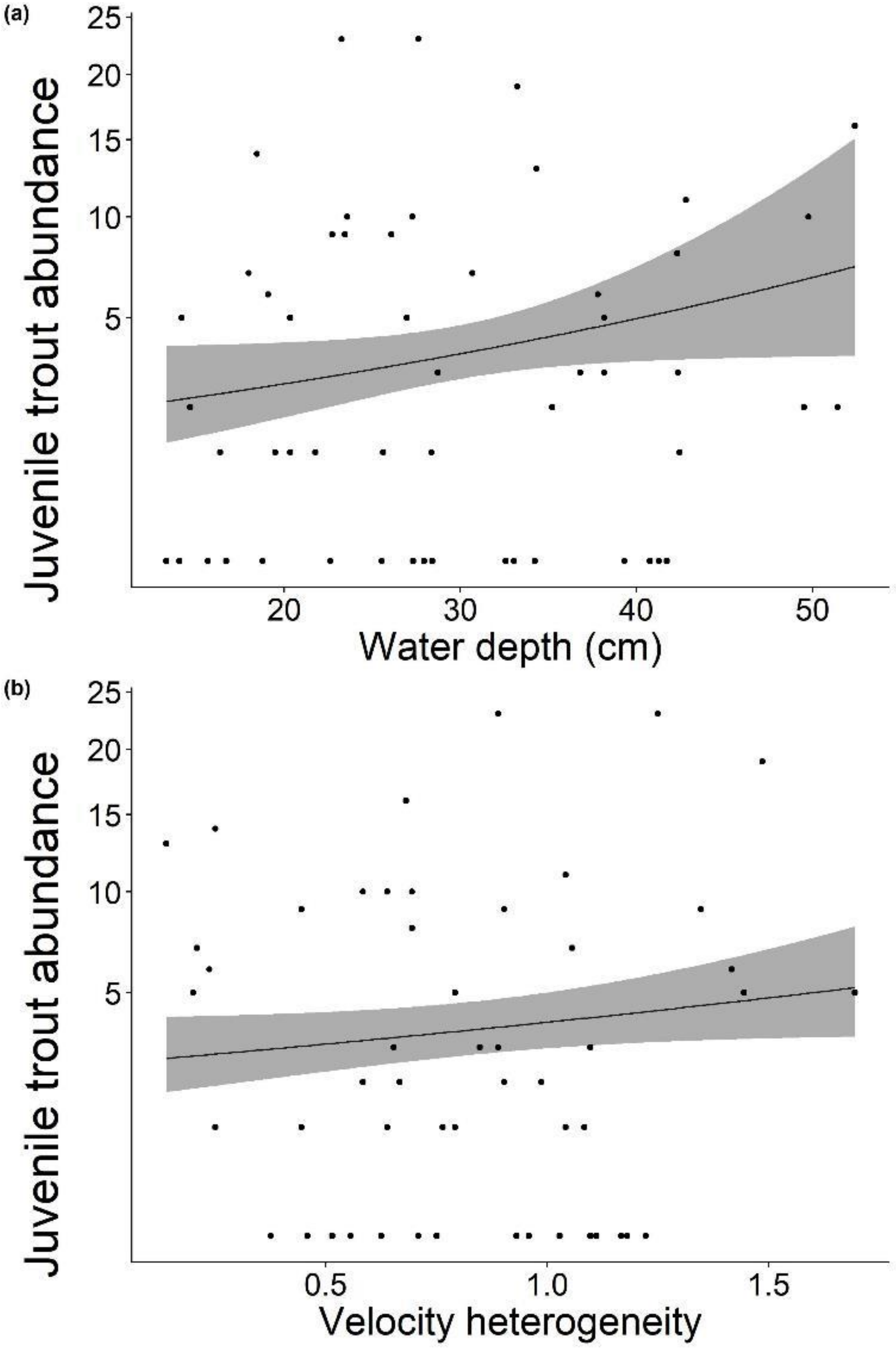


Figure S3.6. Marginal effects of (a) water depth, taken from Model TA6, and (b) velocity heterogeneity, taken from Model TA8, on juvenile trout abundance. Both models were among the top performing models to describe variation in trout abundance. The solid line is the mean estimate, the grey shaded area denotes the 95% confidence interval, and the black circles are the observed trout abundance. Y axis is on a square-root scale for visual clarity.

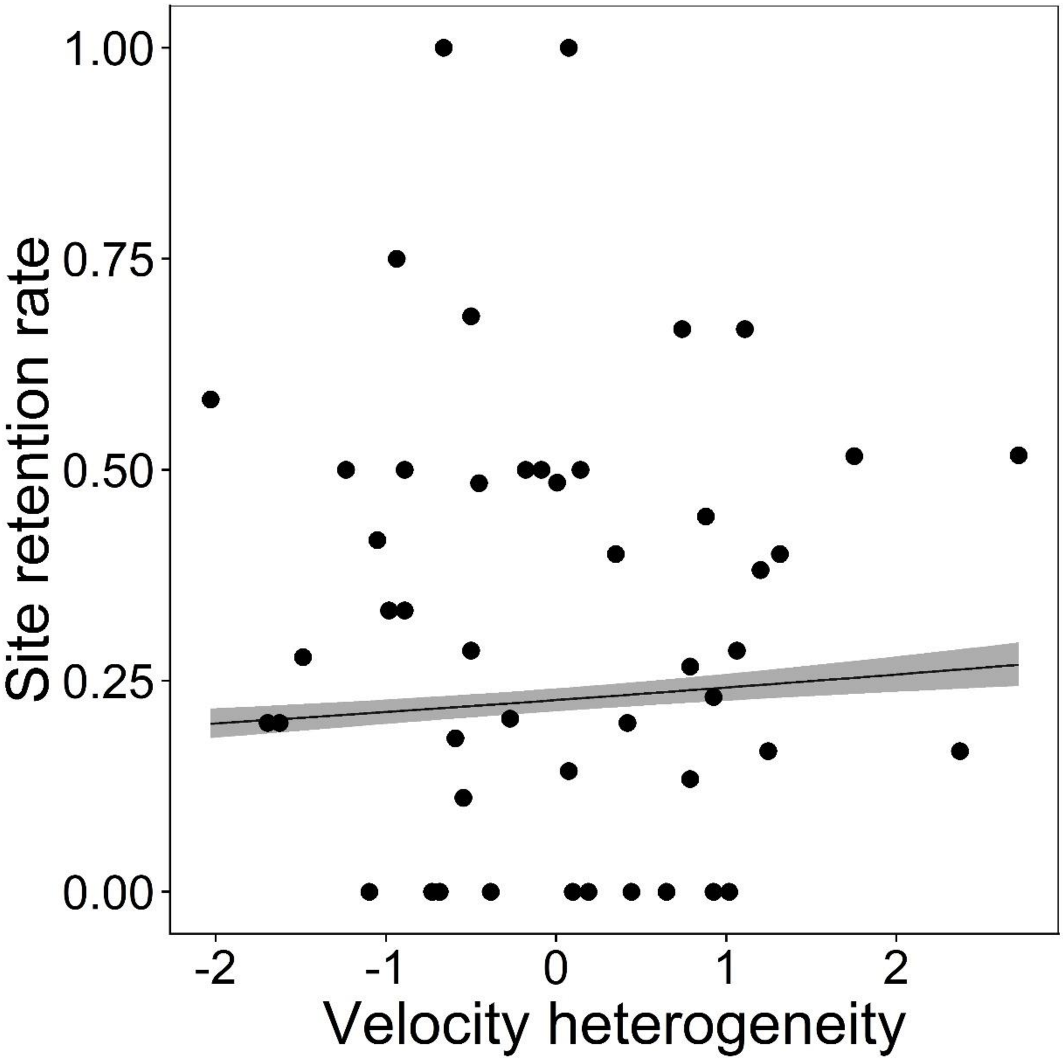


Figure S3.7. Marginal effects of velocity heterogeneity on site rentention rate of juvenile salmon, taken from the best performing candidate model (Model SR3) testing the importance of alternative habitat characteristics. The solid line is the mean estimate, the grey shaded area denotes the 95% confidence interval. Solid circles show the observed site retention rate, 10 data points are omitted from the plot where zero indviduals were caught in the first sample event at a site.

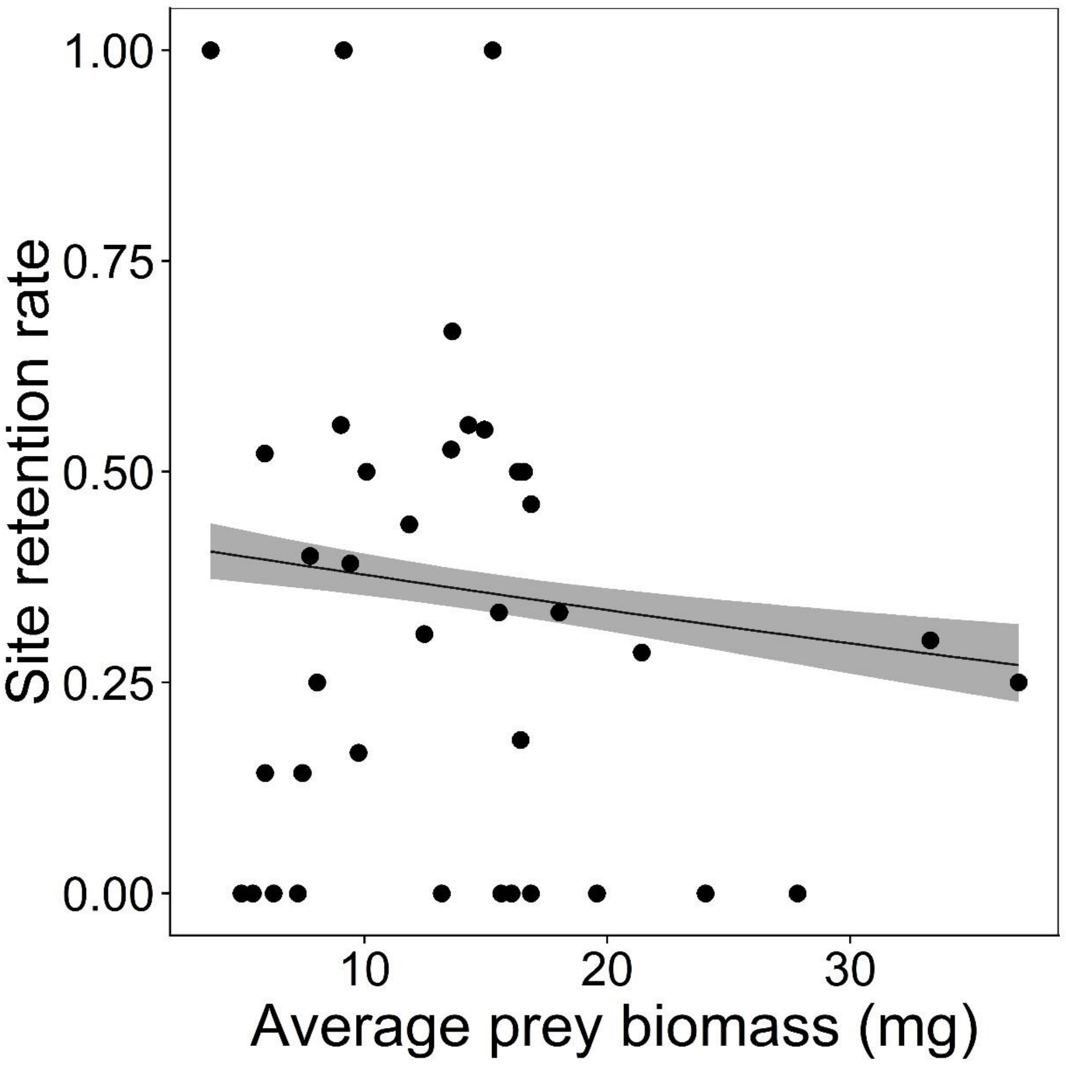


Figure S3.8. Marginal effects of average trout prey biomass on site rentention rate of juvenile trout, taken from the best performing candidate model (Model TR5) testing the importance of alternative habitat characteristics. The solid line is the mean estimate, the grey shaded area denotes the 95% confidence interval. Solid circles show the observed site retention rate, 14 data points are omitted from the plot where no individuals were caught in the first sample event at a site.

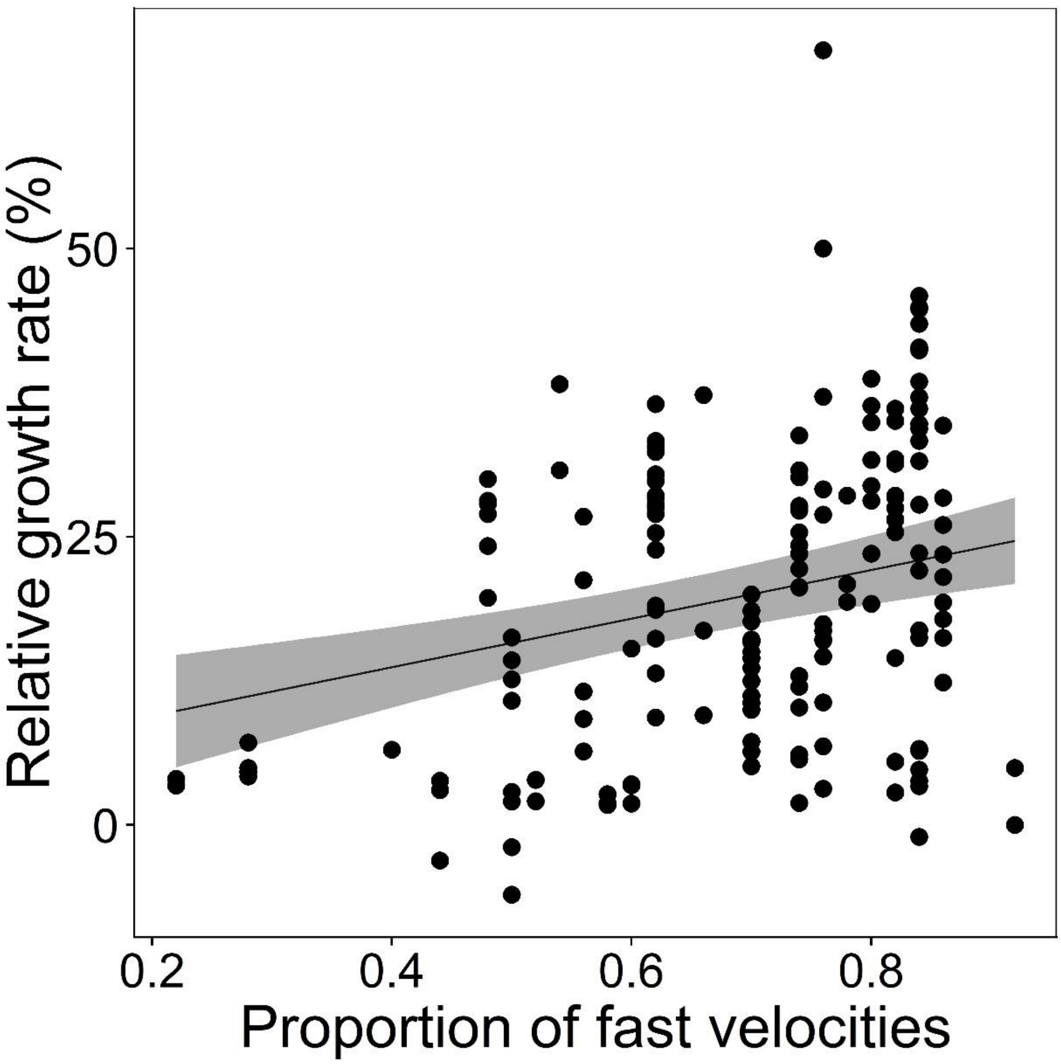


Figure S3.9. Marginal effects of average proportion of fast velocites on the growth rates of recaptured salmon, taken from model SG3. Model SG3 was the top performing models to describe variation in growth rates when considering alternative habitat variables. The solid line is the mean estimate, the grey shaded area denotes the 95% confidence interval, and the black circles are the observed growth rates.

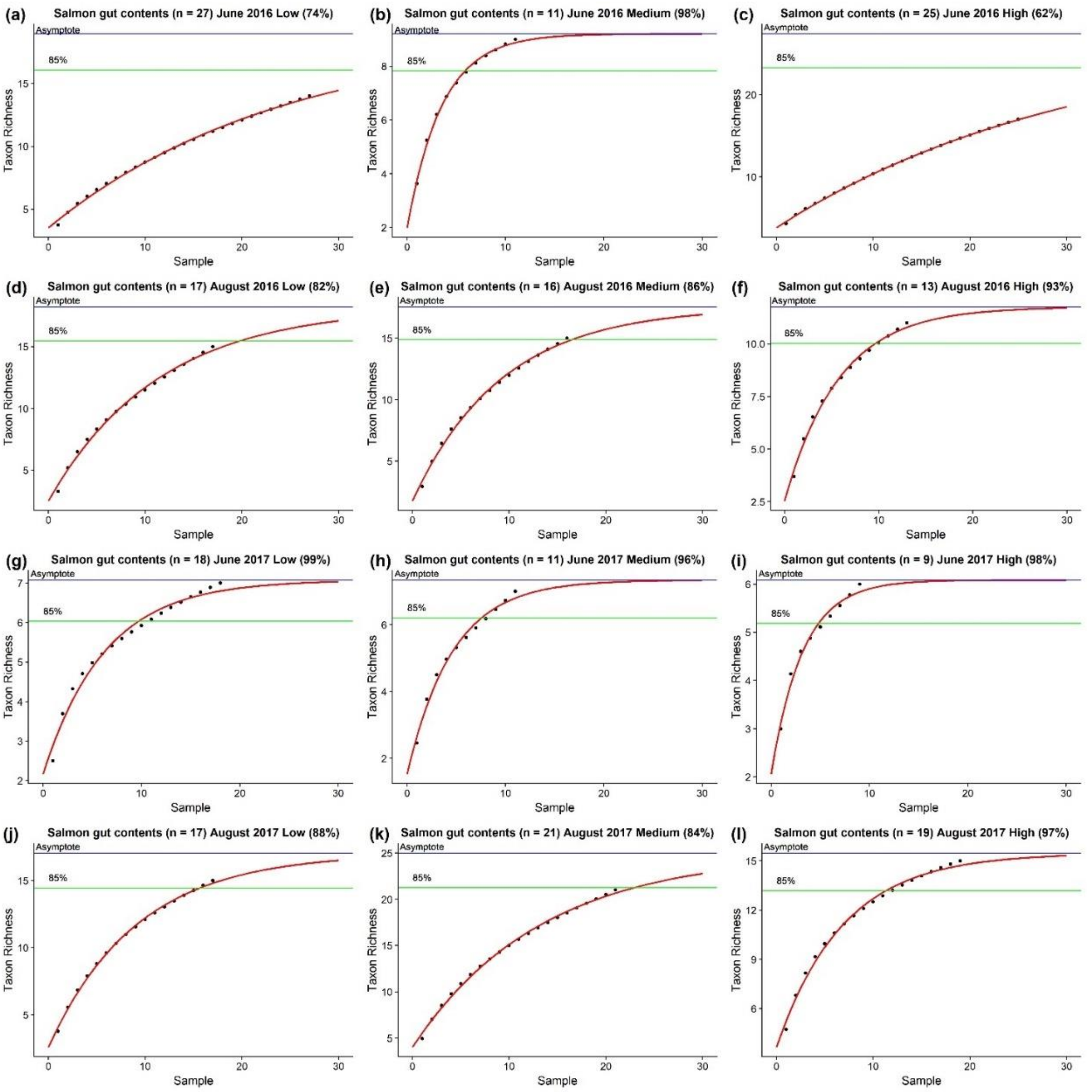


Figure S4.1. Taxa accumulation curves for salmon gut contents (*n* = 204) collected in (a)-(c) June 2016, (d)-(f) August 2016, (g)-(i) June 2017, (j)-(l) August 2017 in different treatment levels of *Ranunculus* cover. Black dots show the taxon richness per gut sample, green line is 85% of the asymptote for reference and blue line is the asymptote. The percentage in brackets is the percent of taxa identified in all samples relative to the asymptote.

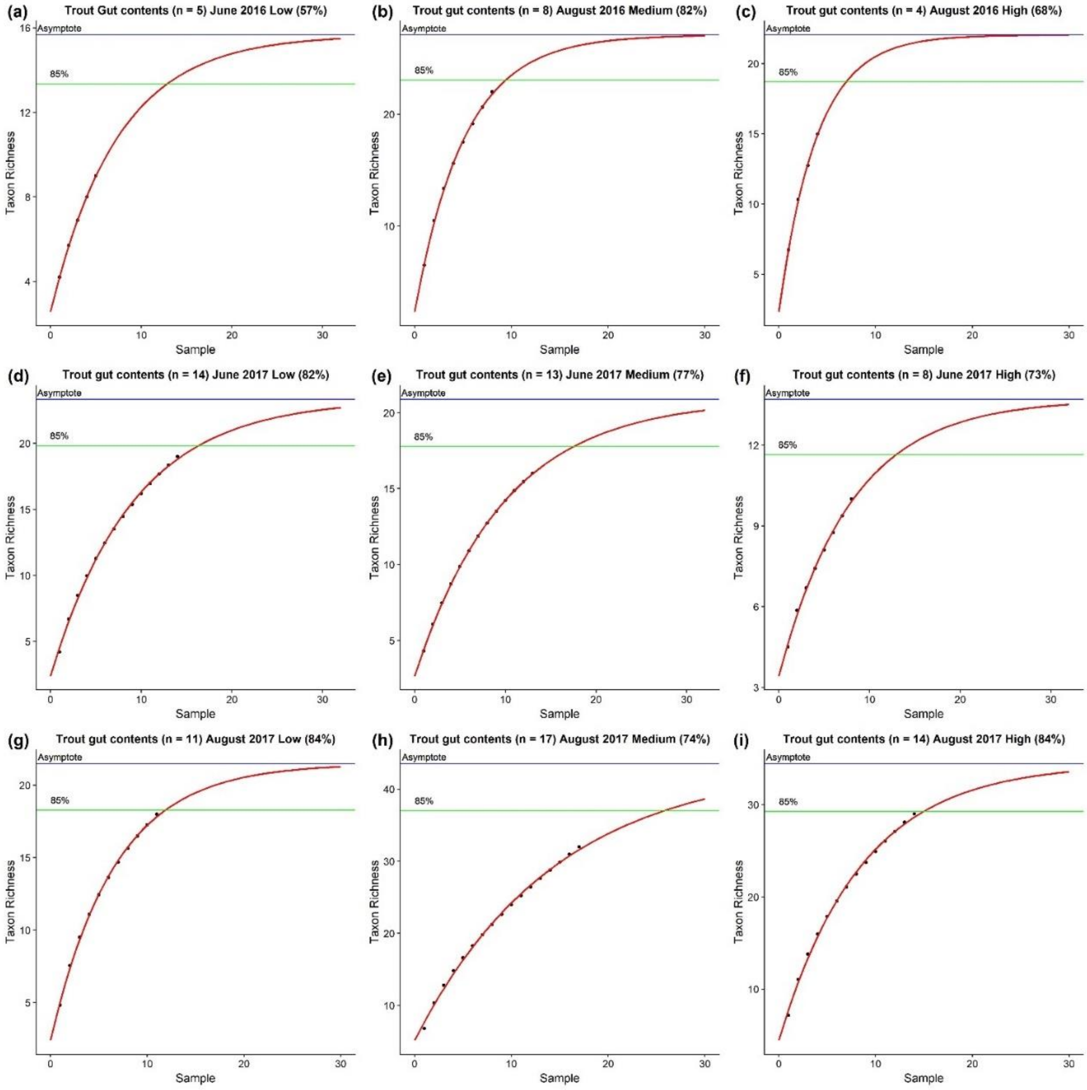
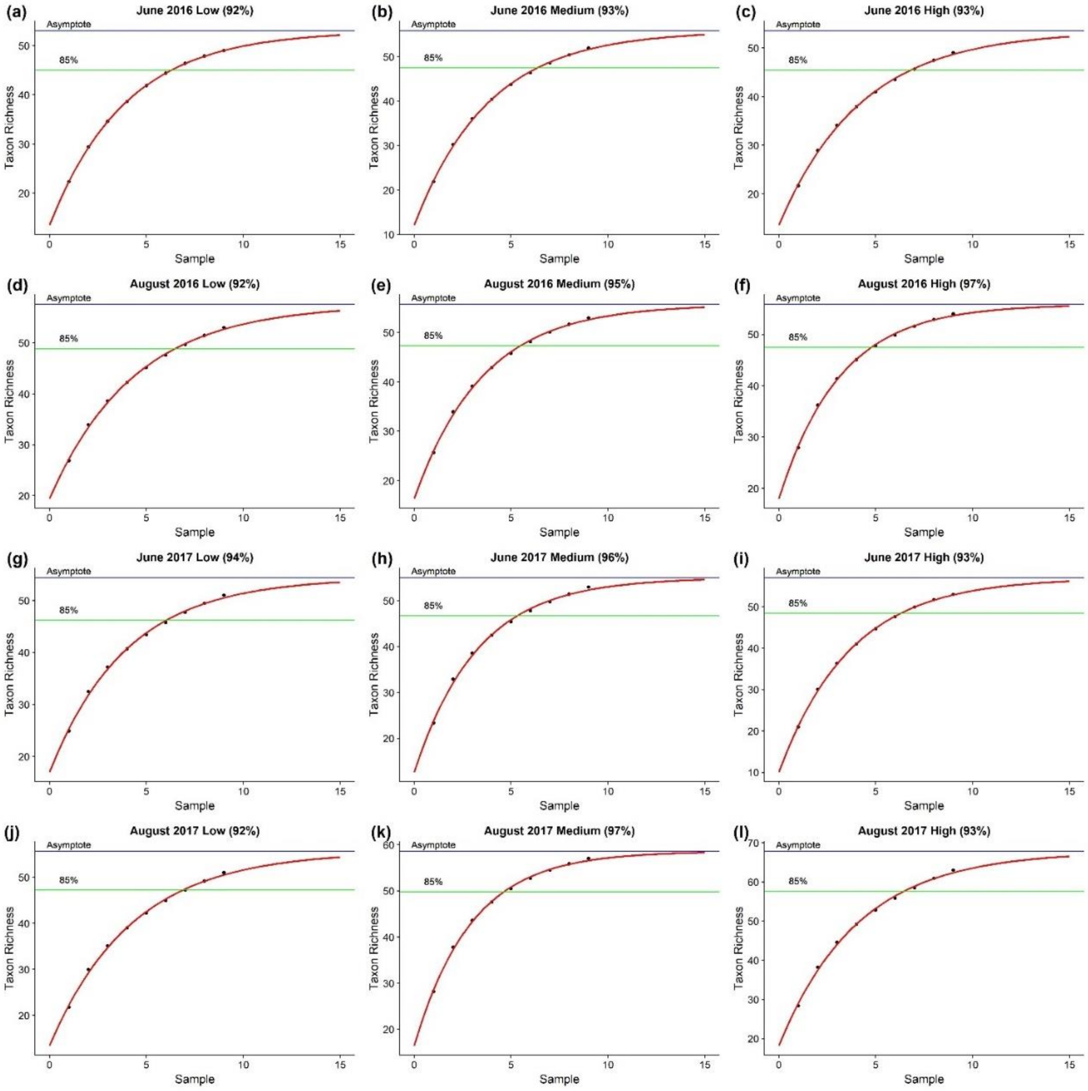


Figure S4.2. Taxa accumulation curves for trout gut contents (*n* = 94) collected in (a) June 2016, (b)-(c) August 2016, (d)-(f) June 2017, (g)-(i) August 2017 in different treatment levels of *Ranunculus* cover. No curve was computed for medium and high treatment levels in June 2016, or low treatment level in August 2016 because there were not enough samples (*n* = 2). Black dots show the taxon richness per gut sample, green line is 85% of the asymptote for reference and blue line is the asymptote. The percentage in brackets is the percent of taxa identified in all samples relative to the asymptote.


(a) June 2016 Low (92%)

(b) June 2016 Medium (93%)

(c) June 2016 High (93%)

(d) August 2016 Low (92%)

(e) August 2016 Medium (95%)

(f) August 2016 High (97%)

(g) June 2017 Low (94%)

(h) June 2017 Medium (96%)

(i) June 2017 High (93%)

(j) August 2017 Low (92%)

(k) August 2017 Medium (97%)

(l) August 2017 High (93%)

Figure S4.3. Taxa accumulation curves for Surber samples (*n* = 108) collected in (a)-(c) June 2016, (d)-(f) August 2016, (g)-(i) June 2017, (j)-(l) August 2017 in different treatment levels of *Ranunculus* cover. Black dots show the taxon richness per Surber sample, green line is 85% of the asymptote for reference and blue line is the asymptote. The percentage in brackets is the percent of taxa identified in all samples relative to the asymptote.

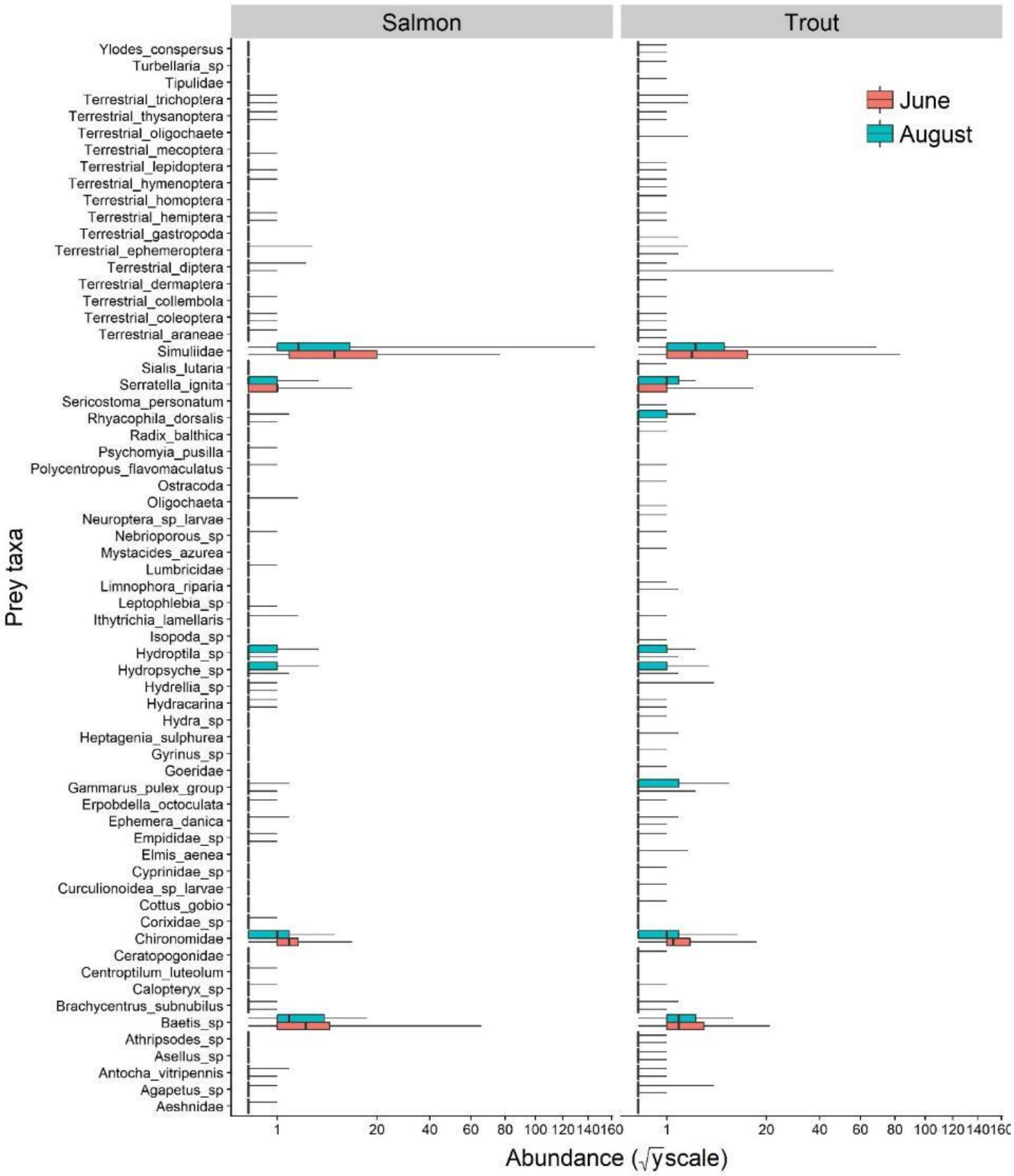


Figure S4.4. Abundance of all prey taxa found in diet contents of salmon and trout. Black line denotes the minimum and maximum abundance of prey taxa, box shows the interquartile range and black line within the box shows the median.

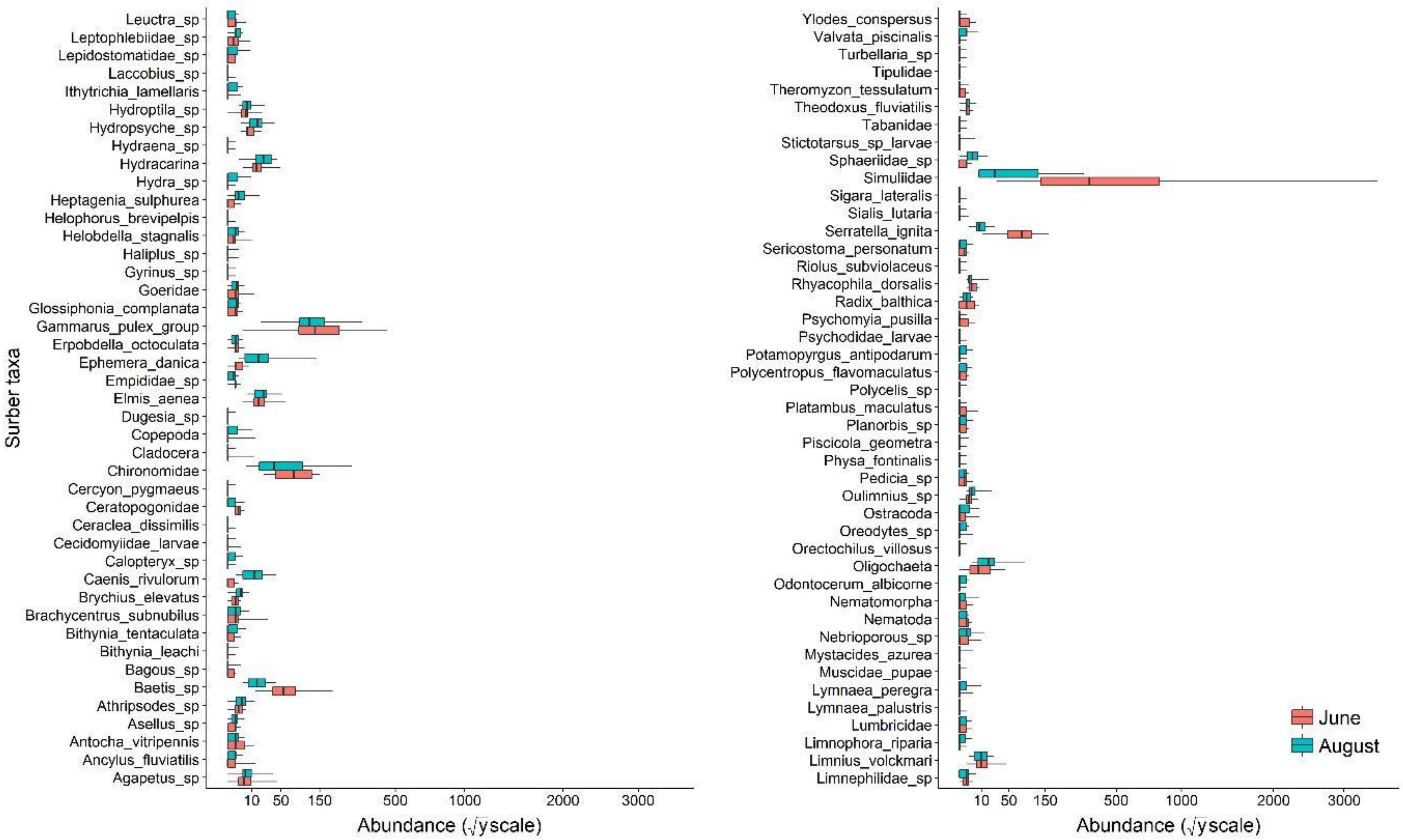


Figure S4.5. Abundance of all prey taxa found in Surber samples. Black line denotes the minimum and maximum abundance of prey taxa, box shows the interquartile range and black line within the box shows the median

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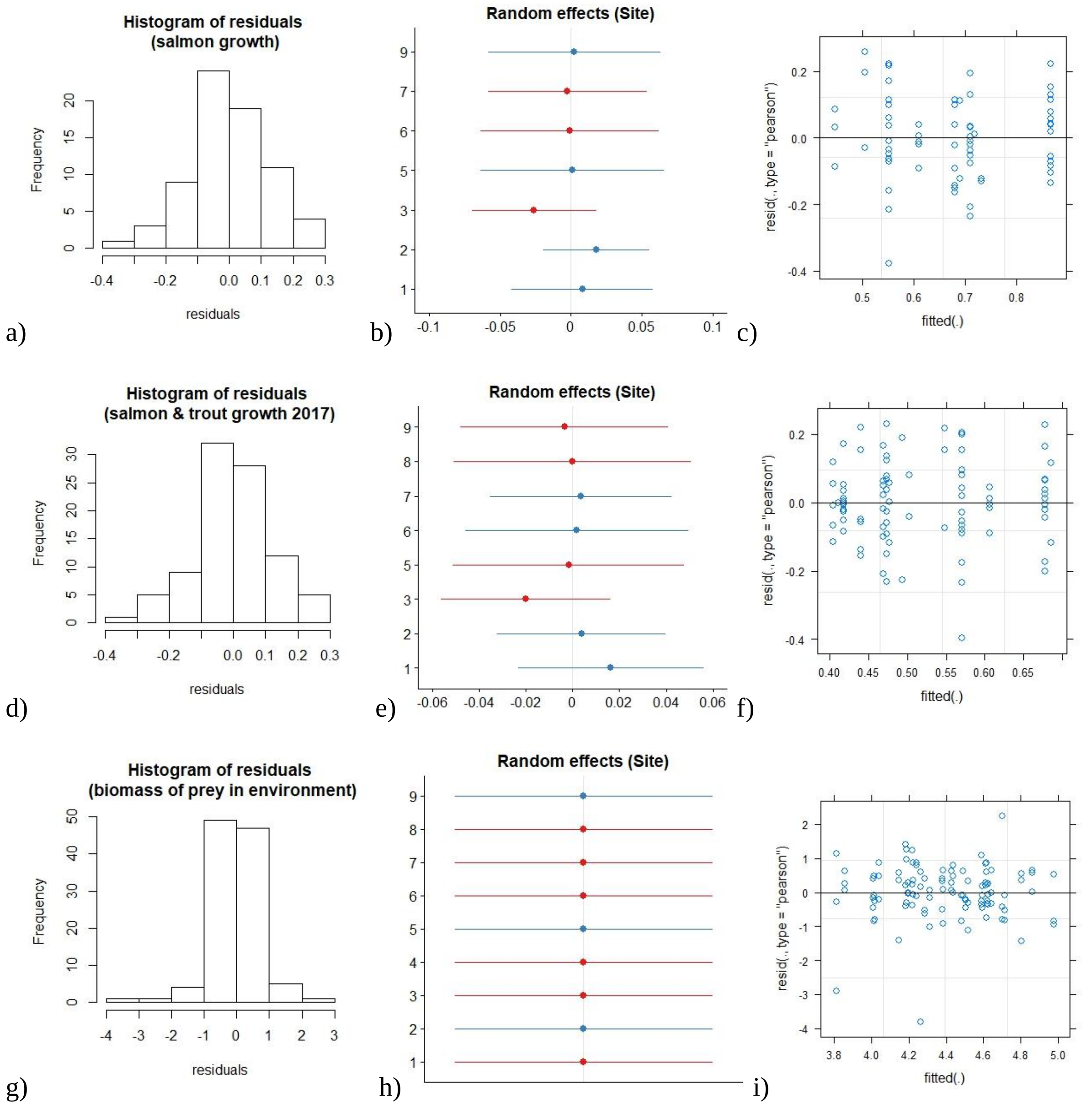

Figure S4.6. Model diagnostic plots for: (a-c) linear mixed effects model for salmon growth, (d-f) linear mixed effects model for salmon and trout growth in 2017, (g-i) linear mixed effects model for biomass of prey in the environment.

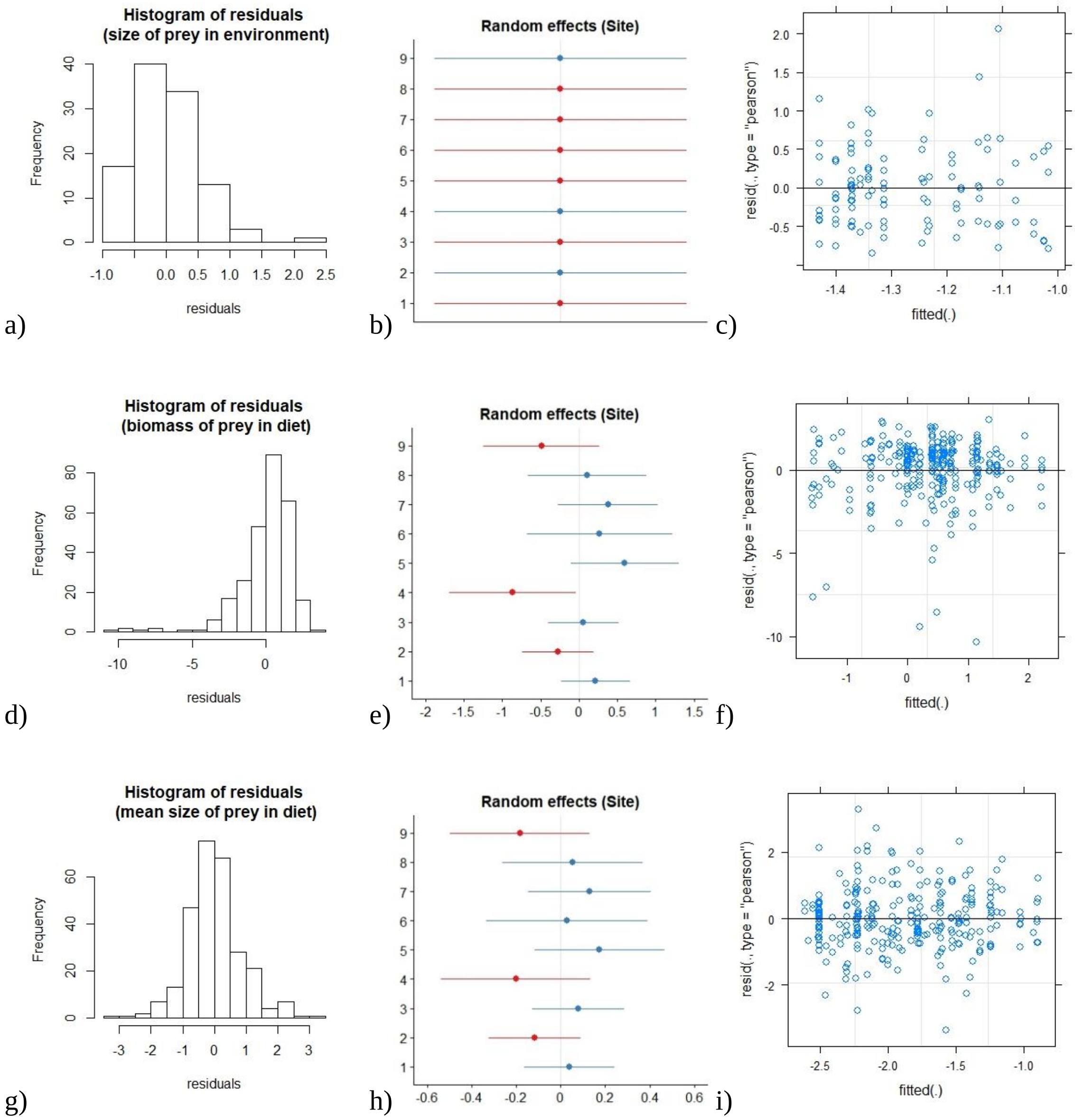

Figure S4.7. Model diagnostics plots for: (a-c) linear mixed effects model for size of prey in the environment, (d-f) linear mixed effects model for biomass of prey in the diet, (g-i) linear mixed effects model for size of prey in the diet.

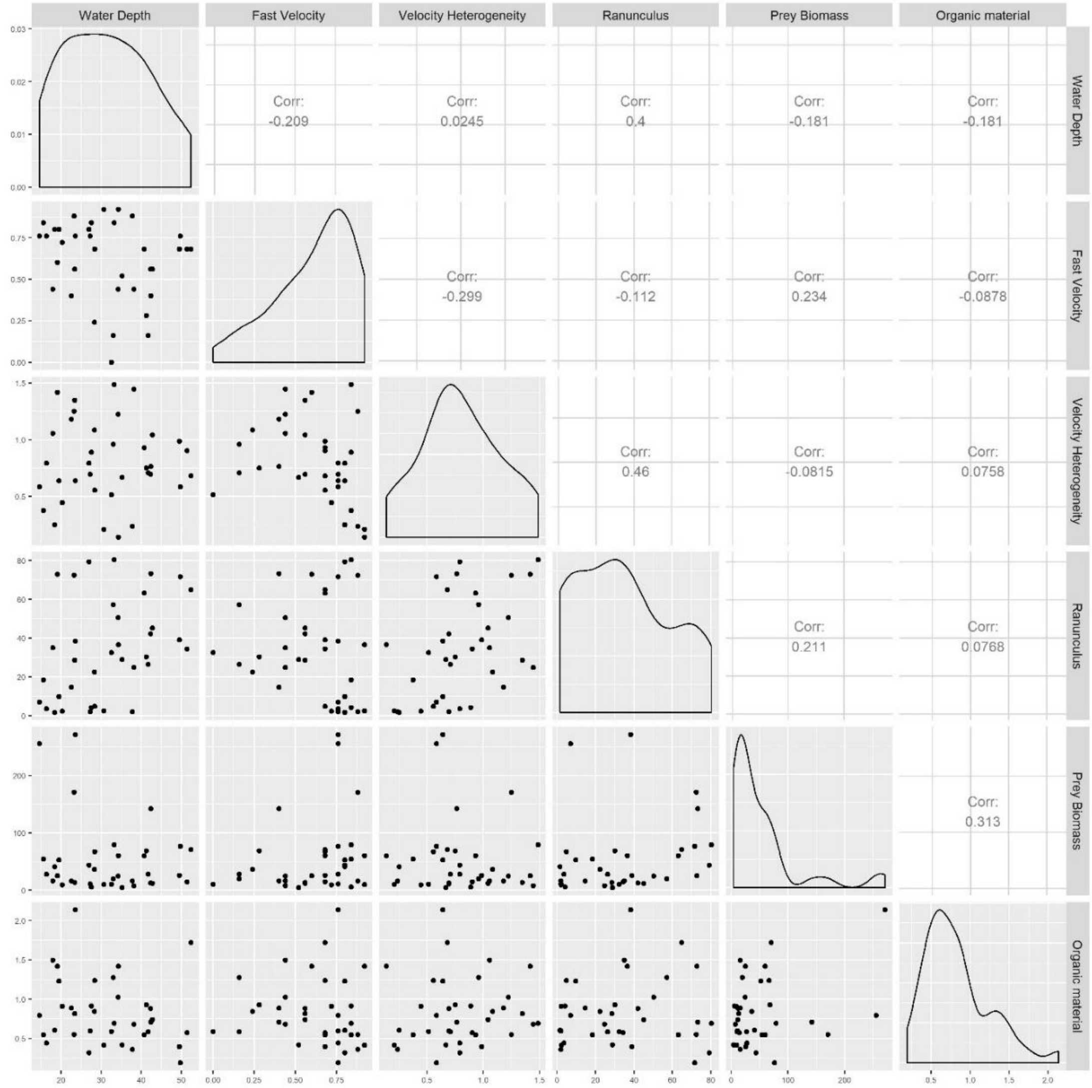

Figure S5.1. Correlation matrix for explanatory variables included in salmon abundance SEM.

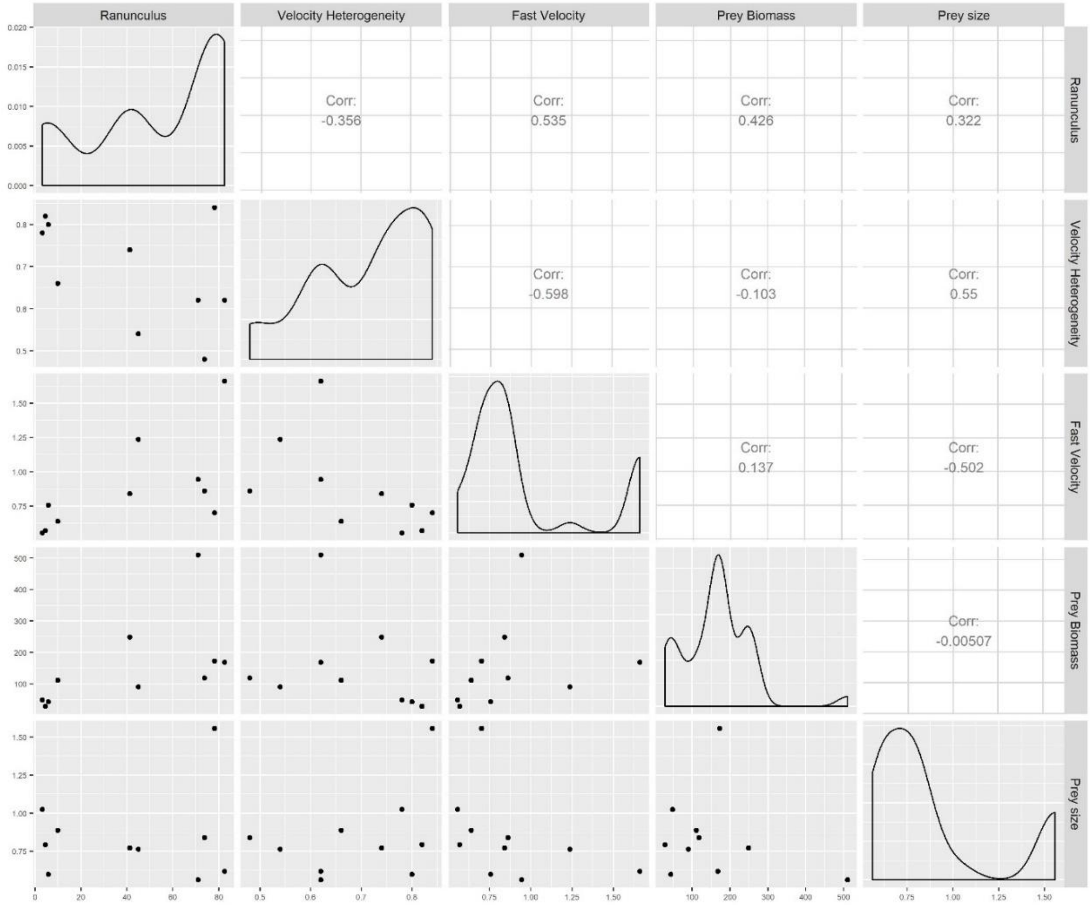

Figure S5.2. Correlation matrix for explanatory variables included in salmon growth rates SEM.