Sex, Parasites and Coevolution:
Improving forecasts for the distribution of the
New Zealand mudsnail *Potamopyrgus antipodarum*

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Abstract

For the fields of invasion biology and conservation science, the ability to predict the distribution of a species is crucial. Even more so, the ability to identify where a species distribution will expand to before it actually occurs can be imperative to mapping and controlling growing distributions. For these issues, Species Distribution Models (SDMs) are used to predict the distribution of the target species by relating the species presence or abundance to a variety of environmental or spatial characteristics. It has been suggested that SDMs are limited in their ability to predict species distributions because ecological theory is not fully integrated in the modelling process. This idea is realised through the lack of inclusion of biotic interactions into SDMs, as SDMs currently are unable to predict the changing range limits of a species that occur due to constantly changing biotic interactions such as competition, predation and dispersal limitation. This thesis was able to show through simulating population growth under different abiotic and biotic conditions that the coevolutionary interaction between *Potamopyrgus antipodarum* and its trematode parasites is important to include in SDMs if they are to accurately predict the distribution of *P. antipodarum*. The research presented in this thesis connects the already well-established field of ecological niche modelling with the complexity of modelling biotic interactions, opening the door for exciting advances in the field of distribution modelling and predicting invasive species ranges.

Chapter 1

Introduction

1.1 Predicting species distributions

For the fields of invasion biology and conservation science, the ability to predict the distribution of a species is crucial (Peterson 2003). Even more so, the ability to identify where a species distribution will expand to before it actually occurs can be imperative to mapping and controlling growing distributions (Ferrier 2002). For these issues, Species Distribution Models (SDMs) are used to predict the distribution of the target species by relating the species presence or abundance to a variety of environmental or spatial characteristics (Elith et al 2006, Elith & Leathwick 2009, Guisan & Thuiller 2005). For example, distribution models have been used to create potential geographic distributions for invasive species (Peterson 2003), to analyse the responses of invasive species to climate change (Petitpierre 2012, Araujo et al 2005, Franklin 2010), to predict the geography of a potential habitat for invasive species (Peterson 2005), and to understand if the abiotic environment is the cause of divergence in species occupying the same habitat (Godsoe et al 2009). The development of computer based programs for manipulating geographic information systems (GIS) has made predicting species distributions much easier. Combining geographic environmental layers with presence/absence datasets obtained through traditional field-based ecology provides scientists with a more advanced toolset to predict and visualise species distributions (Elith et al. 2006).

A good example of this comes from a study measuring the realised niche of five *Eucalyptus* species in south-eastern Australia (Austin et al 1990). The authors used a simple distribution model that included presence and absence data as well as mean annual rainfall, mean annual temperature and a radiation index to predict the response of their *Eucalyptus* species to the three environmental factors. Using their distribution model they were able to assess how the presence of the species changed, and the relative influence of environmental factors on the species realized niche. The authors then displayed the realized niche as probability surface plots with mean annual rainfall on the X-axis and mean annual temperature on the Y-axis, indicating the chance of finding a species based on the level of environmental factor.

Although this seems to be an easy and accurate method of predicting a species distribution, there is more at play. SDMs are plagued with limitations that arise when ecological theory is not properly integrated into the creation of the model, in turn making SDMs difficult to use because of the lack of accuracy in the output (Guisan & Thuiler 2005). Examples of this include correlations between environmental variables not being identified, not using the correct spatial scale and not including species interactions as predicting factors (Guisan & Thuiller 2005).

A major limitation of SDMs comes from using museum data and records in the model (Newbold 2010). Generally, older data only consists of presence data points, when SDMs require both presence and absence to properly predict a species distribution. A solution to this problem is to use 'pseudo-absence data', where absence data points are created from points that do not have a presence associated with them. Zaniewski et al (2002) found that creating environmentally weighted pseudo absences for an SDM was a good alternative to creating random pseudo absences, but noted that these absences, regardless of if they were weighted by the environment or not, were not "true" absences and therefore reduce the overall accuracy of the SDM.

The accuracy of SDMs using pseudo absences also depends on the spatial scale that the absences are taken from (VanDerWal et al 2009). Model performance is significantly lower when the pseudo absences are taken from a smaller and more restricted region than from a larger region of

species occurrence (VanDerWal et al. 2009). Another limitation of using museum data is that the data collected may be biased towards areas with generally a higher probability of occurrence, and also data may vary in sample size and collection methods (Newbold 2010). Both limitations can have large impacts on the accuracy of the SDM used. For example, a study published in 2002 found that accuracy improved dramatically when increasing from ten to twenty data points and levelled off after 50 data points (Stockwell & Peterson 2002).

The main limitation that plagues SDMs is that while they are able to predict distributions based on environmental factors, they are unable to predict the changing range limits of a species that occur due to constantly changing biotic interactions such as competition, predation and dispersal limitation (Elith et al 2006, Thuiller et al 2013, Godsoe and Harmon 2012). By excluding these important biotic interactions from SDMs we limit our ability to accurately predict a species distribution. However, the inclusion of biotic interactions into Species Distribution Models first requires an understanding of how the abiotic environment affects the target species. In freshwater environments, much of what shapes a species distribution can be found in the abiotic environment. The evolutionary pressure of the abiotic environment controls where a species can persist (Jackson et al. 2001). Abiotic factors such as flow rate, nutrient availability and stream stability have been found to influence the abundance, density and community structure of freshwater species. For example, a study conducted on the abiotic and interspecific effects on freshwater fish assemblages found that variability in the mean flow rate and peak flow was a much stronger predictor of fish assemblage and structure than predation or competition for space (Grossman et al. 1998).

Nutrient availability affects freshwater species by preventing individuals from dispersing into new locations where resources cannot be utilised. Streams with higher levels of nutrients can promote growth in some macrophytes and yet be harmful to other macrophyte species (Cronin & Lodge 2003). Nutrient input into a stream caused by land runoff from terrestrial sources and land use of the riparian areas of a stream can influence the water chemistry and stream temperature, enhancing or inhibiting in-stream primary production, resulting in changes in biomass for many of

the species inhabiting the stream (Sponseller et al. 2001). Stream stability can affect freshwater species through a variety of means. For example, streams fed by naturally occurring spring water generally have a more predictable and stable flow regime than streams fed by land runoff as unlike runoff-fed streams, spring-fed streams have a uniform annual temperature and a consistent flow rate (Death & Joy 2004, Gordon et al. 2004).

The abiotic environment plays an important role in controlling species distributions, but biotic interactions have been found to also influence the range limits of a species and the species distribution (Case et al. 2005). Abiotic factors paint only half the picture, whereas, an understanding of biotic interactions such as competition and predation gives us an overall better sense of what controls the distribution of the species. For example, interspecific competition has been shown to influence the distribution of a species through competitive exclusion. Bauer et al. (1994) were able to show this through analysing the distributions of three species of the Equidae family (horses and related animals) in Africa. The authors found that despite the three species being very similar, they existed along an environmental gradient with narrow overlapping geographical ranges, preventing each other from expanding into new habitats through competitive exclusion.

A study published in 2011 again demonstrates this idea of the importance of biotic interactions by showing how an obligate mutualism between a leaf cutter ant species (*Atta texana*) and their fungus (*Attamyces sp.*) has led to an expansion of *A. texana*'s distribution (Mueller et al. 2011). Leafcutter ants depend on the fungus for food, and in turn are constrained in terms of their distribution by the abiotic environment that the fungus can tolerate (Mueller et al. 2011). The evolution of this cold-tolerant fungus has allowed *A. texana* to expand its distribution into climates with colder temperatures where it previously could not persist.

These examples of biotic interactions provide solid evidence that the abiotic environment, while very important to consider, is not the only mechanism controlling the expansion and constraining the range limits of a species distribution.

1.2 Host-parasite coevolution and the mosaic of selection

Alongside competition and predation, coevolution is another biotic interaction with the potential to shape species range limits, although literature on this subject is scarce. Due to climate change and anthropogenic effects, species live in a constantly changing environment.Therefore, over time species niches as well as the interactions they have with other species will evolve and distributions will change as species adapt. Analysis of species' niches is essential for understanding the controls on the boundaries of a species distribution and how these might shift with changes in the environment.

Studies have shown that the interplay between evolution and ecology (eco-evolutionary dynamics) provides a better toolset for understanding niches and how they evolve (Johnson & Stinchcombe 2007). Coevolution incorporates both ecological and evolutionary components making it a worthwhile consideration when examining the role of biotic interactions in distribution modelling. To understand how coevolution influences distributions, first we must understand how coevolution occurs and also how it can be mediated by the abiotic environment. Coevolution can occur very rapidly within decades and can have important influences on the ecological dynamics of communities (Thompson 2005, Thompson 1998). Rapid evolution is best described by the Red Queen hypothesis, which proposes that selection from coevolving pathogens facilitates outcrossing despite the cost of sexual reproduction (Morran et al. 2011). Sexual reproduction is important because it gives rise to genetic differences in offspring, allowing them the potential to be less susceptible to infection and parasitism (Hamilton 1982, Hamilton et al. 1990). When infection rates drop, asexual reproduction takes over and populations begin to fill with clones. Once a parasite evolves and is able to infect a clone, it is not long before all the clones are infected due to the lack of genetic difference that allow them to escape infection and parasitism (Hamilton et al. 1990, King et al 2009). The selection pressure imposed by the high parasitism causes an evolutionary shift to sexual reproduction and the rate of parasitism drops again (Peters & Lively 1999, King et al 2009). This back and forth motion of coevolution between host and parasite is a good example of the rapid

evolution of a defence mechanism, whereby sexual reproduction is used as a defence to parasitism (Hamilton et al. 1990).

Coevolution is an interesting relationship when considering how biotic interactions effect distributions because the outcome of this relationship often has large impacts on where and when a species can persist. Because coevolution occurs between many species in a community, it creates an ever-changing community composition (Thompson 1998). This is best detailed in the book "The Geographic Mosaic of Coevolution" written by John N. Thompson and published in 2005 (Thompson 2005). The backbone of this theory is that the fitness in one species depends on the distribution of genotypes in another species, and that there is often a genotype-by-genotype-by-environment interaction of fitness going on in interacting species (Thompson 2005).

In his book, Thompson also presents the idea of coevolutionary hotspots, where interactions only achieve reciprocal selection, and in turn coevolution, in localised communities. This creates "hotspots" of coevolution where the conditions are right for multiple forms of coevolution to occur in localised parts of an overall distribution (Thompson 2005). On the other hand, this allows for the formation of "coldspots" of coevolution, where local selection is not reciprocal and coevolution does not take place as frequently. These hot and coldspots of coevolution are the basis of the mosaic that Thompson describes in this geographic mosaic of selection theory. Selection mosaics such as this are able to produce spatially variable coevolutionary outcomes throughout the distributions of the species that are interacting with each other (Gomulkiewicz et al. 2000), and are an important determinant of the magnitude of local adaptation (Nuismer 2006).

A study published in 2011 gives an excellent example of how coevolutionary hot and coldspots can be highly dynamic in a metapopulation. The authors conducted a 19 year study on a host-pathogen interaction where infection by the pathogen results in population extinction within the metapopulation. They found that the level of disease and the spatial location of the disease caused by the pathogen varied through time, resulting in an ever-changing pattern of selective

pressure on the host species (Smith et al. 2011). In other words, both hotspots and coldspots were present, and changed through time based on the severity of the rapidly occurring coevolution.

1.3 Coevolution and its role in distribution modelling

From Thompson's theory of the geographic mosaic of selection and the idea of hot and coldspots of coevolution rapidly evolving and changing throughout time and space, we can see how important coevolution is for influencing community composition and the overall distribution patterns of species involved. Yet, it is seemingly unknown how this intricate network of coevolution can influence a Species Distribution Model. Literature on the subject is scarce, making it problematic to understand how coevolution may change distribution models and if it is necessary at all to include. The edges of a distribution, or the range limits, are characterized by increased genetic isolation, genetic differentiation and also variability in the ability of individuals and populations to survive (Sexton et al. 2009). All of these range edge factors fall under the hot and coldspots of coevolution. The nature of the mosaic of selection means that some populations may be genetically isolated in coldspots, where coevolution is not as strong and sexual reproduction is not occurring, leaving individuals and offspring genetically similar without access to gene flow or the necessary evolved defences to survive at the range margin. In contrast, hotspots of coevolution allow for high levels of genetic differentiation through the constant outcrossing obtained from the sexual reproduction occurring in the hotspots.

Many studies highlight the need for the inclusion of biotic interactions and coevolutionary dynamics into distribution models and models of range limits (Sexton et al. 2009, Godsoe & Harmon 2012, Thuiller 2013, Ricklefs 2010), with some stating that the quality and reliability of Species Distribution Models is questionable due to the overlooking of these important biotic interactions (Thuiller 2013). This begs the question, is it necessary to include coevolution among biotic interactions in species distribution models? And will the inclusion of coevolution significantly change the outcome of the predicted distribution?

To determine whether not including coevolution into species distribution models will increase their accuracy in predicting distributions, it is necessary to analyse the ecological impact coevolution has on the species involved. We know how coevolution affects populations through the mosaic of selection (Thompson 2005), but it is important to understand the effects of coevolution on the fitness of species and the potential for ecological change and niche shifts. Species' niches can overlap if their distributions are controlled by a biotic interaction, preventing competitive exclusion (Godsoe et al. 2009). For example, the overlap in niche space between host populations and their pathogens/parasites or mutualists results from localised coevolutionary dynamics (Ricklefs 2010). It is also possible that relationships with pathogens or parasites might actually constrain a species distribution if the diversity of the antagonist increases with the host diversity, resulting in more host switching of the pathogen/parasite and higher rates of disease (Ricklefs 2010). Coevolution at the range margins has the potential to expand and also constrain species distributions, highlighting the need to include coevolution into Species Distribution Models. These studies also highlight how important sampling in the range margin is for the analysis of species ranges. In central populations, the strength of coevolution regardless of its direction (expansion or contraction of the species range) has little effect on the overall distributional patterns observed at a larger scale. High parasitism rates may cause a localised extinction in the central population, but this does not affect the overall distribution of the species. However, when these localised extinctions and/or growths in populations occur at the range margin parasitism rates begins to matter for predicting how a species distribution may change (Pearman et al. 2007, Ricklefs 2010).

1.4 *Potamopyrgus antipodarum* and its trematode parasites

The coevolution between the New Zealand mudsnail *Potamopyrgus antipodarum* and its trematode parasite has been extensively studied and gives us a unique opportunity to test how the relationship influences the range margins and distribution of *P. antipodarum*.

Potamopyrgus antipodarum is a prosobranch New Zealand freshwater snail commonly found in lakes, rivers, ponds and streams (King et al. 2011, Winterbourn 1970). First identified by John Edward Gray in 1843, it has since colonised other countries such as Australia and the United States (Kerans et al. 2005) sparking studies into its invasive success.

This species contains females that can reproduce either by sexual or asexual reproduction (Dybdahl & Lively 1995), leading to populations that contain a combination of sexual and asexual individuals, or populations that are entirely asexual (Lively 1989). Decades of research suggest that the dioecious nature of *P. antipodarum* is a result of parasitism by trematode parasites such as *Microphallus* sp*.* (Lively 1989). *Microphallus* sp*.*, along with other digenetic trematode parasites, use *P. antipodarum* as an intermediate host for reproduction (Lively &Jokela 1996)*.* The parasites eggs are ingested and form hundreds of encysted larvae inside the snail. The final stage of the parasite's reproduction is completed upon the ingestion of the snail by the final host, ducks (Grey Ducks and Mallards) and the encysted larvae hatch (Lively and Jokela 1996).

Successful infection by trematode parasites results in the sterilisation of both sexes of the mudsnail (Lively 1989) through the replacement of the host's gonads and digestive gland by encysted larvae (Koskella & Lively 2007); therefore, in an effort to escape parasitism, *P. antipodarum* populations use sexual reproduction as an adaptation to produce genetically variable offspring that the parasites are not adapted to infect and in turn reducing the overall infection rate in the population (i.e. frequency-dependant selection) (Lively 1989). In other words, the advantage of sex is that it allows for the production of rare phenotypes, giving them a greater chance to avoid becoming parasitised. Sexual populations of *P. antipodarum* have been shown to have higher levels of infection suggesting that parasitism may contribute to the maintenance of sex in *P. antipodarum* (Lively 1987).

Trematode parasites that use *P. antipodarum* as a host species are locally adapted, meaning that they are able to track common snail phenotypes within a local population (Lively 1989, Lively & Dybdahl 2000)). The ability of *P. antipodarum* to reproduce rare phenotypes to escape infection and

the counter-adaptation of the parasite to track the phenotypes as they become more common is the basis of the coevolutionary relationship and is an example that supports the Red Queen hypothesis (Lively 1987, King et al. 2011, Lively 1996, Lively & Dybdahl 2000), where continuous adaptation occurs between the host and the parasite. Recent studies have found this biotic interaction between host and parasite can have interesting effects on both species. This wealth of knowledge on the subject of host-parasite coevolution in *P. antipodarum* gives us the perfect study species for attempting to understand how biotic interactions such as coevolution can influence a range margin or a species distribution as a whole.

1.5 Thesis aims and hypotheses

The overall aim of this thesis is to investigate if the inclusion of a biotic interaction into an SDM will improve the models ability to predict the distribution of the target species. I will explore the prediction that for future SDMs to be accurate and reliable enough for practical use it is necessary to include biotic interactions.

More specifically, Chapter Two of this thesis explores how the abiotic environment influences the presence of *P. antipodarum*, identifying which abiotic factors are important for *P. antipodarum's* distribution and how they relate to each other. The specific aims of Chapter Two are as follows:

(i) To identify which environmental gradients traverse the distribution of *P. antipodarum*

(ii) To identify what environmental predictors shape the distribution of *P. antipodarum.*

By exploring the role of the abiotic environment in determining mudsnail presence I will be able to show which abiotic factors are necessary to include in future modelling of *P. antipodarum's* distribution.

For coevolution to influence the distribution of *P. antipodarum* it is necessary to first test if parasites actually occur in the range margins. If they do not occur there, then coevolution cannot influence the distribution. If parasites do occur in the range margin then the potential for distributional changes related to coevolution exists. Chapter Three of this thesis aims to investigate if coevolution occurs in the range margins of *P. antipodarum* and if the strength of the coevolution can change based on the environment. Specific hypotheses of Chapter Three are:

(i) Coevolution occurs in the range margins of *P. antipodarum*.

(ii) The abiotic environment mediates the strength of coevolution.

Chapter Four aims to combine the findings of Chapters Two and Three into models that show the survivability of *P. antipodarum* populations based on the abiotic environment as well as coevolution resulting from parasitism by trematode parasites. The hypotheses for Chapter Four are:

(i) The simulated growth and survivability of *Potamopyrgus antipodarum* populations change when abiotic and biotic factors are included in population growth models.

(ii) When parasitism is present in simulated populations of *P. antipodarum* that occur in the range margins of the distribution that the potential exists for the range margins to shift.

By the end of this thesis I will have investigated the influence of abiotic factors on the presence of *P. antipodarum*, assessed the potential of host-parasite coevolution on determining the range margins of *P. antipodarum's* distribution, and simulated population growth through models that include abiotic and biotic factors. I will show that parasitised populations that occur in the range margins of the distribution have different growth rates than unparasitised populations, warranting the inclusion of host-parasite coevolution in Species Distribution Models.

Chapter 2

The Abiotic Environment

2.1 Introduction

The abiotic environment is forever changing, and in turn, species distributions change with it. Many abiotic factors are particularly intertwined with the distribution of freshwater species. For example, stream salinity has been found to be a good indicator of species distributions as many species distributions are correlated with salinity level in their resident habitats (Gallardo-Mayenco 1994). One study showed that regions of a stream with salinity levels higher than 10 parts per thousand (ppt) were dominated by larvae of *Epyhydra* and *Culioides (*order Diptera) during periods of aquatic reproduction while in areas with salinity less than 10ppt, species richness increased in a linear fashion with decreasing levels of salinity (Short et al. 1991). Stream salinity plays a role in determining where a species can persist and is linked with the distributional changes that we observe in macroinvertebrates.

On the other end of the spectrum, some abiotic factors have a not so clear link to species distributions. Although macroinvertebrate occupation of different substrate sizes has been demonstrated (Quinn & Hickey 1990), in another study substrate size has been shown to have little to no effect on macroinvertebrate distributions (Culp et al. 1983). Culp et al. (1983) found that the density and biomass of 16 out of the 19 taxa they tested did not change across varying sizes of substrates. Some abiotic factors influence a distribution heavily while some have little to no effect,

which begs the question, what environmental abiotic factors are important for freshwater species? Which factors matter the most for influencing the distribution of a species? Numerous studies have been conducted in an attempt to answer these questions and have shown that factors such as flow variability and stream stability are heavily linked to distributional changes through disturbance events and altered flow regimes.

Flow variability is a major determinant of freshwater habitat in streams (Bunn & Arthington 2002). Low flow habitats are stable, have a low disturbance frequency, contain high levels of organic matter, provide high refugia availability, and support a diverse assemblage of species. In contrast, high flow habitats are unstable, have higher disturbance frequency, and provide less refugia and organic matter, resulting in dramatically lower levels of species diversity and biomass (Scarsbrook & Townsend 1993). Flow variability is especially important for freshwater invertebrates, where flooding events can have large impacts on the distributions of the species involved primarily through a drastically increased water flow accompanied by the movement of substrate. For example, it has been shown that major flooding events can result in a reduction of species richness and biomass by up to 90% (Quinn & Hickey 1990). Flow variability is a major abiotic factor to consider when thinking about what factors are important for the distribution of a species, as it can quickly alter the habitat a species is living in and can create sharp range limits through flooding events.

Alongside flow variability and stream stability, nutrient availability is another abiotic factor that is heavily linked to species distributions. In freshwater ecosystems, invertebrates gain nutrients from a variety of different methods. For example, stream grazers obtain nutrients from algae that form on the substrate of the streams they reside in; detritivores obtain nutrients from detritus that falls into the stream from surrounding vegetation, and filter feeders filter nutrients from the water. Invertebrates rely on the availability of nutrients to survive in their habitats, and in that way, nutrient availability is linked to distributional changes.

A good example of the effects of nutrient availability on invertebrates can be found in a study on the effects light and nutrient manipulations have on invertebrate biomass. The authors

found that with an increase in phosphorus into their treatments a shift in invertebrate functional group composition occurred. Composition shifted from filter feeders to mainly grazers (Bourassa & Cattaneo 2000). From this we can see that an increase in nutrient availability can change the community composition of a stream and in turn the distribution of each species in those functional groups changes.

2.1.1 Potamopyrgus antipodarum in the abiotic environment

SDMs can be used to predict a species distribution based on the environmental factors in their habitat, but before they are used effectively it is essential to understand which environmental factors are important for the target species and how they influence the overall distribution. For my thesis, the target species is the freshwater mudsnail, *Potmopyrgus antipodarum*. As described earlier, there are many environmental factors to which freshwater species are subjected. Which of these are important to consider for the distribution of *P. antipdarum* remains untested. To create an SDM for this species it is first necessary to understand how *P. antipodarum* reacts to its environment and how its distribution is influenced by abiotic factors.

The range of salinity present in different freshwater habitats is an important abiotic factor for many freshwater species (Gallardo-Mayenco 1994). The ability to tolerate different levels of salinity within the freshwater range can create range boundaries for a species, restricting its ability to disperse into new habitats. However, it is unclear if salinity is a stressor for *P. antipodarum*. A study on the impact of salinity on the structure of freshwater gastropod communities found that abundance and species richness increased dramatically from high salinity to lower salinity waters (Gerard et al 2003), showing how important salinity is for freshwater species. Interestingly, regardless of the salinity level, *P. antipodarum* was the most abundant species. *Potamopyrgus. antipodarum* was also the only snail present in the highest salinity sites sampled (Gerard et al 2003). From this we can deduce that salinity, while crucial for understanding other species distributions, is not an important factor to consider for understanding and predicting the distribution of *P.*

antipodarum. The fact that this study was conducted in France may change the importance of salinity for distribution modelling as invasive snails found there may have a high tolerance to salinity than snails found in New Zealand.

Land use surrounding the habitat and the physio-chemical nature of the stream play an important role in determining whether a species can persist at a site (Harding & Winterbourn 1995). Pastoral habitats are surrounded by paddocks with little canopy cover and higher temperatures than covered forested streams, leading to a high level of periphyton in the water (Harding & Winterbourn 1995). Pastoral streams also have different chemicals in the water, with higher levels of iron and potassium (Harding & Winterbourn 1995). Not surprisingly, Harding & Winterbourn (1995) found that *P. antipodarum* dominated pastoral streams, where there were more food resources (periphyton) and where streams were generally more stable.

Alongside the physio-chemical attributes of a stream, flow variability has an effect on the distribution of *P. antipodarum*. Holomuzki & Biggs (2000) found that in experimentally simulated high flow events (in an effort to replicate natural flooding events) mudsnails burrow into the sediment as to protect themselves from being washed away, burying deeper than both mayflies and caddisflies. *P. antipodarum* numbers also decreased with an increase in flow velocity but with snails still present at flows of 100 cm/s. There was a higher dislodgement rate of *P. antipodarum* in unstable patches versus stable patches (19% and 8% respectively) and a higher mortality rate in unstable vs stable patches (8% and 4% respectively). While mudsnails are able to survive in habitat with varying flow and flooding events, there is still mortality occurring during flooding events and the possibility for flow variability influencing the distribution of *P. antipodarum* exists.

2.1.2 Aims

From these few examples of how the environment influences the distribution of *P. antipodarum* we can see that there are abiotic factors that have the potential to shape the range margins of a species and the overall distribution, factors that are necessary to understand first in

order to create a SDM that is both accurate and also useful for distribution predictions. Therefore, the aims of this chapter were to identify;

Which environmental gradients traverse the distribution of *P. antipodarum.*

What environmental predictors shape the distribution of *P. antipodarum*.

2.2 Methods

The sample design was informed by existing distribution models, which provide a good synopsis of the distribution of *Potamopyrgus antipodarum*. In 2009, Leathwick *et al*. published a report detailing the predicted national-scale distributions for several freshwater macro-invertebrates across New Zealand. Statistical models relating to the various macro-invertebrates were combined with environmental variables describing characteristics of streams around New Zealand, resulting in topographical maps that gave visual representations of predicted distributions and the probability of macro-invertebrate presence. Leathwick *et al.* (2009) used a large dataset of 2883 presences to predict sites likely to contain *P. antipodarum*. They summarized this information using the predicted probability of occurrence, where probabilities range from 0 to 1 with 0 representing sites unlikely to contain *P. antipodarum* and 1 representing sites likely to contain this species (Figure 2.1).
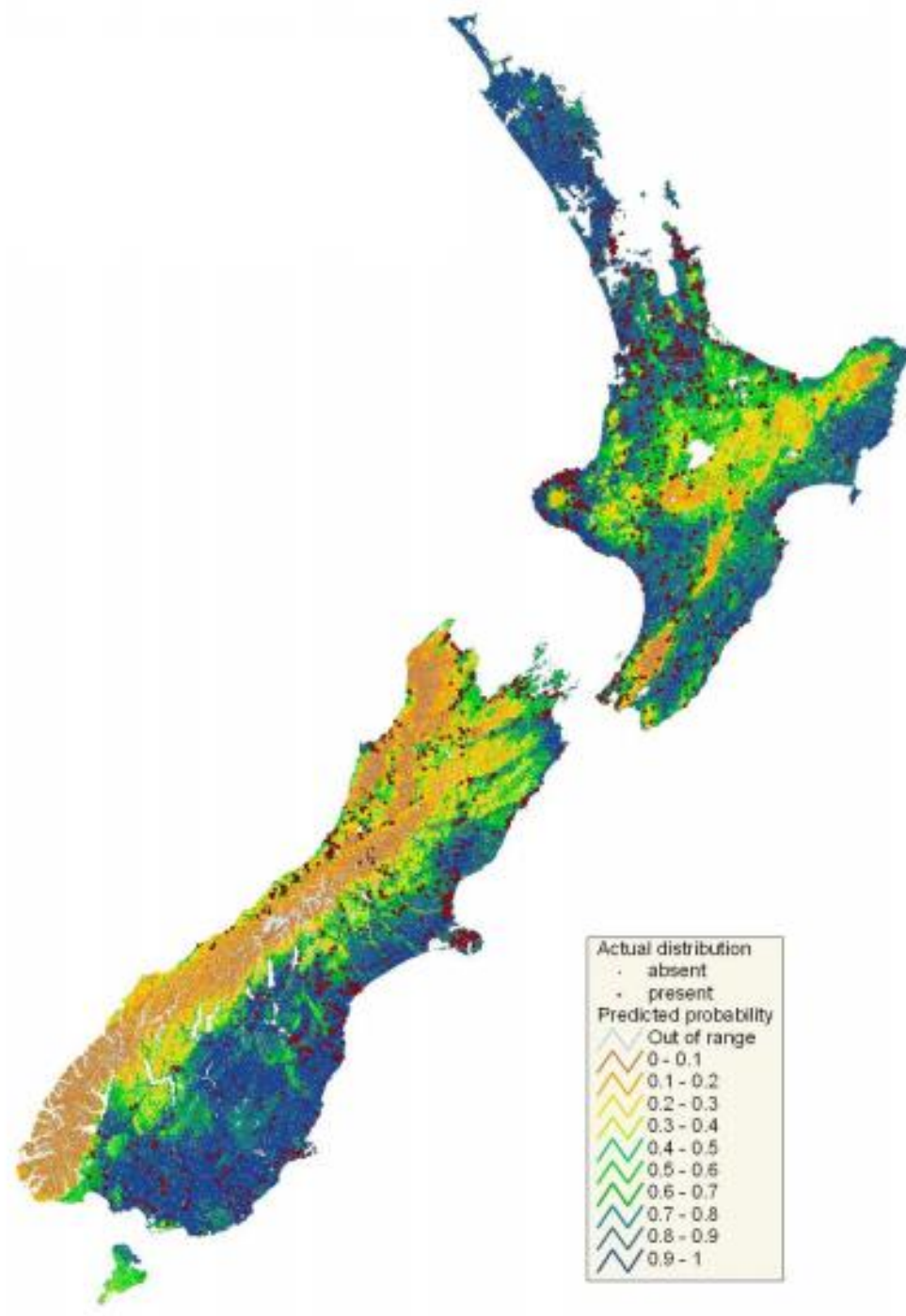
Figure 2.1. The predicted probability of occurrence and observations of *Potamopyrgus antipodarum* (Leathwick et al. 2009).

Alongside a detailed map of *P. antipodarum's* distribution, Leathwick et al. (2009) also detailed various important abiotic factors for predicting the distribution of *P. antipodarum*; stream

nitrogen load, flow stability, days with rainfall greater than 25 mm and average phosphorus concentration. I extracted these four variables from Leathwick's dataset using the statistical programs ArcGIS and R (version 3.0.3). Elevation was also used in statistical analysis and was extracted from the "Hydro1K Australia" data set uploaded to the internet for the purpose of hydrological analysis by the USGS/EROS Center (Earth Resources Observation and Science). 1000m cell size was used in this data set and the Lambert Azimuthal Equal Area projection was used to project the DEM (digital elevation model). I used the statistical program R (version 3.0.3) to extract elevation values. The five environmental variables used in this chapter are described in Table 2.1, which names the variables, describes their units of measure and gives a brief explanation of what each variable is.

Table 2.1. Descriptions of the five environmental variables used in the analysis, including the variable name, the unit of measurement and an explanation of the variable.

Variables	Measurement	Explanation
Elevation	Metres	Describes the relative metres above sea level.
Flow Stability	Annual low flow/annual mean flow	Describes the ratio of mean annual low flow to the mean average flow. High values indicating minimal within-year variation in stability and low values indicating high within-year variation in stability.
Phosphorus	1 = very low, 5 = very high	Describes the average phosphorus concentration of underlying rocks.
Nitrogen Load	log10 transformed parts per million	Describes the nitrogen concentration of a river segment. Used as an indicator of land-use intensity.
Days Rain	Days/Years	Describes the frequency of days in a year with significant rainfall (>25mm) in the upstream catchment. Indicates the likelihood of an elevated flow.

To understand which environmental gradients traverse the distribution of *P. antipodarum,* I explored the relationships between the environmental variables and the presence of *P. antipodarum* *using* topographical maps I generated in the geographical information system (GIS) program ArcMAP of each environmental variable. The topographical map of elevation was generated in the statistical program R (version 3.0.3). I then produced a pairwise plot and a table of correlation coefficients in R (version 3.0.3) to determine if there were any apparent correlations between variables.

In an effort to assess which environmental variables were important for predicting the presence of *P. antipodarum* I ran a general linear model (GLM) with binomial error because the data being used has response variables with two possible outcomes (parasitised/unparasitised, male/female). using the five environmental variables on presence/absence data collected in the field (methods described in Chapter Three) combined with a data set obtained from King at al (2010) and also from a summer student working out of the University of Canterbury (Gamlen-Greene unpublished). As nitrogen load was the only variable to return a significant result in the first GLM and flow stability has been shown in the past to be important for predicting *P. antipodarum* presence (Holomuzki & Biggs 2000, Holomuzki & Biggs 1999), I ran another GLM with binomial error on nitrogen load and flow stability, comparing the AIC score to the first GLM to determine which model was the most efficient in explaining the relationship between the environment and *P. antipodarum* presence.

2.3 Results

Comparing elevation across the Canterbury-Westland area of New Zealand (Figure 2.2) to the map of the predicted probability of *P. antipodarum* occurrence (Figure 2.1) shows a consistent trend. As elevation increases towards its peak in the Southern Alps, the probability of mudsnail occurrence decreases. Mudsnails are most likely to be found in areas where the elevation is lower and are least abundant in areas with higher elevation (Figure 2.1).

Flow stability follows a similar trend, comparing the environmental gradient of flow stability (Figure 2.3) to the predicted probability of *P. antipodarum* being present (Figure 2.1) shows that in streams and rivers that are less stable (lower values) there is a higher chance of *P. antipodarum* being present.

Phosphorus concentration (Figure 2.4) is a variable that does not traverse the distribution of *P. antipodarum* (Figure 2.1) as predominately as elevation or flow stability. Comparing the map of phosphorus concentration (Figure 2.4) to the map of the predicted probability of *P. antipodarum* presence; (Figure 2.1) the concentration of phosphorus appears to stay high across the mudsnail distribution, with a slight inclination to higher phosphorus levels in the areas with highest mudsnail occurrence.

Nitrogen load (Figure 2.5), much like elevation and flow stability, traverses the distribution of *P. antipodarum* (Figure 2.1); increasing in concentration with increased probability of mudsnail presence.

The environmental gradient of Days Rain (Figure 2.6) does not appear to change in relation to *P. antipodarum* presence (Figure 2.1). The frequency of days with large rainfalls dramatically increases from around 12 to upwards of 65 upon reaching the Southern Alps (Figure 2.6), whereas the probability of *P. antipodarum* presence decreases slowly as it approaches the Southern Alps (Figure 2.1). There are patches on the West Coast of New Zealand where probability of mudsnail presence is high, as is as the frequency of days with high rainfall.

There are a few modest correlations between variables (Table 2.2 and Figure 2.7). Nitrogen load has a mild negative correlation (r = -0.54) with flow stability, with higher levels of nitrogen being found in streams that are not very stable (i.e. have more variation in their flow regime). Nitrogen load also has a modest correlation with phosphorus concentration (r = 0.46). With increased levels of nitrogen we see a mild increase in phosphorus concentration as well (Figure 2.7). Flow stability has a moderate correlation with elevation (r = 0.54), showing that streams have a more stable and less variable flow in areas with higher elevation (Figure 2.7). Other slight

correlations exist between nitrogen load and the days rain (r = -0.37), nitrogen load and phosphorus (r = 0.46) and phosphorus and days rain (r = -0.38). Out of all the variables, nitrogen load seems to be the variable correlated to some degree with all the other variables tested (Table 2.2).

Results from the general linear model using the five environmental variables on the presence and absence data show only one abiotic factor with a significant influence on *P. antipodarum* presence. Stream nitrogen load returned a significant result (P<0.001, df=117), indicating that as stream nitrogen load increases; the probability of *P. antipodarum* presences increases as well (Figure 2.8). As Holomuzki & Biggs (1999) showed that flow disturbances can create distribution responses in *P. antipodarum*, the second GLM model with binomial error that was run contained just nitrogen load and flow stability. Results from this model mirror the original model, with nitrogen load returning a significant result (P<0.001, df=117) and flow stability returning a non-significant result (P = 0.83, df=117).

A comparison of AIC scores between the two GLM models and a third GLM model containing just nitrogen load alone show that the most efficient model to explain the variation of presences and absences of *P. antipodarum* is the model containing just nitrogen load (AIC = 137.49). The model containing nitrogen load as well as flow stability had an AIC score of 139.45, and the main model containing all five variables had an AIC score of 142.2.
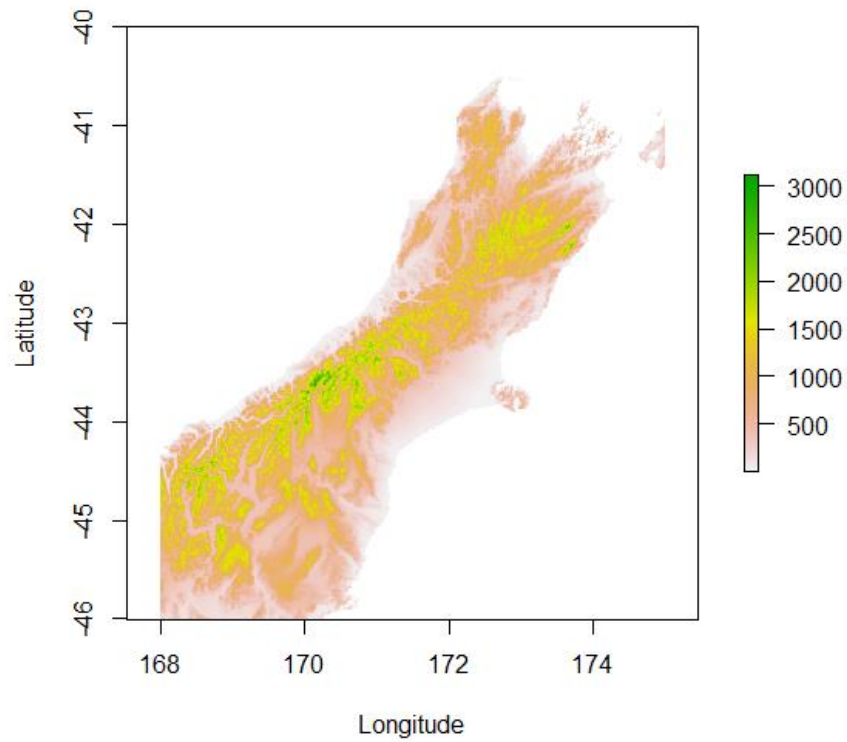
Figure 2.2. Elevation in metres above sea level across the Canterbury-Westland area obtained from the Hydro1K Australia data set publically available online.
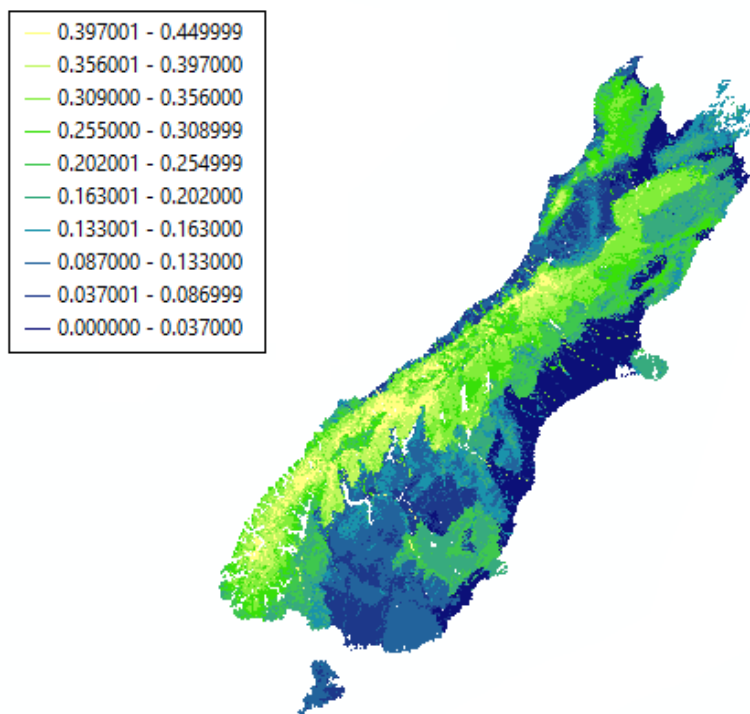
Figure 2.3. Flow stability across the South Island of New Zealand using the data extracted from Leathwick et al. (2009)'s dataset.
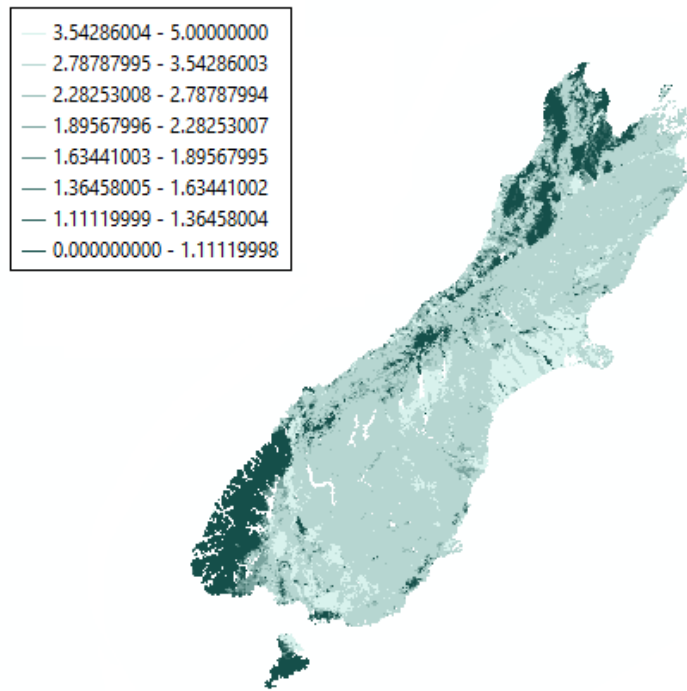
Figure 2.4. Phosphorus concentration across the South Island of New Zealand using the data extracted from Leathwick et al. (2009)'s dataset.
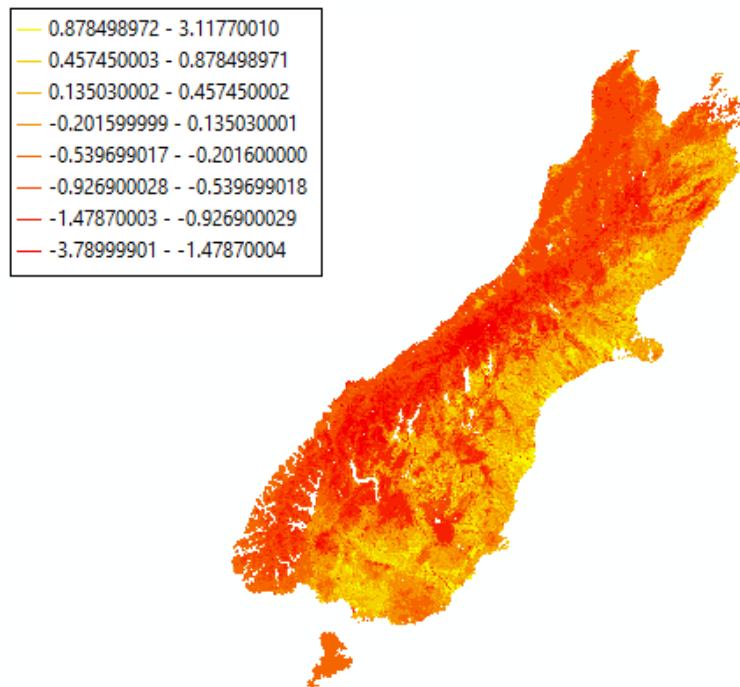
Figure 2.5. Nitrogen load across the South Island of New Zealand using the data extracted from Leathwick et al. (2009)'s dataset.
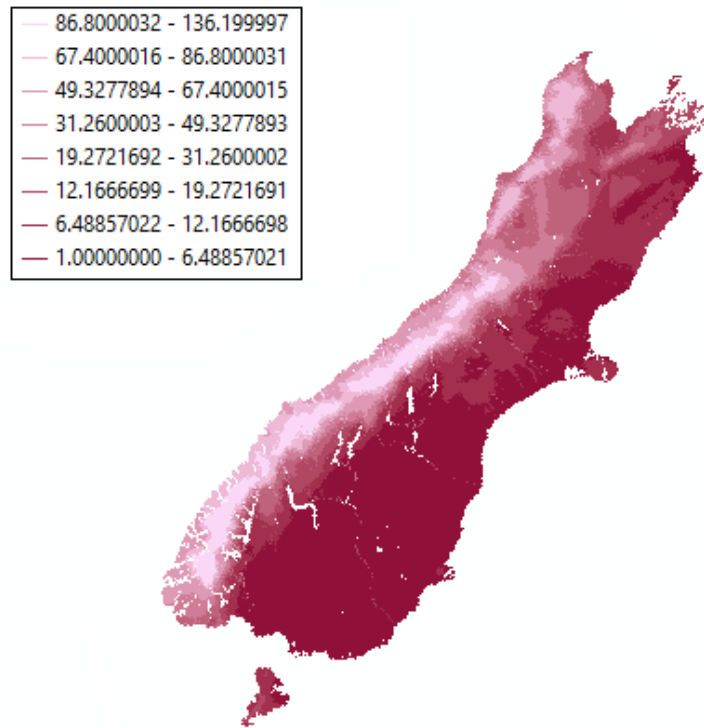
Figure 2.6. Average days rain across the South Island of New Zealand using the data extracted from Leathwick et al. (2009)'s dataset.

Table 2.2. Correlation coefficients (r) for the five environmental variables used in data analysis, obtained from Leathwick et al. (2009).

	Elevation	Flow Stability	Nitrogen Load	Days Rain	Phosphorus
Elevation	1	0.54	-0.21	-0.5	-0.26
Flow Stability	0.54	1	-0.54	-0.02	-0.023
Nitrogen Load	-0.21	-0.54	1	-0.37	-0.46
Days Rain	-0.5	-0.02	-0.37	1	-0.38
Phosphorus	0.26	0.03	0.46	-0.38	1
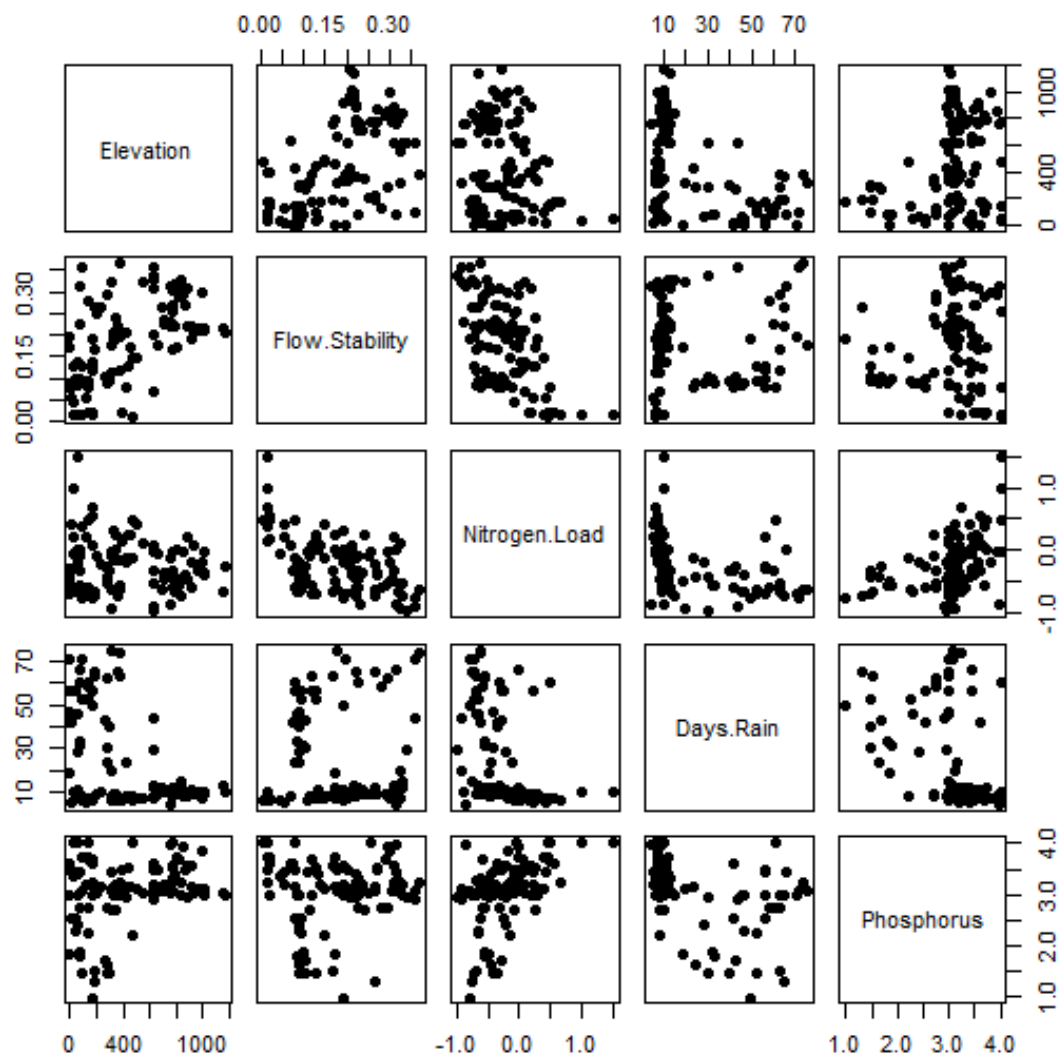
Figure 2.7. Pairwise correlations between all variables collected from a dataset created by Leathwick et al. (2009).
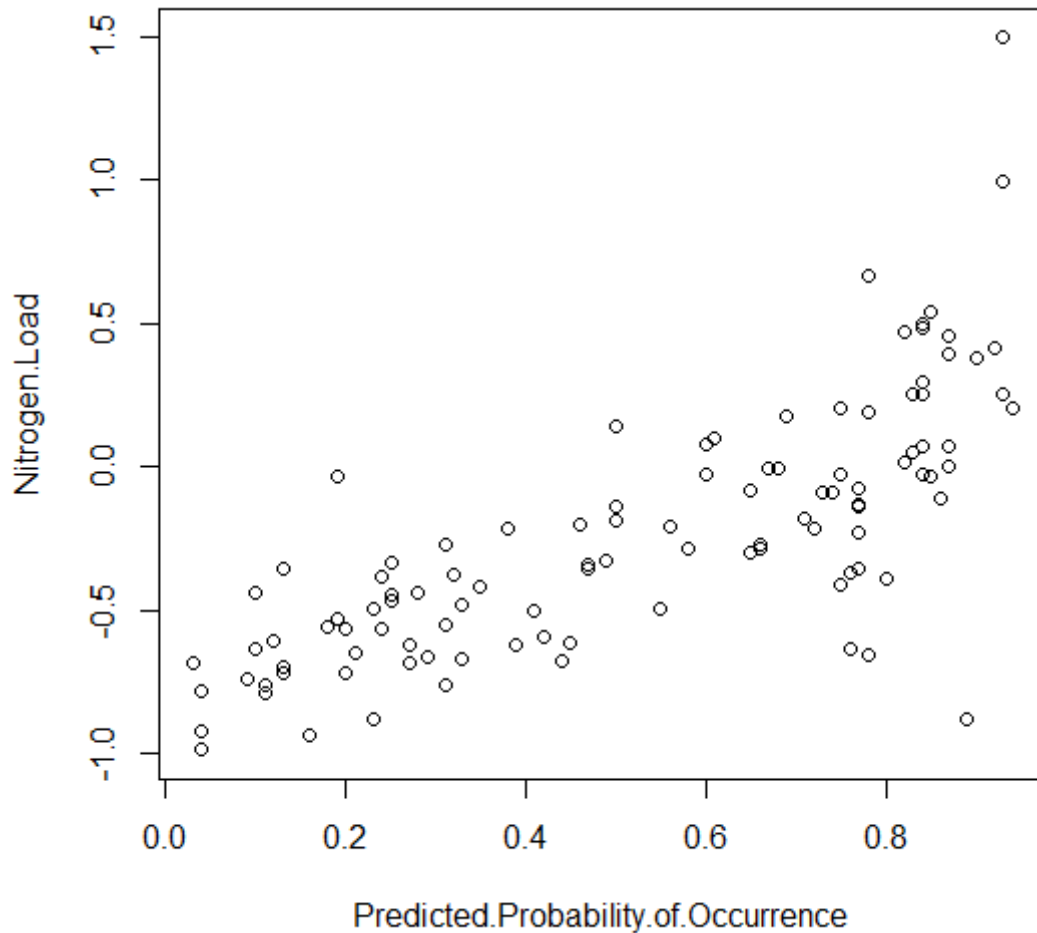
Figure 2.8. Nitrogen load plotted against the predicted probability of *Potamopyrgus antipodarum* occurrence, data obtained from Leathwick et al. (2009)'s dataset.

2.4 Discussion

Environmental gradients that change across the distribution of *P. antipodarum* are more likely to have a significant influence on where *P. antipodarum* is found while environmental gradients that stay the same and do not change in relation to *P. antipodarum*'s distribution won't be as important to consider when creating an SDM for predicting mudsnail presence.

Results from the first GLM show that out of the five environmental variables, nitrogen load is the only variable to have a significant influence on the probability of *P. antipodarum* being present. A study conducted in 2003 that found that *P. antipodarum* consumed 75% of the primary production in the streams around Yellowstone National Park, Colorado, USA (Hall et al. 2003). The mudsnails seemed to dominate the consumption of nitrogen and the excretion of ammonia in the streams,

leading to the potential for large shifts in community consumption through competitive exclusion (Hall et al. 2003). *Potamopyrgus antipodarum* also has been found to have a higher tolerance to nitrogen and ammonia compared to other aquatic invertebrates, allowing it to potentially thrive in sites with nutrient levels that would normally cause toxic effects to other invertebrates (Alonso & Camargo 2003). This would explain both the high probability of occurrence in streams with very high levels of nitrogen and also *P. antipodarum's* invasive success. Mudsnails may be able to survive in harsher, high nitrogen load habitats where other species cannot persist.

Contrary to the results of these studies, Riley and Dybdahl (2015) showed through an experiment where they manipulated resource levels and measured growth rate, that *P. antipodaum* did not grow faster when resources were abundant, and had a similar growth rate to when resources were scarce. Growth remained relatively constant across both levels of resource. Another study has shown that high levels of nitrogen can impair the behaviour and reproduction of *P. antipodarum (*Alonso *&* Camargo 2013)*.* The authors were able to show that when exposed to chronic, but realistic levels of nitrate, *P. antipodarum* exhibits reduced mobility and also reduces the number of live new-borns. These results indicate that nitrogen may be a limiting factor in regards to the presence of *P. antipodarum* rather than a factor that gives populations of *P. antipodarum* a competitive advantage in habitats with high nitrogen levels.

The results of the analysis in this chapter combined with results from studies on the subject of nitrogen and *P. antipodarum* pose a problem when trying to identify whether nitrogen is an important factor to consider when creating an SDM. On one hand, because of the high tolerance to nitrogen, high nitrogen habitats give *P. antipodarum* new options to disperse to where competition with other species is low and populations can thrive on the high nitrogen. On the other hand, there is a trade-off between reduced competition and a lower fecundity. Snails have the space and the resources to thrive but as a result experience lower fecundity and mobility. It is possible that the competitive advantage of high nitrogen levels is negated by the disadvantage of lower fecundity and mobility. The similar growth rates between low and high resource levels would seem to give

evidence for this idea and indicate that nitrogen load is not an important abiotic factor to include in distribution models, despite the significant result of the binomial GLM.

Not surprisingly, nitrogen load is mildly correlated with phosphorus concentration (Table 2.2, Figure 2.7). Alongside the need for nitrogen, *P. antipodarum* also needs other essential nutrients. Phosphorus is associated with growth and fecundity in *P. antipodarum (*Tibbets et al. 2010). Mudsnails exposed to low levels of phosphorus have slower growth rates, have significantly smaller offspring and mature at a later stage, whereas mudsnails exposed to higher levels of phosphorus concentration experience the opposite (Tibbets et al. 2010).

The topographical map of phosphorus concentration over the South Island of New Zealand (Figure 2.4) show that phosphorus concentration does not exhibit a strong environmental gradient and does not traverse or change as much across the gradient of mudsnail occurrence (figure 2.1) as other environmental predictors observed previously in this chapter. It is important to note that despite there being little change in concentration of phosphorus across the mudsnail distribution, phosphorus concentration remains relatively high in the majority of locations *P. antipodarum* is likely to occur in, indicating that populations of *P. antipodarum* in New Zealand are not limited by phosphorus concentrations. This idea is supported by a paper published in 2011, describing the effects of light availability on *P. antipodarum* growth rates (Liess & Lange 2011). The authors manipulated streams to produce differing nutrient ratios and light levels in an effort to assess changes in growth rates in the different scenarios. Results show that snails grew faster and were more active in low light conditions than high light conditions. They found that growth rates were not mediated by food quality but by light level. This would explain why the binomial GLM returned a non-significant result for phosphorus concentration. Other studies have found similar results, showing medium-scale factors such as shade ratio and riparian land use to be important to stream community composition (Collier 1995).

Another abiotic factor that was tested in this chapter was flow stability. While the binomial GLM results show no relationship between flow stability and presence of *P. antipodarum*,

comparisons between the topographical map of flow stability (Figure 2.3) and the predicted probability of mudsnail presence (figure 2.1) indicate a trend in mudsnail presence, with the probability of mudsnail occurrence being higher in sites that are unstable. It is at first puzzling as to why highly unstable streams are linked to the highest abundance of mudsnails . Stable streams have higher macrophyte biomass due to less dislodgement from high, variable flows (Riis & Biggs 2003), and aquatic macrophyte beds are a primary food source and refugia for mudsnails, resulting in decreases in mudsnail abundances when they are in decline (Vinson et al 2007), so it is very interesting to see that *P. antpodarum* is more likely to be found in these high/variable flow sites where the food source can become scarce.

A study by Schreiber et al. (2003) found that the presence of *P. antipodarum* was positively related to high flow variability where mudsnails were found more often in higher flow sites because flooding events facilitate their invasion. Large floods dislodge other invertebrate species and create a gap in the stream community that *P. antipodarum* can easily fill due to its highly successful ability to invade new areas. Holomuzki & Biggs (1999) showed through analysis of 48 streams across New Zealand, as well as laboratory flow tank experiments that during disturbance flooding events where flows were unstable, snails moved to low-velocity areas of the stream to avoid dislodgement (Holomuzki & Biggs 1999, Holomuzki & Biggs 2000). The sediment type mediates the mortality and drift in mudsnails that is usually associated with high-flow streams and flooding events (Holomuzki & Biggs 2003). This way, they can avoid mortality usually suffered by invertebrates during flooding events.

Schreiber et al. (2003) also noted that *P. antipodarum* was more likely to be present in sites that were closer to the sea and closer to human activities. The authors stated that this was because being in closer proximity to the sea and human activity facilitates the invasion of the species. Sites close to the sea and human activity are generally sites with lower elevation and lower flow stability. Another study concurred with Schreiber et al. (2003) by showing that low elevation sites were found to be more suitable for *P. antipodarum* because they were closer to major cities and popular fishing

destinations where it was easier for the mudsnails to have a vector for dispersal (Vinson et al. 2007).

Pastoral environments which have been described as favoured by *P. antipodarum* (Harding &

Winterbourn 1995) are also found in low to mid elevation sites. Lower elevation areas experience

higher variation in stability due to the level of rainfall they experience. Increases in rainfall will see

low elevation/higher order streams undergo an influx of new rainwater, having a domino like effect

the lower down the stream flows. Higher elevation sites will have less of an influx of new water and,

therefore, will experience a more stable and consistent flow regime. This is mirrored by the

correlation between elevation and flow stability (Table 2.2, Figure 2.1), but is contrary to the weak

negative correlation between flow stability and days rain (Table 2.2, Figure 2.1).

As elevation and flow stability have mild correlations with each other (Table 2.2) and

together can explain why *P. antipodarum* is found in low flow stability sites with low elevation, it

would seem that they should have some significant effect on the present of *P. antipodarum*.

Observations from the topographical maps (figure 2.2 and figure 2.3) and the probability of *P.*

antipodarum occurrence (figure 2.1) seem to suggest all three of these environmental factors are

good predictors of mudsnail distributions; it may be that because all three variables are mildly

correlated with each other that by themselves they are not statistically significant in influencing *P.*

antipodarum's distribution but as a whole they have a combined effect on where *P. antipodarum* is

found.

The combination of flow stability and nitrogen showed that both variables were highly

significant. This result is contrary to my initial belief that flow stability on its own would explain more

of the variance in mudsnail distribution because of the combined effect of elevation and flow

stability.

In conclusion, nitrogen load, phosphorus concentration, flow stability, and elevation were all

environmental variables that traversed the distribution of *P. antipodarum*.. Despite nitrogen load

returning a significant result in the binomial GLM that determines which variables significantly

influence the presence of *P. antipodarum,* I determined that nitrogen load was not a good predictor

of *P. antipodarum* presence as there is a trade-off between the positive effects of high nitrogen loads and negative effects of high nitrogen loads. Mudsnails have access to high nutrient levels through competitive exclusion but experience reduced fecundity when nitrogen is high. This trade-off was reaffirmed by a study that showed growth rates of *P. antipodarum* populations do not change significantly between high and low resource levels (Riley and Dybdahl 2015). Therefore, I will not be including nitrogen load in the model simulating *P. antipodarum* survivability (Chapter 4). I also showed that phosphorus concentration did not change much over the distribution of *P. antipodarum* and is not an effective predictor of mudsnail presence.

I found that flow stability also changed across the distribution of *P. antipodarum*, and that the reason this variable returned a non-significant result may have been because of the correlation between flow stability and elevation. *Potamopyrgus antipodarum* is more likely to be found in sites where elevation is low and flow stability is high because of the dispersal potential flooding events and proximity to the sea/human activity creates. Contrary to the results of the binomial GLM I ran, I will be including flow stability in models that predict *P. antipodarum* survivability as I believe it is an important factor if species distribution models are to accurately predict new habitats to which *P. antipodarum* can potentially disperse.

Running a second binomial GLM using only nitrogen load and flow stability was a better model for predicting the presence of *P. antipodarum*, and despite indicating flow stability was not an important predictor, it showed that days rain, phosphorus concentration and elevation were not important for predicting the presence of *P. antipodarum.*

Chapter 3

Host-Parasite Interaction in the Range Margins

3.1 Introduction

3.1.1 Biotic interactions shape range limits

Much like abiotic factors, biotic interactions have the potential to influence where a species can persist. Biotic interactions occur when a living component of an ecosystem interacts in such a way that the action affects the life of another. The best example of a biotic interaction is the relationship between a predator and its prey. The action of the predator hunting and consuming directly influences the life of the prey species, constraining the prey's population growth and preventing the prey's dispersal into high predator populated habitats (Case et al 2005, Holt & Barfield 2009). Competition works in the same way, when Species A out-competes Species B for a resource it constrains the population growth of the Species B and results in competitive exclusion, forcing Species B to find a new resource (Case et al. 2005). A species can be prevented from expanding into a new area because competition for resources is too high and the species is out competed, or predation rates are too high for a species to establish successfully (Godsoe & Harmon 2012). Studies have incorporated competition and predation into theoretical models and show that they have significant effects on geographic range limits, by constraining them or in some specialist cases even expanding them (Holt & Barfield 2009, Araujo & Luoto 2007).

Another biotic interaction that can influence where a species can persist is mutualisms. When two species have a mutualistic relationship their ability to disperse into new environments is intertwined. One species' ability to disperse and persist in a different environment may "open the door" per say for the other species in the mutualism to disperse as well. For example, this is seen in a 2011 study on the mutualism between a cold-tolerant fungus (*Attamyces*) and its leaf-cutter ant mutualist (*Atta texana*). The leaf-cutter ants are able to survive in colder, northern climates because of the evolution of cold-tolerance in the fungi they cultivate, whereas similar ant species without mutualistic relationships could not survive (Mueller et al 2011). Another example of a mutualism influencing where a species can persist is seen in the pollination mutualism between the Joshua Tree (*Yucca brevifolia*) and its pollinating Yucca moths. Two varieties of *Y. brevifolia* are able to coexist within the same environment as they have not specialized on distinct habitats. The pollination mutualisms between the varieties of Joshua tree and the two sister-species of Yucca moth, who live parapartically (their ranges do not overlap), have allowed the different Joshua tree varieties to coexist in the same habitat. Each variety is pollinated by a different species of Yucca moth, preventing competitive exclusion of one variety over the other and in turn expanding the distributions of each variety (Godsoe et al. 2009). It is apparent that a species range limit can be directly influenced by the biotic interactions they have with other species around them.

3.1.2. Strength and importance of biotic interactions

Not only can biotic interactions shape a species distribution, the strength of the biotic interaction plays an important role in shaping a species range limit. What controls the strength of biotic interaction? Literature on the subject suggests that the abiotic environment mediates biotic interactions, and that there is a clear link between the climate of a habitat and the strength of the interaction (Schemske et al 2009, Bertness & Ewanchuk 2002). Schemske et al (2009) demonstrates this idea by showing that the importance of biotic interactions changes along a latitudinal gradient. The authors stated that in equatorial climates, where abiotic stress was minimal, biotic interactions could flourish, in turn leading to higher biodiversity and more specialised species. Biotic interactions

are more important and stronger, but species are more specialised and have fewer interactions on the whole. In contrast, in temperate climates where conditions are harsher, abiotic stress is the determining factor in species diversity (Louthan et al. 2015). In this scenario, biotic interactions are less important and species are generalists who have weaker interactions with more species. This would suggest that at a large scale, biotic interactions are weaker at the range limits of a species distribution and abiotic factors are more important for determining distributional change.

Contrary to this idea, a strong biotic interaction in a harsh abiotic environment may have been the key for allowing the species to expand its range limit into that new environment. In the central populations of a species distribution, the strength of the biotic interaction has little effect on the overall distributional patterns observed at a larger scale. Strong biotic interactions such as predation and competition may cause a localised extinction or growth in the central population but this does not affect the range limits at all. It's when these localised extinctions and/or growths caused by strong biotic interactions occur in populations at the range margin that we begin to see a species range change and shift over spatial and temporal scales (Pearman et al. 2007, Ricklefs 2010). Petitpierre (2012) supports this idea by implying through his study on niche conservatism in invading terrestrial plants that niche shifts to new, non-native habitat will be facilitated only when changes in biotic interactions occur in the range margins of the species distribution. In this way, the strength of a biotic interaction can be as important as abiotic factors in aiding or preventing a species from dispersing into a new habitat.

Alongside the abiotic environment mediating the strength of biotic interactions, climate may change biotic interactions completely, with harsher climates hosting a different array of biotic interactions because of the physical stress imposed by the abiotic conditions. Callaway et al. (2002) was able to show in an experiment conducted in alpine and subalpine plant communities that competition was the dominant interaction in lower elevations where conditions were more favourable, while at higher elevation sites where conditions were harsher and abiotic stress was

higher that positive interactions where species facilitate each other were dominant. This indicates that the strength and type of biotic interaction changes based on the climate and the species involved.

3.1.3. Host-parasite coevolution

As described earlier, the main goal of this thesis is to understand how coevolution can influence the range limits of the species *Potamopyrgus antipodarum*. Coevolution is a biotic interaction where one species coevolves with another. The actions of Species A directly affect Species B, causing Species B to evolve traits in response to these actions that directly affect Species A. This causes Species A to then evolve traits in response to Species B and so on and so forth (Janzen 1979). John Thompson describes coevolution in his 2005 book as "one of the most important ecological and genetic processes organising earth's biodiversity" (Thompson 2005), therefore, we should be considering coevolution as one of the important biotic interactions shaping species range limits. Literature on the subject is limited, with only a few examples that show how coevolution has the potential to shift a species range margin. For example, the potential for an expansion in a species range limit can occur through coevolution between neighbouring species, where populations in the range margins rapidly evolve with other species on the edge of their distribution (Pearman et al 2007).

Many studies have been conducted on the coevolutionary relationship between *P. antipodarum* and its trematode parasites. The literature shows that coevolution between the snails and parasites occurs when snail populations begin reproducing sexually instead of asexually, producing genetically diverse offspring that is more difficult for the parasite to infect. In turn, leading to rapid evolution in parasite populations to infect sexual lineages as they become more locally common (King et al. 2009, King et al. 2011). Further studies have demonstrated that this host-parasite coevolution can be found over a gradient of interaction strength. In 2009 a study by King et al (2009) showed a habitat-specific cline existed in the frequency of sexual reproduction. The

authors found that in shallow lake habitat the frequency of males was dramatically higher than in deeper lake habitats, indicating that sexual reproduction is more prevalent and coevolution is stronger. These areas are known as "hot spots" of coevolution, as described in Chapter One of this thesis under the geographic mosaic of selection.

The same authors published another study in 2011 repeating the experiments of King et al. 2009 to ensure that their data was robust over time. The same results were achieved, confirming that the strength of coevolution between *P. antipodarum* and its trematode parasites changed across a habitat gradient. Another study on the same subject found that by comparing the genetic structure of snail and parasite populations from eight lakes around the South Island of New Zealand they were able to show that snail populations dispersing in to new lakes are followed by their trematode counterparts in a "stepping-stone" fashion (Dybdahl & Lively 1996).

Parasites follow their snail hosts from lake to lake, and coevolution occurs across a habitat-gradient of interaction strength. These conclusions from recent studies seem to suggest that there could be a link between coevolution and the expansion of *P. antipodarum*'s range limits. This is where a gap in our knowledge exists, we are uncertain of the role coevolution plays at a larger distributional scale.

3.1.4 Hypotheses

In this chapter I will be building from previous work of how coevolution occurs in *P. antipodarum,* moving to a larger scale to understand how local host-parasite adaptation can affect the species' distribution and range limits. For this biotic interaction to have an influence on the range limits of *P. antipodarum* then it must occur in the range limits of the distribution (i.e., marginally suitable habitat). If biotic interaction does not occur in the range limits then there is no potential for it to influence the range limit. If it does occur, then the strength of the coevolutionary relationship needs to be determined to investigate further if coevolution can influence the range limits of *P. antipodarum*. Therefore, my hypotheses are:

(i)   Coevolution occurs in the range margins of *P. antipodarum*.

(ii)   The abiotic environment mediates the strength of coevolution.

3.2 Methods

3.2.1. Field work

Approximately 100 individuals were collected from forty seven sites located in the predicted range within the Canterbury and Westland region where the predicted probability of occurrence for *P. antipodarum* was lower than 0.5. The predicted range margin was obtained from an existing distribution model of *P. antipodarum* published in 2009 by Leathwick et al., details regarding this distribution model can be found in Chapter 2 of this thesis. I focused sampling in previously un-sampled regions that are marginally suitable to *P. antipodarum*. Sampling with the outer range limits of *P. antipodarum*'s distribution where probability of occurrence was lower than 0.1 was not possible. The Southern Alps and land immediately adjacent are high in elevation and streams/rivers running throughout this area are too steep to sample and did not fit the habitat requirements for *P. antipodarum*. Further into the range margin, the land becomes flatter and more easily accessible for sampling. Sites chosen for sampling were visited on separate occasions, with specific stream/river choice occurring on the day and taking into account the accessibility of the streams themselves. During the field work season, a storm hit the west coast of New Zealand, causing rivers and streams in the area to flood. Collection of *P. antipodarum* in the region where this storm hit occurred after the storm had passed and the water levels of the various streams and rivers had returned to normal.

My sampling protocol was based on protocols from previous studies (King et al. 2011) and designed to assess both presence and absence of snails and if they were present, to collect enough snails for dissection. Upon arrival at a chosen stream, I identified a 10 m stretch of stream for sampling. Using kick-nets, I sampled all available microhabitats within the 10 m sampling area to ensure mudsnails were collected evenly and results were not skewed by an underlying microhabitat preference of the mudsnails. Kick-net samples collected were emptied into white trays for sorting.

Using forceps, I collected 100 mudsnails per stream/river and transported them to ice cream containers for transport to the lab. In some cases, where time and mudsnail abundance were constraining factors, less than 10 snails were collected. If *P. antipodarum* was not present in more than ten kick-net samples across the various microhabitats, that 10 m zone was recorded as being absent of *P. antipodarum*. GPS coordinates and elevation data were taken at each of the sampled locations using a Garmon GPS device.

Mudsnails collected during sampling were stored in folded, wet paper towels inside the ice-cream containers to ensure that the mudsnails were kept wet and still during transport. Ice cream containers were then placed inside a cooled chilli bin to keep the mudsnails at a temperature similar to the streams they were found in. Upon returning to the University campus, we transported the mudsnails from paper towels to containers filled with water obtained from the streams from where they were collected for later dissection.

To assess the sex and parasite load of the samples I used a protocol developed by Curt Lively, shown to me during Curt's visit to the Edward Perceval Field Station in Kaikoura, New Zealand. To identify the sex of each mudsnail, the shell of the snail was cracked using forceps and if a penis was present that mudsnail was recorded as being male. Once the sex had been recorded, the shell was further cracked to examine the internal organs of the mudsnail and identify possible parasites and also if a brood was present. If a parasite was found, its genus, and species if possible, was determined using a guide on the different *Potamopyrgus antipdarum* parasites and the methods for correct identification (Hechinger 2012).

3.2.2. Data analysis

The data set I used in my analysis was also used in the previous chapter, comprising data from two other datasets, one published by King et al. 2011 which contains information on parasite load and sex ratio alongside GPS coordinates for the sampled locations, and the other from a summer student working out of the University of Canterbury (Gamlen-Greene unpublished).

If coevolution occurs in the range limits of *P. antipodarum*'s distribution, parasitised snails and male snails would be present in locations where the predicted probability of *P. antipodarum* occurring was low, as they are both indicators of coevolution. To test the hypothesis that coevolution occurs in marginally suitable habitat I ran two binomial GLMs. The first GLM I ran using data on the parasite load of the snails to test whether there is a relationship between the parasite load and the predicted probability that *P. antipodarum* occurs at a given location. The second GLM I ran was similar to the first, instead using data on the sex ratio of the snails. Binomial GLMs were used for this analysis because the data being used has response variables with two possible outcomes (parasitised/unparasitised, male/female).

To determine if the abiotic environment can mediate coevolution there needs to be an abiotic factor that has a significant relationship with either parasite load or sex ratio. To test the hypotheses that the abiotic environment mediates coevolution I ran another two binomial GLMs. In the previous chapter, I concluded that flow stability would be included in a model to predicted probability of *P. antipodarum* occurrence and therefore it is the only abiotic factor to be included in the analysis. The first GLM used data on parasite load of the snails to test for a significant relationship between parasite load and flow stability. The second GLM was the same but using sex ratios instead of parasite loads. All analyses and production of figures were carried out in the statistical program R (version 3.0.3).

3.3 Results

Results of the binomial GLMs run to test the first hypothesis yielded non-significant results. There was no significant relationship between parasite load and the predicted probability of *P. antipodarum* occurrence (P=0.437, df=47). Nor was there a significant relationship between sex ratio and the predicted probability of *P. antipodarum* occurrence (P=0.347, df=64). Parasitised snails occurred across the whole distribution of *P. antipodarum* (Figure 3.1), with the highest amount occurring at the probability 0.84, where there would be an 84% chance of *P. antipodarum* occurring.

Even at probability 0.11, where there would be an 11% chance of *P. antipodarum* occurring, parasitised snails were found. There was no significant trend occurring in the presence of parasitised snails over the distribution, but parasitised snails occur in central populations as well as populations residing in the range limits of the distribution. Male snails occurred across the whole distribution of *P. antipodarum* (Figure 3.2), with the highest amount being found at probability 0.77. Much like parasitised snails, male snails occurred in both central populations and in the range limits of the distribution.

Results of the binomial GLMs to test the hypothesis that the abiotic environment can mediate the strength of coevolution had mixed results. The first GLM found a significant result for a relationship between parasite load and flow stability (P=0.02 df=47). Flow stability had a significant effect on where parasitised snails were found. The second GLM found a non-significant negative result for a relationship between sex ratio and flow stability (P=0.764, df=64).
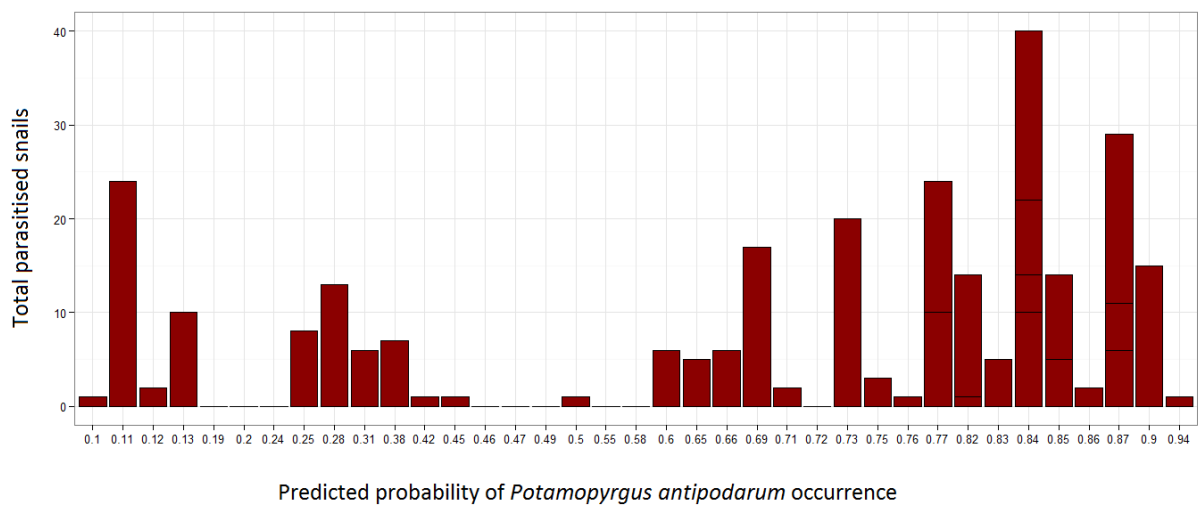
Figure 3.1. The total number of parasitised snails found in field collections across the predicted distribution of *P. antipodarum* in the South Island of New Zealand.
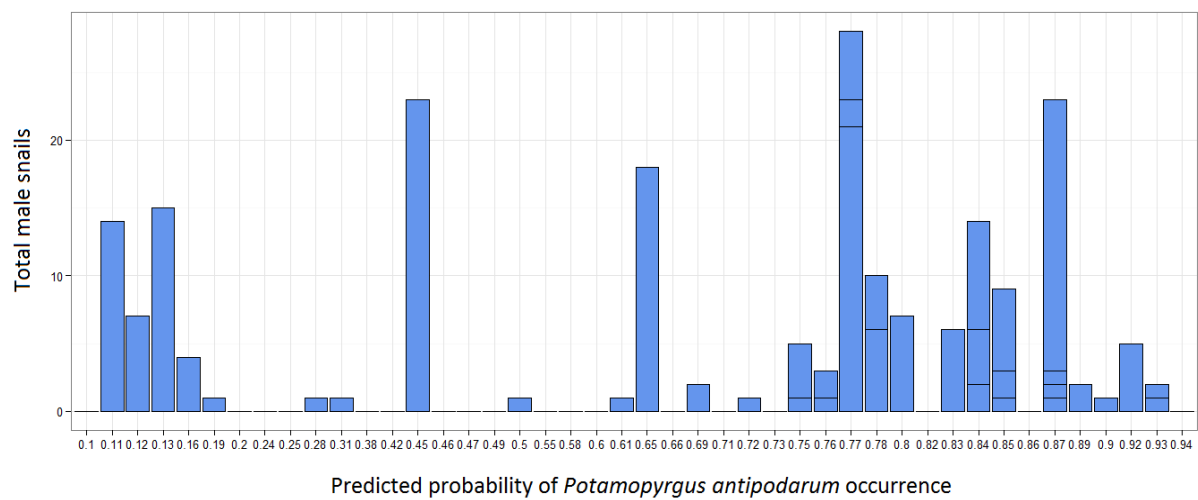
Figure 3.2. The total number of male snails found in field collections across the predicted distribution of *P. antipodarum* in the South Island of New Zealand.
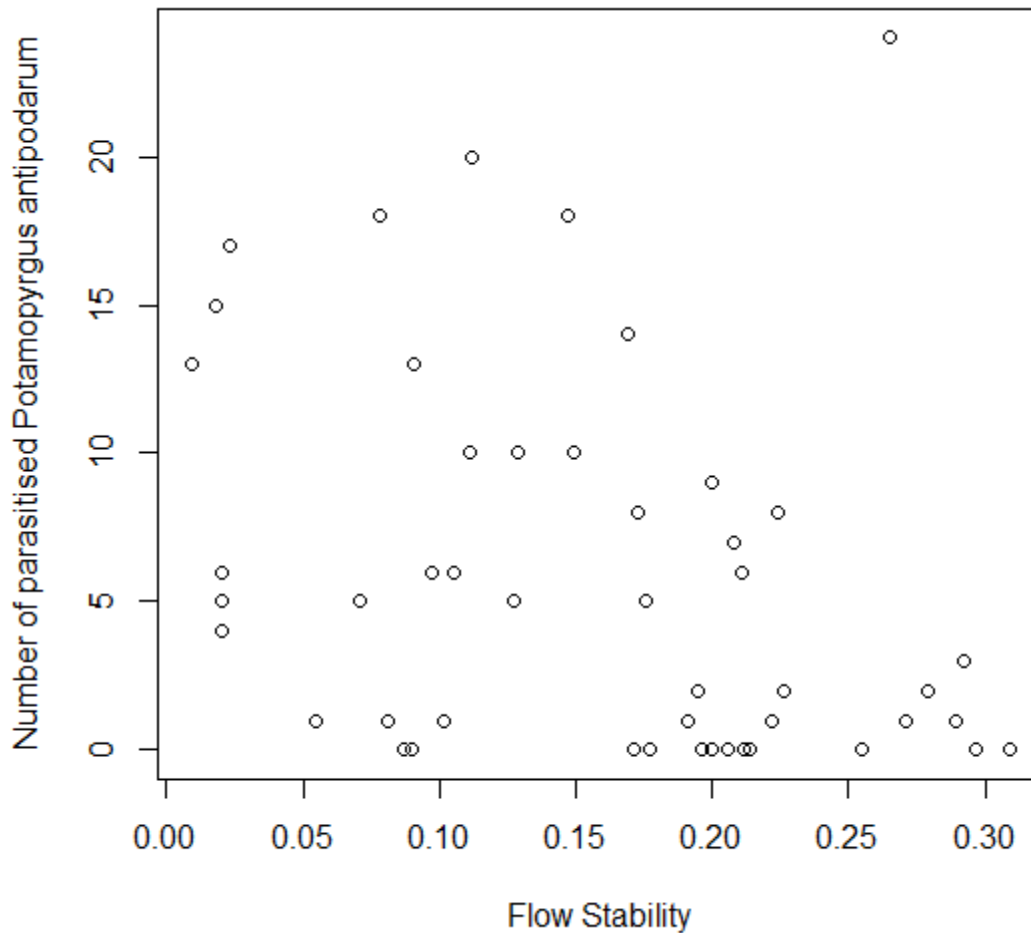
Figure 3.3. The number of parasitised *Potamopyrgus antipodarum* individuals collected in the field plotted against flow stability, data obtained from Leathwick et al. (2009)'s dataset.

3.4 Discussion

The first hypothesis of this chapter is that coevolution occurs in the range margins of *P. antipodarum*. For coevolution to occur in the range margins, parasites must be present, and the non-significant GLM results show that parasites are present across the whole distribution of *P. antipodarum*. From Figure 3.1 we can see that even in sites with a very low predicted probability of *P. antipodarum* occurring parasites are found. Figure 3.2 shows us that at these low probability sites, males are present in the population as well. Because the coevolutionary response of *P. antipodarum*

to increasing rates of parasitism is to favour sexual reproduction (Lively 1989), males are being produced. Essentially, coevolution is taking place in these sites of where the probability of occurrence is low , confirming my initial hypothesis.

The next step is to understand how coevolution occurring in the range margins can affect the expansion or contraction of *P. antipodarum*'s distribution. Coevolution between *P. antipodarum* and its trematode parasites can cause behavioural changes in the snails that could have the potential to contract the range margins through predator-induced mortality. A study conducted in 2000 was able to show that *Microphallus* parasites that infect *P. antipodarum* individuals were able to alter the mudsnail behaviour to increase the likelihood that the parasite would be transmitted to their waterfowl final hosts (Levri & Lively 1996). Uninfected brooding female snails hide under rocks and refugia during the early morning when their waterfowl predator is present, and forage during the late morning and afternoon to avoid predation. Infected snails with encysted parasites flip this behaviour with parasitism causing a behavioural change in the snail, causing them to forage during the early-morning to increase the chance of predation by waterfowl, the parasite's final host. Infected snails with parasites not yet encysted mirror the foraging behaviour of uninfected brooding females in an effort to decrease predation so the parasite has a chance to grow before being transmitted (Levri & Lively 1996). This behavioural change in *P. antipodarum* caused by parasitism may contract the range margins as populations in the range margins that are parasitised are more likely to be predated, lowering the overall density and the potential for range expansion.

Alternatively, the opposite could occur and behavioural changes caused by parasitism could in fact expand the range margins of *P. antipodarum*'s distribution. A 1998 study found that fish predate on *P. antipodarum* during the late hours of the morning and early afternoon, while the infected snails are hiding under refugia. They author also examined the gut contents of fish who predate on *P. antipodarum* and found that snails eaten by these fish are less likely to be infected (Levri 1998). This indicates that high levels of parasitism may prevent fish predation, giving the

population the potential for "predator-release". This phenomenon was shown to occur in an understory shrub *Macropiper excelsum*, where the release from its primary herbivore supported enhanced growth and survival, facilitating the establishment of *M. excelsum* outside of its natural range (Lakeman-Fraser & Ewers 2013).

These studies indicate that infection by parasites can cause an increase in waterfowl predation and also a decrease by fish predation. The behavioural changes in foraging caused by parasitism may decrease the likelihood of *P. antipodarum* populations dispersing into areas with high waterfowl populations, but may increase the ability to disperse into areas with higher fish populations. Although, whether or not a population experiences higher predation rates or predator-release is dependent on the levels of water-fowl and fish populations.

Another way that distributions of *P. antipodarum* may experience range limit shifts is through the reproductive disadvantage of sexual reproduction over asexual reproduction. Populations under heavy parasitism shift from asexual reproduction to sexual reproduction, producing males to increase genetic differences in offspring to reduce the likely hood of infection (Lively 1989). When a population is entirely asexual it experiences a two-fold increase in reproduction that comes from not requiring two individuals to produce an offspring (Smth & Maynard-Smith 1978). A study from 1998 that compared survivorship of sexual and asexual snails when starved and fed found that sexual and asexual individuals survived at the same rate, despite predictions that asexual snails would die faster due to a higher mutation load (i.e. asexual snails are loaded with deleterious mutations that arise from clonal reproduction). These results indicate that populations of asexual, clonal snails have nothing more than a two-fold reproductive advantage. Because of this, populations under heavy parasitism who are reproducing sexually may not have a high enough population growth rate to reach carrying capacity, and are unable to expand the range margins of the distribution, while asexual populations can expand the distribution through increased

reproduction, linking asexual reproduction with the invasive success of *P. antipodarum* (Alonso & Castro-Diez 2008). In this way, parasitism prevents the expansion of *P. antipodarum*'s distribution.

Alongside behavioural changes caused by parasitism and the increased reproductive effort of asexual snails, a range margin shift can occur from poor host condition caused by heavy parasitism. A review published in 2015 on the role of biotic interaction strength compared to abiotic stress in determining range limit shifts stated that in areas of high abiotic stress, parasite loads will have larger effects on host performance because of the decreased ability of the host to recover from infection (Louthan et al 2015). This would result in *P. antipodarum* populations in the range margins having poor conditions and potentially a higher mortality rate. For example, Jokela et al. (1999) showed through an experiment where natural mortality was measured between parasitised and unparasitised snails when subjected to two food treatments; with food and without food, snails that were parasitised had a higher mortality rate than snails that were unparasitised. Extrapolating this out to the population level, populations in the range margins that are under heavy parasitism, and are in habitats that endure high abiotic stress, are less likely to survive and may go extinct, creating the potential for a contraction of *P. antipodarum*'s range margin.

This idea links in to the second hypothesis of this chapter, that abiotic stress can mediate the strength of coevolution. If abiotic stress is high in the range margins of *P. antipodarum* it is possible that the effect of coevolution on the shifting of the range margins is negated. In the review on biotic interactions compared to abiotic stress in determining rage limit shifts, the authors propose a hypothesis called the "Species Interactions-Abiotic Stress Hypothesis" which states that the effects of species interactions are stronger in more benign habitats, and in habitats with high abiotic stress, biotic interactions are not important in determining range limit shifts (Louthan et al. 2015). Relating this concept to the results of the binomial GLM on the relationship between parasite load and flow stability, this hypothesis suggests that in habitats that are frequently disturbed by high flows (low flow stability), the effect of coevolution on influencing the range margins of the distribution should

not be an important factor. Results from the GLM run on parasite load and flow stability contradict this hypothesis, with parasitised snails being more likely to be found in habitats with low flow stability (frequently disturbed, high flow habitats) (figure 3.3). This confirms my second hypothesis that the abiotic environment can mediate the strength of coevolution as higher parasite loads are an indicator of strong coevolution.

This chapter has shown that coevolution between *P. antipodarum* and its trematode parasites occurs in the range margins of *P. antipodarum*'s distribution, confirming my first hypothesis, and that because of this there are multiple ways that *P. antipodarum*'s distribution can undergo both expansion and contraction of its range margins. This chapter has also shown that the abiotic environment can mediate the strength of coevolution, confirming my second hypothesis. Low levels of flow stability appear to have higher parasite loads. These findings are evidence that if species distribution models are too accurately predict the distribution of *P. antipodarum* and forecast new potential habitats for invasion, then coevolution must be included in these models.

At this point in time, there are no studies that explore the role of flooding disturbance and low flow stability on the facilitation of host-parasite coevolution. This is an area that requires more research if species distribution models are too accurately predict potential habitats for *P. antipodarum* to disperse to. Few studies seem to step away from the physiological and life-history effects of parasitism on *P. antipodarum*, focussing too heavily on the individual level of the interaction despite the obvious implications for the whole distribution. For example, studies seem to focus more on the physiological implications of parasitism, such as juvenile susceptibility to infection and the effect of parasitism on growth rates (Krist & Lively 1998), but pay no attention to how these may influence the dispersal ability of the species despite *P. antipodarum* being a highly successful invader. A large gap exists in transferring knowledge of small-scale effects to the larger scale. This is the gap my thesis is trying to fill, by showing that coevolution between host and parasite occurs in the range margin of the *P. antipodarum* distribution and, in the next chapter, by adding this

coevolutionary relationship into a distribution model where we should be able to see any changes in the predicted distribution of *P. antipodarum* and begin to understand how these individual level parasitism effects can influence the species at a distributional scale. This creates a gap for new exciting research contributions, and provides the oppourtunity to apply the findings of research into this area to improving distribution models for species other than *P. antipodarum*.

Chapter 4

Simulations of *Potamopyrgus antipodarum* Population Growth

4.1 Introduction

Models that predict the growth of a species' population are commonplace in biology. They are used to predict how a population will respond to repairing fragmented habitat (Hudgens & Haddad 2003), how threatened species will respond to varying management alternatives (Crouse et al. 1987), the survivability and the speed of growth of an invasive species (Kot et al. 1996), and how different abiotic factors control species' growth dynamics (Higgins et al. 2006). Using models to predict species growth allows for the ability to simulate different conditions and observe population growth over timescales that would be too difficult to assess in real-time. They also provide us with the unique opportunity to answer questions about population growth by simply changing a variable in the model.

Previous chapters of this thesis have focused on identifying variables that should be included in a model that predicts the growth of *Potamopyrgus antipodaum*. In chapter two I identified flow stability as an important abiotic factor for predicting *P. antipodarum's* distribution and described how snails are more frequently found in habitats that are more disturbed and have high variability in their flow. I also described how flow stability can facilitate the dispersal of *P. antipodarum* populations through highly variable flows and frequent floods. In chapter three I was able to show that coevolution occurs in marginal habitats, and that parasitism in the range margins of *P.*

antipodarum's distribution can result in the contraction or expansion of those range margins. I was also able to show that the strength of coevolution can be mediated by the abiotic environment. Combining the results of this chapter involves the inclusion of flooding events and coevolution into a model that predicts the survivability and growth of *P. antipodarum* populations. The purpose of this chapter is to take these results and create models that will predict the growth of *P. antipodarum* under different abiotic and biotic conditions.

The first model is a simple exponential growth model, where the number of *P. antipodarum* individuals (N) changes over time based solely on the intrinsic growth rate. Exponential growth models are used to predict the change in the density of a species when populations are not limited by anything (Tsoularis 2001). The second model will take a step further and include density dependence, where a population is limited by its own density. This type of model is known as a logistic growth model, first described by Pierre-Francois Verhulst in 1838 (Verhulst 1838), and is an extension of the exponential growth model that includes interspecific competition (where a species competes with itself for resources and space).

The next model will focus on how flow stability influences the growth of a population. In the model, flow stability has been measured by the frequency of flooding events, where a flood is defined as flows three times larger than the median flow (Clausen and Biggs 1997, Holomuzki and Biggs 1999). This measure of flow stability has been found to be the most ecologically useful overall flow variable (Causen and Biggs 1997). Using this model I will be able to show how *P. antipodarum* populations respond to frequently disturbed, harsh environments.

The final models will analyse how the host-parasite biotic interaction can influence growth, through differing sex ratios and the reduced fecundity that comes from *P. antipodarum* individuals being castrated by parasites that infect them (Koskella & Lively 2007, Lively 1989). As asexual populations have the advantage of a two-fold reproductive success (Lively 1996, Lively 2010) and sexual populations who experience parasitism have reduced fecundity, the model will show how

asexual and sexual populations differ in their growth rates and survivability in the face of harsh environments.

All models were run in the statistical program R (version 3.0.3) using the deSolve package. The models have been set-up in a way that shows the step-by-step procedure for arriving at the final model.

Hypotheses:

(i)   The inclusion of flow stability into a model predicting *P. antipodarum* growth will result in the population experiencing lower density and decreased growth rates.

(ii)   The inclusion of host-parasite coevolution into a model predicting *P. antipodarum* growth will result in sexual populations experiencing lower density and decreased growth rates than asexual populations.

(iii)   Including parasite-induced castration into the same model will result in lower density and decreased growth rates of sexual populations.

I predict that the results of this model will show populations of *P. antipodarum* decreasing in size and experiencing lower growth rates as the frequency of flooding events increases. I also predict that there will be a limit whereby after a certain number of floods and disturbance, the population begins to decline towards extinction. I also predict that the results of the model where host-parasite coevolution is included will show that host parasite coevolution hinders a population's growth and survival in harsh environments and that the further inclusion of parasite-induced castration will lower the density and growth rates of sexual populations even more.

4.2 The Models

4.2.1 Potamopyrgus antipodarum growth ignoring density

$$\frac{dN}{dt} = rN \tag{1}$$

The first form of the model explains only the exponential growth of a *P. antipodarum* population. Simulations run using this model will show how a snail population grows when resource availability is unlimited and the population is without environmental mortality, density dependence, parasitism or local evolution. The first parameter, *rN* looks at how the number of snails in the population (N) changes based on the population's intrinsic growth rate (*r*). Simulations using this model will provide a baseline of unhindered population growth against to statistically compare simulations that contain new parameters.. The intrinsic growth rate of Potamopyrgus (*r)* can be defined as (*b-d*), whereby *b* is the birth rate per individual and *d* is the death rate per individual (Birch 1948).

Studies have shown birth rates per individual for *Potamopyrgus antipodarum* range from as high as 0.63 juveniles per female per day to as low as 0.1 juveniles per female per day (Jacobsen & Forbes 1997, Hall et al. 2006). Jensen et al. (2001) showed through an experiment on the effects of Cadmium uptake on the life history traits of *P. antipodarum* that *P. antipodarum* females produce 0.5 individuals per day. One of the life history traits used in the experiment was reproductive output, or the number of juveniles produced per female over the course of the experiment. The experiment had four levels of cadmium exposure with one control where no cadmium was added. Fifteen snails were placed in each treatment and the number of juveniles produced per female was measured by counting the number of juveniles each week for eight weeks. Results show that for the treatment where no cadmium was added, there was an average of 28 juveniles per female. Over the eight week experiment (fifty six days), this equated to 0.5 individuals born per female per day or *b* = 0.5.

Estimates of natural death rates are harder to come by. One study gave an estimate for *d* (Jokela et. al. 1999) through an experiment on the effects of starvation on parasite-induced

mortality of *P. antipodarum*. The experiment consisted of two treatments, "with food", where the snails were fed *ad lib* and "no food", where no food was added. One hundred snails were used per treatment with each treatment being replicated 15 times. The authors ran the experiment for 90 days and found that in treatments with food and no parasites, 40% of snails died over the 90 day period. This means that snails died at a rate of 0.44 individuals per day. After converting this estimate for death rate to the same units the birth rate from Jensen et. al. 2001, I arrived at a death rate of 0.0044 individuals per individual per day.

Using these values for births and deaths gives an estimate for *r* of 0.4956 individuals/individual/day. Substituting this value into the model and simulating exponential population growth results in a population of 100 *P. antipodarum* snails that increases dramatically in size over the course of just five days (Figure 1). Without the pressure of intraspecific competition through density dependence, environmental mortality, or biotic factors, the population of *P. antipodarum* will grow infinitely large.
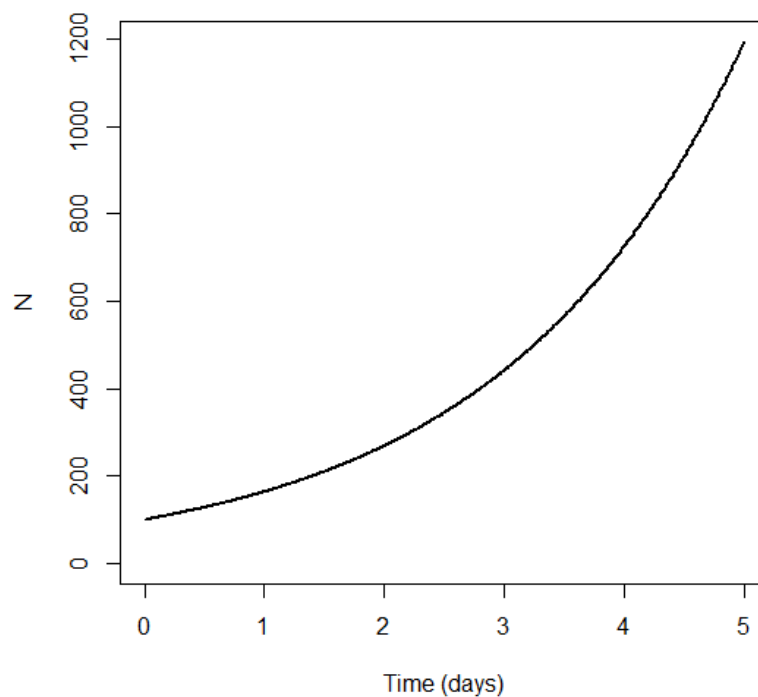
Figure 4.1. Simulation of a *Potamopyrgus antipodarum* population experiencing exponential growth, where N = 100 and *r* = 0.4956.

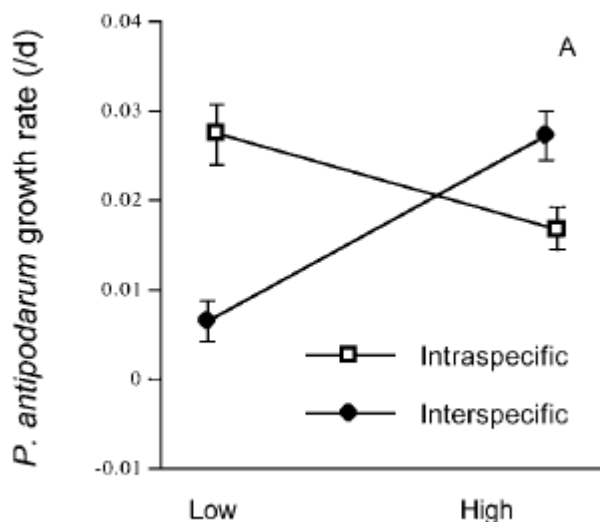*4.2.2 Potamopyrgus antipodarum growth with density dependence*

The second iteration of the model includes a parameter for density dependence as well as the original intrinsic growth rate, changing the model from one of exponential growth to a model of logistic growth. Density dependence is a form of feedback which reduces the rate of population growth (Hassel 1975). Through density dependence, a population limits itself at a certain point known as the "carrying capacity". An environment's carrying capacity is defined as its maximum persistently supportable load (Catton 1986), or in an ecological sense, the maximum number of individuals a habitat can support. With this in mind, adding a density dependence parameter into the model allows a more accurate prediction of *P. antipodarum* population growth in the range margins of the distribution. In the logisitic growth model, density dependence is denoted as α (alpha).

$$\frac{dN}{dt} = rN - \alpha N^2$$

<div align="right">(2.1)</div>

The method I used for obtaining a density dependence parameter consisted of using estimates of population growth data from Riley et al. (2008), inputting them into the logistic growth model and solving for α. After obtaining an estimate for α, simulating population growth became problematic when trying to convert units of α to work with the estimate of *r* that was used in the exponential growth model (0.4956 individuals/individual/day), and so from this point onwards it was decided that the value for *r* would be estimated using the same methods of obtaining the estimate for α to keep the units consistent throughout the models.

Riley et al. (2008) detailed how growth rates of *P. antipodarum* change under the stress of intraspecific competition. Snails were collected from Marmot Spring in Yellow Stone Park, USA, and were subjected to both inter- and intra-specific competition at low snail density (0.66 g/m^2 ash free dry mass (AFDM)) and high snail density (4.98g/m^2 AFDM). The study found that in high density

populations, *P. antipodarum* biomass increased at a slower rate (0.017 g/day) than in low density

populations (0.028 g/day), indicating that intraspecific competition can limit population growth.

Figure 4.2. Mean *Potamopyrgus antipodarum* growth rates when exposed to intra and interspecific

competition in Marmot Spring (Riley et al. 2008).

Substituting growth rate values from Riley et al. (2008) into the logistic growth model

required the model to be rearranged because of the squared term attributed to α. Without

rearrangement, when the model is plotted the result is parabolic. Therefore, I arranged the equation

according to Bodine et al. (2014) to remove the squared term and to give a straight line when

plotted, making it easier to obtain estimates of α and *r*. After transformation the equation becomes:

$$\frac{1}{N}\frac{dN}{dt} = r - \alpha N$$

(2.2)

The same model can be seen in Mallet et al. (2012) and is described as the *r-a* model, a

simpler, polynomial form of the logistic equation. Because the data presented in Riley et al. (2008)

fits the logistic growth model, it needs to be converted to fit the new, rearranged model. We can

convert the data by dividing the growth rates (0.028 g/m^2 & 0.017 g/m^2) by the population biomass

(0.66 g/m^2 & 4.98 g/m^2), converting the growth of biomass per day to the biomass increase per unit

(1 g/m^2), a per capita growth rate. Low density biomass (0.66 g/m^2) results in a growth per 1g/m^2 of

0.04g, and at high density biomass (4.98 g/m^2) we see a growth per 1g/m^2 of 0.0035g. Substituting

these values into the equation above, we can solve for per capita growth rate (r) and density

dependence (α).

r = 0.046 g/(g*day)

α = 0.0085 g/(g*day)

To keep the units of the estimates consistent with other parameters being added into the

model they were converted into years rather than days. This was done by multiplying both values by

the number of days in a year.

r = 16.79 g/(g*year)

α = 3.1025 g/(g*year)

The next issue is converting from grams to individuals. Converting α into individuals requires

it to be multiplied by the biomass of an individual snail. Richards (2004) developed an equation for

finding out the biomass per snail of a population based on shell length. Average shell length of 3.04

mm was obtained from Riley et al. (2008). After conversion to individuals instead of biomass, α =

0.0093 individuals/(individuals*year).

Running the simulation with the estimates of *r* and α from Riley et al. (2008) results in a plot

that shows a population of 100 snails increase in size until reaching the carrying capacity. From this

simulation it can be seen that density dependence drastically limits the growth of the *P.*

antipodarum population. The population grows at an increasing rate similar to the simulation of

exponential growth (Figure 4.1), but at the half-year mark the population experiences a decelerated

growth rate (Figure 4.3). Using this model over the exponential growth model allows for a more

accurate prediction of *P. antipodarum* population growth, where the population is limited by its own density (through intraspecific competition), but is not limited by environmental mortality or biotic interactions.
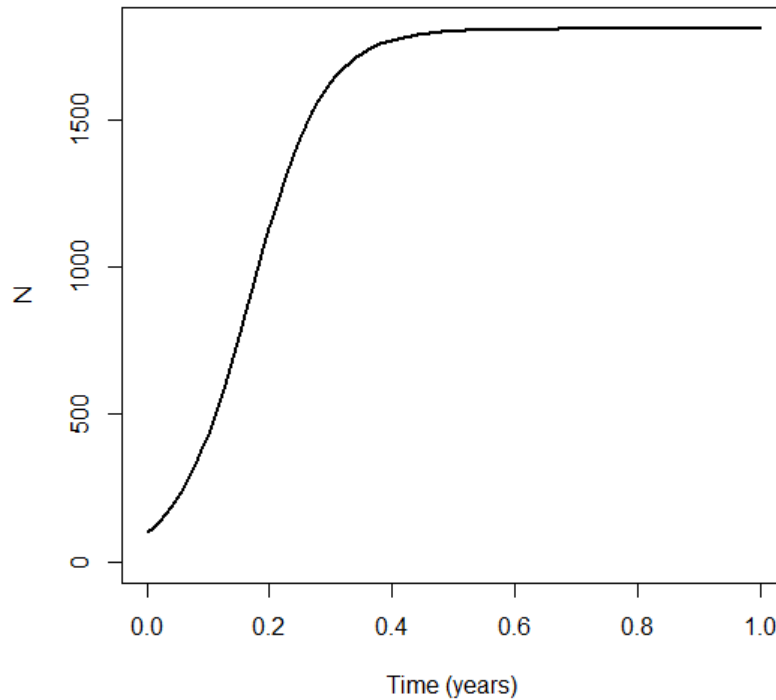
Figure 4.3. Simulation of a *Potamopyrgus antipodarum* population experiencing logistic growth, where N = 100.

4.2.3 The effect of harsh environments

The next step in creating an accurate model for predicting *P. antipodarum* population growth is to include a parameter estimate for mortality that arises from inhabiting a harsh environment. Creating a model that incorporates environmental mortality involved altering the logistic growth model to include the chance of surviving a flooding event as well as the frequency of flooding events. In the new environmental mortality model, the chance of surviving a flooding event is denoted as *dFlood* and flood frequency is denoted as *f*. Holomuzki & Biggs (2000) gave an estimate for *dFlood* by showing that the average percent mortality after a flood for Potamopyrgus is around 5%. In other words, 95% of a population survives during a major flooding event, and therefore

dFlood = 0.95. Flood frequency was found to be the most ecologically useful flow variable in New Zealand streams and averaged about 10 floods a year (Clausen & Biggs 1997). The value of *f* will change based on how harsh the environment is. Habitats that are more frequently disturbed will have a higher *f* value than habitats that are more stable. Therefore, *dFlood^f = 0.95^f,* where *f* can vary between habitats, and *dFlood* is in units of survivability per year. With the addition of flooding events, the logistic growth model becomes:

$$\frac{dN}{dt} = b(dFlood^f)N - dN - \alpha N^2$$

(3)

In this model, the per capita growth rate needed to be split into a birth rate and death rate so that *dFlood* could be incorporated. *dFlood* is the probability of survival after a flooding event, and therefore *b(dFlood^f)* is the amount of reproducing snails that survived *f* amount of floods in one year. This also required the addition of a natural mortality rate (*d*). After converting the natural mortality rate (*d*) from the exponential growth model to units of years rather than days, *d* = 1.78 deaths/(individual*year).

From the results of running a simulation of the environmental mortality model it is easy to see how flooding events can affect the population growth rate of *P. antipodarum*. When flooding events are introduced, the growth rate slows and the population takes longer to reach carrying capacity. Flooding events also cause the carrying capacity to drop from above 1500 snails (Figure 4.3) to 1000 snails (Figure 4.4).
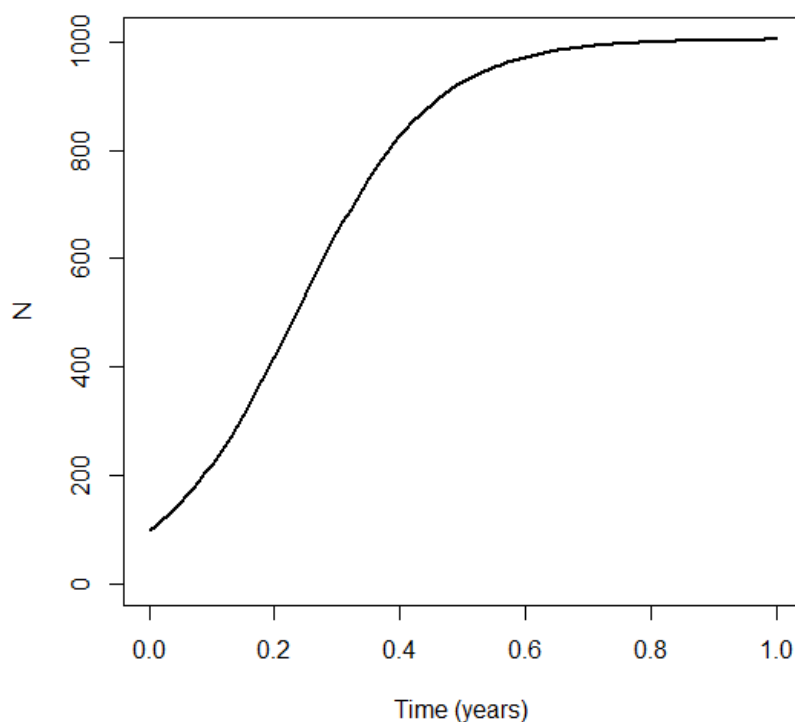
Figure 4.4. Simulation of a *Potamopyrgus antipodarum* population experiencing a disturbed environment, where N = 100, dFlood = 0.95, f = 10.

Increasing the value of *f* in the model from 10 floods per year to 35 floods per year changes *P. antipodarum*'s population growth rate dramatically (Figure 4.5). The rate of increases slows to the point where over the course of a year the population has increased by only a fraction. When the flood frequency is larger than 37 floods per year the *P. antipodarum* population begins to decline from day 1 (Figure 4.6) and will eventually go extinct. Flooding events affect *P. antipodarum* populations in a similar way to density dependence, by imposing limits on how many individuals can survive in the habitat. This has implications for species distribution models that incorporate environmental mortality, as high flooding frequency can result in populations situated in the range margin of the distribution going extinct, in turn preventing the expansion of the distribution. Although, the effect of flooding on *P. antipodarum* populations may not be realistic in New Zealand, as the average number of floods per year is 10 floods per year and the range is 0 to 35 floods per year (Clausen & Biggs 1997).
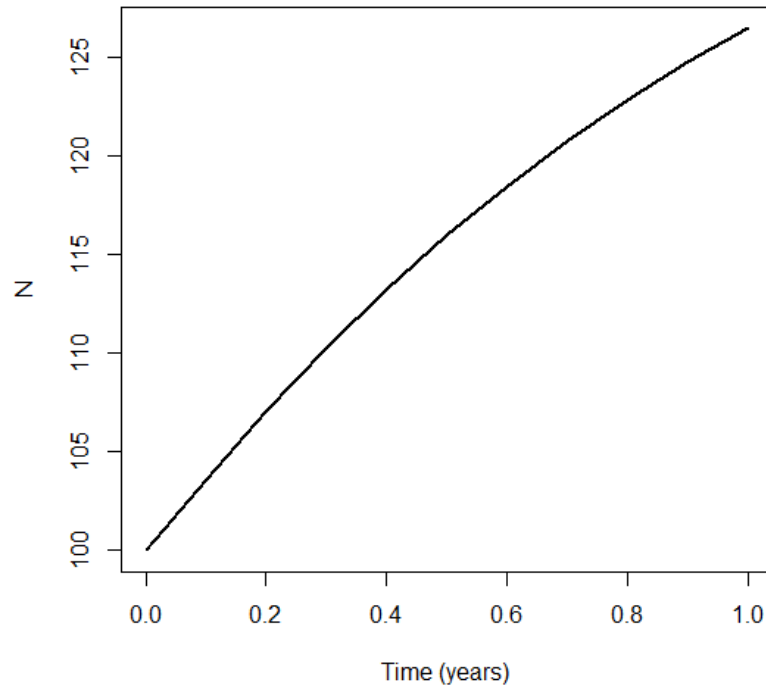
Figure 4.5. Simulation of a *Potamopyrgus antipodarum* population experiencing a disturbed environment, where N = 100, dFlood = 0.95, f = 35
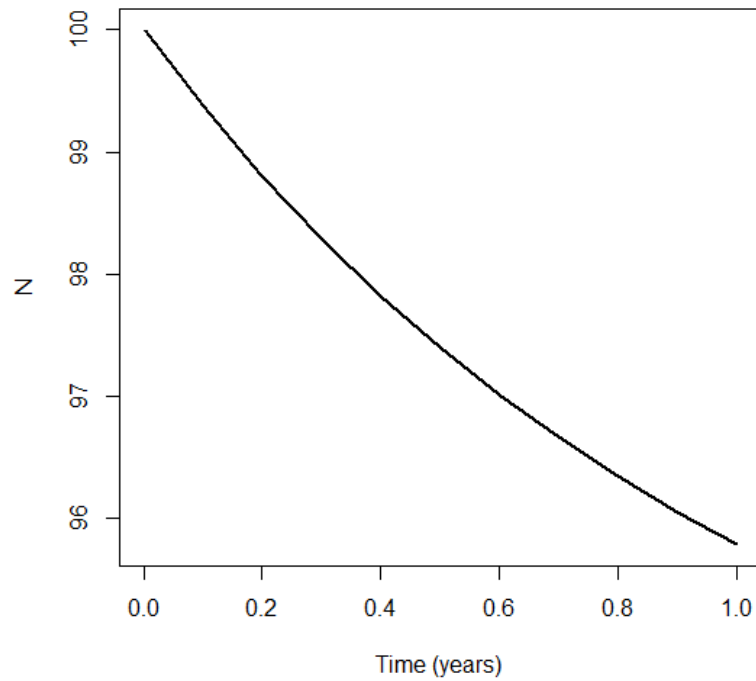

Figure 4.6. Simulation of a *Potamopyrgus antipodarum* population experiencing a disturbed environment, where N = 100, dFlood = 0.95, f = 38

4.2.4 Sexual versus asexual populations

When parasites are present in a population of *P. antipodarum*, the evolutionary response of Potamopyrgus snails causes the population to shift from asexual reproduction to sexual reproduction in an effort to reduce the risk of infection (Lively 1996, Lively 2010). Because of the cost of sexual reproduction, sexual populations suffer from a decrease in their reproductive rate (Lively 1996, Lively 2010). This can have significant implications for a population when both density dependence and environmental mortality are taken into consideration. To incorporate the effect of parasitism into predicting the population growth rate of *P. antipodarum*, a sex ratio parameter was added into the growth model. This is denoted as *S*:

$$\frac{dN}{dt} = b(dFlood^f)SN - dN - \alpha N^2$$

(4)

The parameter *S* controls how sexual a simulated population is and how parasitism affects the per capita growth rate of the simulated *P. antipodarum* population. When *S* is set to a value of 2, the population is entirely asexual and no parasites are present in the population. When *S* is set to a value of 1, the population is entirely sexual with a sex ratio of 0.5, c and experiences a 2-fold decrease in reproduction. Using the *S* parameter it is possible to simulate *P. antipodarum* populations that experience different levels of parasitism and therefore have different sex ratios.

Through running simulations of both sexual (Figure 4.7) and asexual (Figure 4.8) *P. antipodarum* populations, it can be seen that the asexual population has a significantly larger per capita growth rate and a larger carrying capacity that comes with the 2-fold increase in reproduction. This can be very important as it can have significant effects on the population when other parameter values are changed. For example, results from the growth model where flooding disturbance was introduced showed that when the frequency of floods was larger than 37 floods per

year the *P. antipodarum* population began to decline rather than increase (Figure 4.6). Running the

parasitism model again with flood frequency (*f*) at 38 floods per year and both asexual (*S* = 2) and

sexual (*S* = 1) populations present, it is clear that with no parasites present to force the population to

start reproducing sexually the two-fold increase in reproduction prevents the asexual population

from going extinct when flood frequency is high (Figure 4.9).
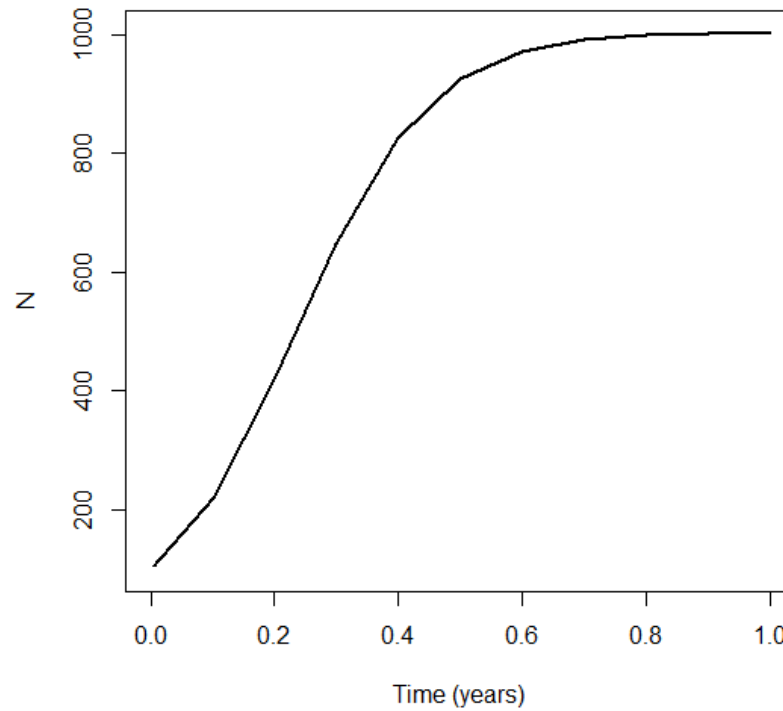
Figure 4.7. Simulation of a sexual *Potamopyrgus antipodarum* population, where N = 100, dFlood = 0.95, f = 10, *S* = 1.
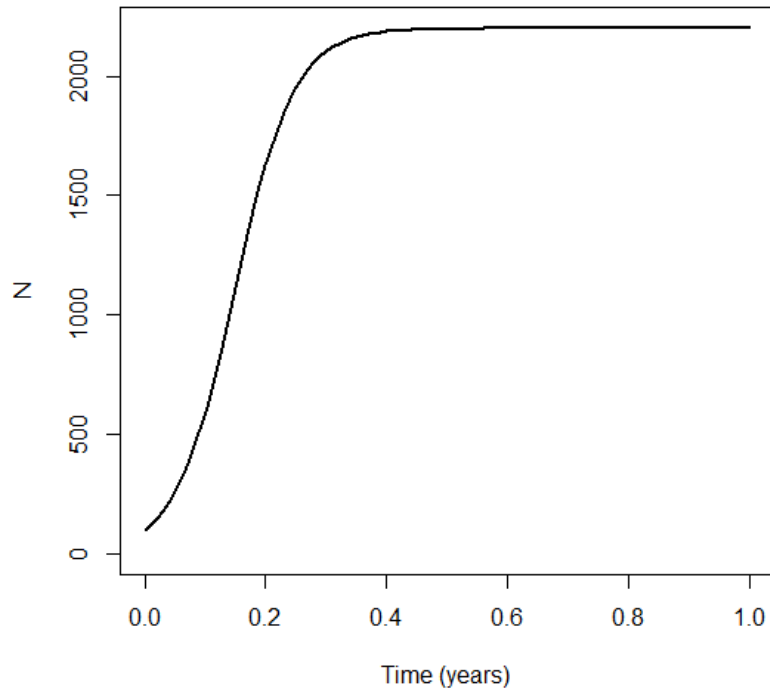
Figure 4.8. Simulation of an asexual *Potamopyrgus antipodarum* population experiencing a two-fold increase in reproduction, where N = 100, f = 10, *S* = 2
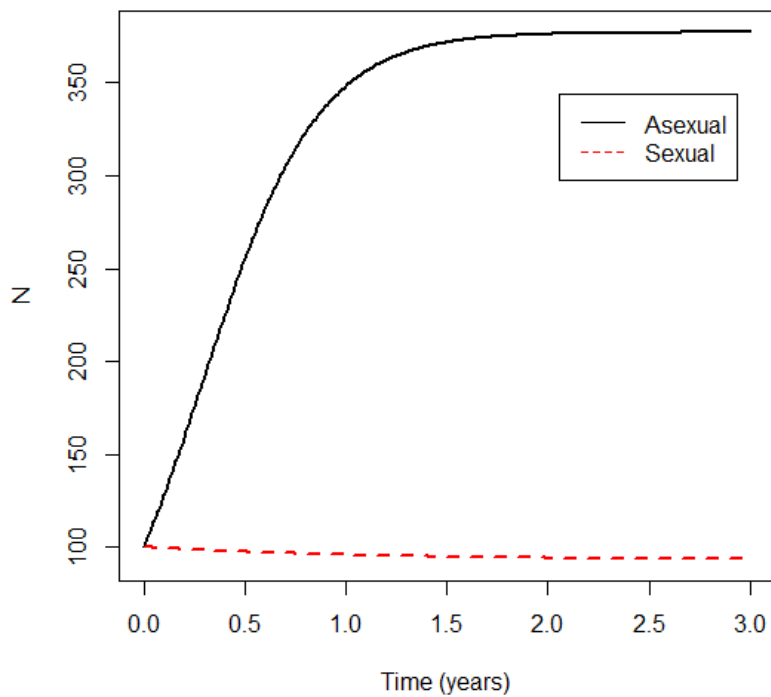
Figure 4.9. Simulation of a both asexual (*S* = 2) and sexual (*S* = 1) *Potamopyrgus antipodarum* populations experiencing a harsh environment, when N = 100 and *f* = 38.

These results show that a population who is experiencing parasitism and is entirely sexual (50% male, 50% female), in a harsh and frequently disturbed environment the population may go extinct. Whereas, a population that is not experiencing parasitism (100% female), can survive at high levels of flooding disturbance. When a population of *P. antipodarum* experiences lighter parasitism (25% males, $S = 1.5$) at high levels of flooding disturbance, the population survives but with a lower growth rate, density, and carrying capacity (Figure 4.10).

This has major implications for SDMs, as asexual populations in the range margin of the distribution can survive harsh habitats while sexual populations in the range margins who experience parasitism, even if it is weak parasitism, may go extinct and prevent the distribution from expanding past its range limits.
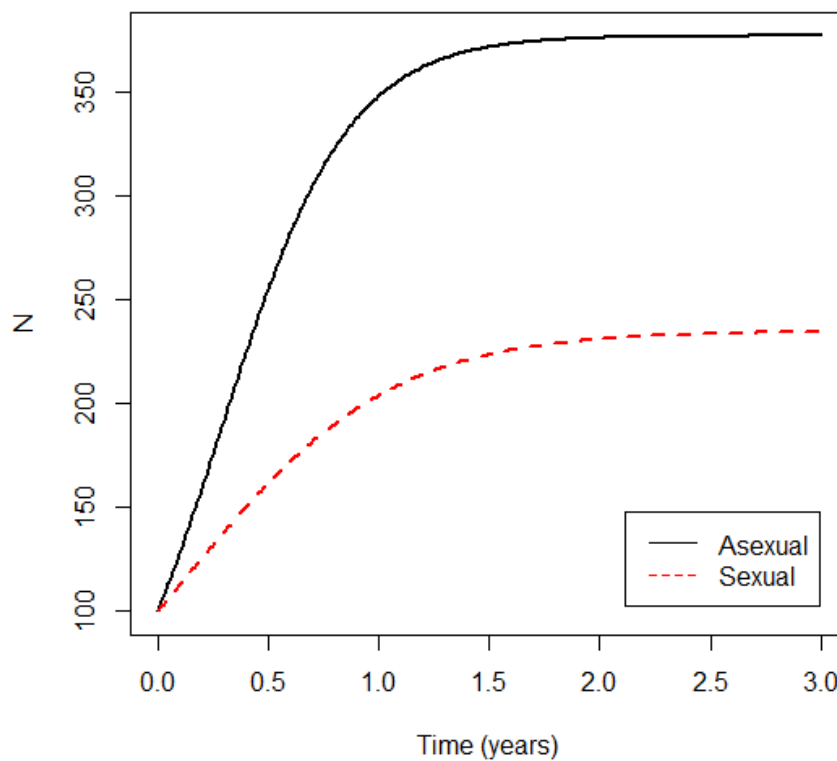
Figure 4.10. Simulation of a both asexual ($S = 2$) and sexual ($S = 1.5$) *Potamopyrgus antipodarum* populations experiencing a harsh environment, where N = 100 and $f = 38$.

4.2.5 Parasite-induced castration

Alongside the decreased reproductive output that results from sexual reproduction, the host-parasite relationship between *P. antipodarum* and its trematode parasites has other impacts on individuals who are parasitised. When a *P. antipodarum* individual becomes infected by a parasite, the parasite castrates the snail through the replacement of the host's gonads and digestive gland with encysted larvae, preventing it from producing any offspring (Koskella & Lively 2007, Lively 1989). If a population of 100 snails incudes 10 snails that are parasitised and have been castrated then it would cause a 10 percent reduction in the population's birth rate. Only 90 of the original 100 snails will be producing any offspring.

In sampled field populations of *P. antipodarum* located in the range margins of the distribution, the number of parasites present in a population varies from 1 parasite, to 24 parasites (Figure 3.1). A population that has 24 snails castrated and not able to reproduce will experience a 24 percent reduction in the number of offspring produced. Simulating this population (Figure 4.11) shows a sexual population will survive 10 floods per year with a carrying capacity of around 600 N when a large parasite load causes reduced fecundity through castration and with a reduced growth rate from being an sexual population (two-fold advantage of asexual populations). In an environment that is not as harsh (around ten floods per year) castration does result in a significantly lower population growth rate and carrying capacity, but the population still persists. The presence of parasites in this sexual population does not appear to hinder or facilitate the expansion of the distribution.
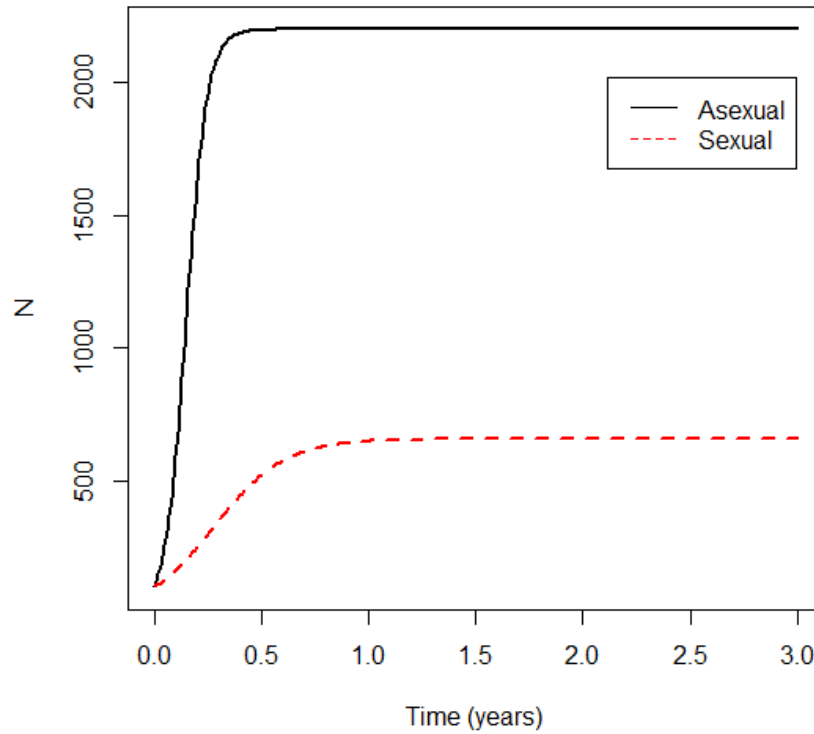
Figure 4.11. Simulation of a both asexual (*S* = 2) and sexual (*S* = 1) *Potamopyrgus antipodarum* populations, where N = 100, *f* = 10, and the sexual population has a 24 percent reduction in birth rate.

A sexual population that experiences parasitism begins to decline to extinction when the amount of floods per year exceeds thirty two (Figure 4.12). A population that does not experience reduced fecundity associated with castration begins to decline to extinction to the limit of thirty eight floods per year (Figure 4.9). The addition of castration into the model reduced the amount of floods a sexual population can survive by 5 floods per year.
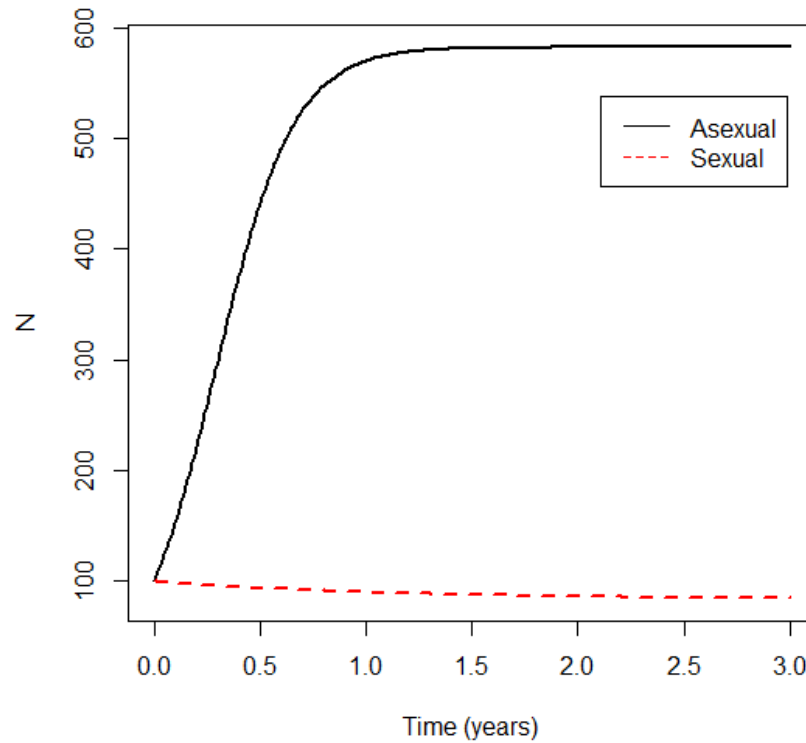
Figure 4.12. Simulation of a both asexual (S = 2) and sexual (S = 1) *Potamopyrgus antipodarum* populations experiencing a harsh environment, where N = 100, f = 33, and the sexual population has a 24 percent reduction in birth rate.

The highest parasite load that was found in the field collections of Chapter Three was 40 infected snails out of a sample of 100. This population, while not found in the range margin of the distribution, would experience a 40 percent reduction in fecundity. This large drop in fecundity results in the population going extinct when the number of floods per year exceeds twenty eight (Figure 4.13), only three floods per year behind a population that experiences a 29 percent reduction in fecundity.
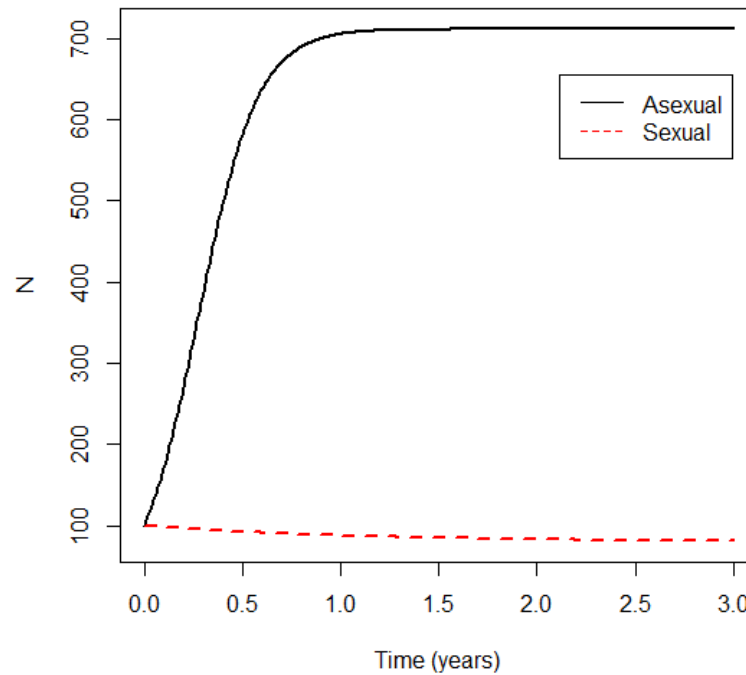
Figure 4.13. Simulation of a both asexual (*S* = 2) and sexual (*S* = 1) *Potamopyrgus antipodarum* populations experiencing a harsh environment, where N = 100, *f* = 29, and the sexual population has a 40 percent reduction in birth rate.

Results of simulations run on populations that experience reduced fecundity associated with castration of infected snails shows that populations will only begin to go extinct when parasite loads are high and populations are located in very harsh environments that are frequently disturbed by flooding events. Populations of *P. antipodarum* that live in streams and rivers have a lower parasite infection rate than populations that live in lakes. Infection frequencies in lake populations have been observed as high as 50 percent of snails infected (King et al. 2011b); while infection frequencies in streams have been found to be much lower (King et al. 2011). In this regard, marginal populations of stream/river dwelling snails will not experience an infection frequency high enough to cause any likelihood of population extinction.

4.3 Conclusions

The results from running the model simulations clearly show that both abiotic and biotic factors can influence the growth and survivability of *P. antipodarum* populations in the range margins. My first hypothesis was confirmed; running a model that simulates disturbance through flooding events resulted in a lower density and growth rate for the simulated population. In the range margins of a distribution, a population experiencing frequent floods will experience a slower growth rate, and at the limit of 38 floods per year, the population began to go extinct. My second hypothesis was also confirmed, simulated sexual populations experienced lower densities and growth rates that would be expected from the disadvantage of sexual reproduction. The parasite-induced castration model confirmed my third hypothesis, with simulated sexual populations experiencing lower density and growth than sexual populations, which were not hindered by parasite-induced castration.

The purpose of this chapter was to understand how abiotic and biotic factors can influence the distribution of *P. antipodarum*, be it through the expansion or contraction of the range limits. As high levels of parasitism result in sexual populations declining to extinction in harsh environments, populations that experience parasitism and occur in the range margins of the distribution do not have the potential to expand the range of the distribution. On the other hand, these populations do have the potential to contract the distribution, although this only occurs in habitats where the parasite load is very high (upward of an infection frequency of 29 percent) and the habitat is very harsh and frequently disturbed (upward of 29 floods per year). To conclude, the likelihood of the conditions being just right for a population of sexual snails to decline is low and because of this, the chance of the distribution's range limits shifting due to abiotic and biotic factors is also low.

Chapter 5

Final Discussion

5.1 Final discussion

The overall aim of this thesis was to improve the forecasts for the distribution of the New Zealand mudsnail (*Potamopyrgus antipodarum*) through the inclusion of abiotic factors shown to be important for predicting *P. antipodarum* presence, and mainly through the inclusion of the host-parasite coevolutionary relationship between *P. antipodarum* and its trematode parasites.

The second chapter of this thesis showed that there is substantial variability in elevation, flow stability and nitrogen load across the distribution of *P. antipodarum*. High levels of nitrogen in a habitat is associated with a higher chance of *P. antipodarum* being present, although the literature suggested that nitrogen may not be responsible for potamopyrgus presence as populations experience a trade-off between competitively excluding other species (Alonso & Camargo 2003) and the reduced fecundity associated with high levels of nitrogen (Alonso & Camargo 2013). Populations also do not change in their growth rates between high and low resource levels (Riley & Dybdahl 2015). Flow stability returned a non-significant result for predicting *P. antipodarum* presence, which may have been affected by *P. antipodarum's* ability to burrow into sediment to reduce flood-induced mortality. Flow stability has been found to facilitate dispersal through flooding events (Schreiber et al. (2003). Because of this, flow stability was chosen over nitrogen load to include in simulations of *P. antipodarum* population growth.

The third chapter showed that both parasites and male snails occur in populations of *P. antipodarum* that are present in the range margins of the distribution (0.11 predicted probability of occurrence, Figure 3.1, Figure 3.2). The switch to sexual reproduction is a coevolutionary response of *P. antipodarum* to the pressure of parasitism (Lively 1989), and the presence of both parasites and males in marginal populations indicate that coevolution occurs in the range margins of the distribution and has the potential to shift those range margins. The second chapter also showed that parasites are more likely to be found in habitats with low flow stability, and that as flows become more unstable, there is an increased likelihood of *P. antipodarum* being present (Figure 3.3). The strength of the relationship between *P. antpodarum* and parasites can be mediated by flow stability.

The fourth chapter of this thesis showed that through modelling simulated *P. antipodarum* populations, a high frequency of flooding events (upwards of 38 floods per year) can cause local extinction of sexual populations residing in the harsh range margins of *P. antipodarum*'s distribution, although this may not be realistic in New Zealand where the average number of floods is 10, and the range of the number of floods per year is 0 to 35. This chapter also showed that asexual populations have a higher survivability in the face of frequent flooding disturbance. Factors that favour the switch from asexual to sexual reproduction (i.e. the presence of parasites) have the potential to contract the range of *P. antipodarum*, while factors that favour the opposite (i.e. lack of parasitism) have the potential to expand the range of *P. antipodarum*. Furthermore, it was shown that parasite-induced castration can reduce the fecundity of sexual populations, lowering growth rates and driving populations to extinction faster than without castration. In regards to the *P. antipodarum* distribution in New Zealand, the effects of these abiotic and biotic factors may be negligible because the levels at which these effects occur are higher than the realistic levels that have been observed in the field.

The question still remains, what does this mean for the creation of species distribution models? If models are to accurately predict potential new habitats for *P. antipodarum* outside of New Zealand, where flood frequency and parasite frequency are higher, they must include both important abiotic factors such as flow stability and biotic interactions such as host-parasite coevolution. Without including these factors, SDMs are not able to grasp the full scope of what controls the distribution of *P. antipodarum*. Flow stability can expand a distribution through facilitated dispersal but also contract a distribution when flooding events are too common. Host-parasite interactions can contract a distribution through the switch to sexual reproduction and parasite-induced castration, and expand a distribution through switching to asexual reproduction.

Guisan and Thuiller (2005) suggest that limitation in SDMs arise from ecological theory not being fully integrated into the modelling process. This idea is realised through the lack of inclusion of biotic interactions into SDMs, as SDMs currently are unable to predict the changing range limits of a species that occur due to constantly changing biotic interactions such as competition, predation and dispersal limitation (Elith et al 2006, Thuiller 2013, Godsoe and Harmon 2012). Including biotic interactions such as host-parasite coevolution is a step in the right direction for improving SDMs. The research presented in this thesis connects the already well-established field of ecological niche modelling with the complexity of modelling biotic interactions, opening the door for exciting advances in the field of distribution modelling and predicting invasive species ranges.

Literature Cited

Alonso, A., Camargo, J.A. (2003) Short-term toxicity of ammonia, nitrite, and nitrate to the aquatic snail *Potamopyrgus antipodarum* (Hydrobiidae, Mollusca). *Bulletin of Environmental Contamination and Toxicology*, **70**, 1006-1012.

Alonso, A., Camargo, J.A. (2013) Nitrate causes deleterious effects on the behaviour and reproduction of the aquatic snail *Potamopyrgus antipodarum* (Hydrobiidae, Mollusca). *Environmental Science and Pollution Research*, **20(8)**, 5388-5396.

Alonso, A., Castro-Diez, P. (2008) What explains the invading success of the aquatic mud snail *Potamopyrgus antipodarum* (Hydrobiidae, Mollusca)?. *Hydrobiologia*, **614**, 107-116.

Araujo, M.B., Luoto, M. (2007) The importance of biotic interactions for modelling species distributions under climate change. *Global Ecology and Biogeography*, **16**, 743-753.

Araujo, M.B., Pearson, R.G., Thuiller, W., Erhard M. (2005) Validation of species-climate impact models under climate change. *Global Change Biology*, **11**, 1-10.

Austin, M.P., Nicholls, A.O., Margules, C.R. (1990) Measurement of the realized qualitative niche: environmental niches of five Eucalyptus species. *Ecological Monographs*, **60**, 161-177.

Bauer, I.E., McMorrow, J., Yalden, D.W. (1994) The historic ranges of three equid species in North-East Africa: a quantitative comparison of environmental tolerances. *Journal of Biogeography*, **21(2)**, 169-182.

Bertness, M.D., Ewanchuk, P.J. (2002) Latitudinal and climate-driven variation in the strength and nature of biological interactions in New England salt marshes. *Oecologia*, **132(3)**, 392-401.

Birch, L.C. (1948) The intrinsic rate of natural increase of an insect population. *The Journal of Animal Ecology*, 15-26.

Bodine, E. N., Lenhart, S., & Gross, L. J. (2014). *Mathematics for the life sciences*. Princeton University Press.

Bourassa, N., Cattaneo, A. (2000) Responses of a lake outlet community to light and nutrient manipulation: effects on periphyton and invertebrate biomass and composition. *Freshwater Biology*, **44**, 629-639.

Bunn, S.E., Arthington, A.H. (2002) Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. *Environmental Management*, **30(4)**, 492-507.

Callaway, R. M., Brooker, R. W., Choler, P., Kikvidze, Z., Lortie, C. J., Michalet, R., ... & Armas, C. (2002). Positive interactions among alpine plants increase with stress. *Nature*, **417(6891)**, 844-848.

Case, T.J., Holt, R.D., McPeek, M.A., Keitt, T.H. (2005) The community context of species' borders: ecological and evolutionary perspectives. *Oikos*, **108**, 28-46.

Catton, W. (1986). Carrying capacity and the limits to freedom. *Social Ecology Session*, *1*, X1.

Clausen, B., Biggs, B.J.F. (1997) Relationships between benthic biotic and hydrological indices in New Zealand streams. *Freshwater Biology*, **38**, 327-342.

Colliet, K.J. (1995) Environmental factors affecting the taxonomic composition of aquatic macroinvertebrate communities, in lowland waterways of Northland, New Zealand. *New Zealand Journal of Marine and Freshwater Research*, **29**, 453-465.

Cronin, G., Lodge, D.M. (2003) Effects of light and nutrient availability on the growth, allocation, carbon/nitrogen balance, phenolic chemistry, and resistance to herbivory of two freshwater macrophytes. *Ecophysiology*, **137(1)**, 32-41.

Crouse, D.T., Crowder, L.B., Caswell, H. (1987) A stage-based population model for loggerhead sea turtles and implications for conservation. *Ecology*, **68(5)**, 1412-1423.

Culp, J.M., Walde, S.J., Davies, R.W. (1983) Relative importance of substrate particle size and detritus to stream benthic macroinvertebrate microdistribution. *Canadian Journal of Fisheries and Aquatic Sciences*, **40(10)**, 1568-1574.

Death, R.G., Joy, M.K. (2004) Invertebrate community structure in streams of the Manawatu-Wanganui region, New Zealand: the roles of catchment versus reach scale influences. *Freshwater Biology*, **49**, 982-997.

Dybdahl, M. F., & Lively, C. M. (1996). The geography of coevolution: comparative population structures for a snail and its trematode parasite. *Evolution*, 2264-2275.

Dybdahl, M.F., Lively, C.M. (1995) Diverse, endemic and polyphyletic clones in a mixed populations of a freshwater snail (*Potamopyrgus antipodarum*). *Journal of Evolutionary Biology*, **8(3)**, 385-398.

Elith, J., Graham, C.H., Anderson, R.P., Dudik, M., Ferrier, S., Guisan, A., Hijmans, R.J., Huettmann, F., Leathwick, J.R., Lehmann, ... & Zimmermann, N.E. (2006) Novel methods improve prediction of species' distributions from occurrence data. *Ecography,* **29**, 129-151.

Elith, J., Leathwick, J.R. (2009) Species distribution models: ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution, and Systematics*, **40**, 676-697.

Ferrier, S. (2002) Mapping spatial pattern in biodiversity for regional conservation planning: where to from here? *Systematic Biology*, **51(2)**, 331-363.

Gallardo-Mayenco, A. (1994) Freshwater macroinvertebrate distribution in two basins with different salinity gradients (Guadalete and Guadaira river basins, south-western Spain). *International Journal of Salt Lake Research*, **3**, 75-91.

Gerard, C., Blanc, A., Costil, K. (2003) *Potamopyrgus antipodarum* (Mollusca: Hydrobiidae) in continental aquatic gastropod communities: impact of salinity and trematode parasitism. *Hydrobiologia*, **493**, 167-172.

Godsoe, W., Harmon, L.J. (2012) How do species interactions affect species distribution models? *Ecography*, **35**, 001-010.

Godsoe, W., Strand, E., Smith, C.I., Yoder, J.B., Esque, T.C., Pellmyr, O. (2009) Divergence in an obligate mutualism is not explained by divergent climatic factors. *New Phytologist* , **183**, 589-599.

Gomulkiwicz, R., Thompson, J.N., Holt, R.D., Nuismer, S.L., Hochberg, M.E. (2000) Hot spots, cold spots, and the geographic mosaic theory of coevolution. *The American Naturalist*, **156(2)**, 156-174.

Grosman, G.D., Ratajczak, R.E., Crawford, M., Freeman, M.C. (1998) Assemblage organization in stream fishes: effects of environmental variation and interspecific interactions. *Ecological Monographs*, **68(3)**, 395-420.

Guisan, A., Thuiller, W. (2005) Predicting species distribution: offering more than simple habitat models. *Ecology Letters*, **8**, 993-1009.

Hall, R.O., Dybdahl, M.F., VanderLoop, M.C. (2006) Extremely high secondary production of introduced snails in rivers. *Ecological Applications*, **16(3)**, 1121-1131.

Hall, R.O., Tank, J.L., Dybdahl, M.F. (2003) Exotic snails dominate nitrogen and carbon cycling in a highly productive stream. *Frontiers in Ecology*, **1(8)**, 407-411.

Hamilton, W.D. (1982) Pathogens as causes of genetic diversity in their host populations. *Population Bology of Infectious Diseases*, **25**, 269-296.

Hamilton, W.D., Axelrod, R., Tanese, R. (1990) Sexual reproduction as an adaptation to resist parasites. *Proceedings of the National Academy of Sciences*, **87**, 3566-3573.

Harding, J.S., Winterbourn, M.J. (1995) Effects of contrasting land use on physio-chemical conditions and benthic assemblages of streams in a Canterbury (South Island, New Zealand) river system. *New Zealand Journal of Marine and Freshwater Research*, **29**, 479-492.

Hassell, M.P. (1975) Density-dependence in single-species populations. *Journal of Animal Ecology*, **44(1)**, 283-295.

Hechinger, R.F. (2012) Faunal survey and identification key for the trematodes (Platyhelminthes: Digenea) infecting *Potamopyrgus antipodarum* (Gastropoda: Hydrobiidae) as first intermediate host. *Zootaxa*, **3418**, 1-27.

Higgins, S.N., Hecky, R.E., Guildford, S.J. (2006) Environmental controls of *Cladophora* growth dynamics in eastern Lake Erie: application of the *Cladophora* growth model (CGM). *Journal of Great Lakes Research*, **32(3)**, 629-644.

Holomuzki, J.R., Biggs, B.J.F. (1999) Distributional responses to flow disturbance by a stream-dwelling snail. *Oikos*, **87(1)**, 36-47.

Holomuzki, J.R., Biggs, B.J.F. (2000) Taxon-specific responses to high-flow disturbance in streams: implications for population persistence. *Journal of the North American Benthological Society*, **19(4)**, 670-679.

Holomuzki, J.R., Biggs, B.J.F. (2003) Sediment texture mediates high-flow effects on lotic macroinvertebrates. *Journal of the North American Benthological Society*, **22(4)**, 542-553.

Holt, R.D., Barfield, M. (2009) Trophic interactions and range limits: the diverse roles of predation. *Proceedings of the Royal Society of Biological Sciences*, **276**, 1435-1442.

Hudgens, B.R., Haddad, N.M. (2003) Predicting which species will benefit from corridors in fragmented landscapes from population growth models. *The American Naturalist*, **161(5)**, 808-820.

Jackson, D.A., Peres-Neto, P.R., Olden, J.D. (2001) What controls who is where in freshwater fish communities – the roles of biotic, abiotic, and spatial factors. *Canadian Journal of Fisheries and Aquatic Sciences*, **58**, 157-170.

Jacobsen, R., & Forbes, V. E. (1997). Clonal variation in life-history traits and feeding rates in the gastropod, *Potamopyrgus antipodarum*: performance across a salinity gradient. *Functional Ecology*, **11(2)**, 260-267.

Janzen, D.H. (1979) When is it coevolution? *Evolution*, **34(3)**, 611-612.

Jensen, A., Forbes, V. E., & Parker, E. D. (2001). Variation in cadmium uptake, feeding rate, and life-history effects in the gastropod *Potamopyrgus antipodarum*: Linking toxicant effects on individuals to the population level. *Environmental Toxicology and Chemistry*, **20(11)**, 2503-2513.

Johnson, M.T.J., Stinchcombe, J.R. (2007) An emerging synthesis between community ecology and evolutionary biology. *Trends in Ecology and Evolution*, **22(5)**, 250-257.

Jokela, J., Lively, C.M., Taskinen, J., Peters, A.D. (1999) Effect of starvation on parasite-induced mortality in a freshwater snail (*Potamopyrgus antipodarum*). *Oecologia*, **119(3)**, 320-325.

King, K.C., Delph, L.F., Jokela, J., Lively, C.M. (2009) The geographic mosaic of sex and the red queen. *Current Biology*, **19**, 1438-1441.

King, K.C., Delph, L.F., Jokela, J., Lively, C.M. (2011b) Coevolutionary hostspots and coldspots for host sex and parasite local adaptation in a snail-trematode interaction. *Oikos*, **120(9)**, 1335-1340.

King, K.C., Jokela, J., Lively, C.M. (2011) Parasites, sex, and clonal diversity in natural snail populations. *Evolution*, **65(5)**, 1474-1481.

Kot, M., Lewis, M.A., van den Driessche, P. (1996) Dispersal data and the spread of invading organisms. *Ecology*, **77(7)**, 2027-2042.

Krist, A.C., Lively, C.M. (1998) Experimental exposure of juvenile snails (*Potamopyrgus antipodarum*) to infection by trematode larvae (Microphallus sp.): infectivity, fecundity compensation and growth. *Oecologia*, **116(4)**, 575-582.

Kroskella, B., Lively, C.M. (2007) Advice of the rose: experimental coevolution of a trematode parasite and its snail host. *Evolution*, **61(1)**, 152-159.

Lakeman-Fraser, P., Ewers, R.M. (2013) Enemy release promotes range expansion in a host plant. *Oecologia*, **172**, 1203-1212.

Leathwick, J. R., Julian, K., & Smith, B. (2009). Predicted national-scale distributions of freshwater macro-invertebrates in all New Zealand's rivers and streams. *NIWA client report HAM2009–042*.

Levri, E.P. (1998) The influence of non-host predators on parasite-induced behavioural changes in a freshwater snail. *Oikos*, **81(3)**, 531-537.

Levri, E.P., Lively, C.M. (1996) The effects of size, reproductive condition, and parasitism on foraging behaviour in a freshwater snail, *Potamopyrgus antipodarum*. *Animal Behaviour*, **51**, 891-901.

Liess, A., Lange, K. (2011) The snail *Potamopyrgus antipodarum* grows faster and is more active I the shade, independent of food quality. *Oecologia*, **167**, 85-96.

Lively, C.M. (1987) Evidence from a New Zealand snail for the maintenance of sex by parasitism. *Nature*, **328**, 518-521.

Lively, C.M. (1989) Adaptation by a parasitic trematode to local populations of its snail host. *Evolution*, **43(8)**, 1663-1671.

Lively, C.M. (1996) Host-parasite coevolution and sex. *Bioscience*, **46(2)**, 107-114.

Lively, C.M. (2010) A review of red queen models for the persistence of obligate sexual reproduction. *Journal of Heredity*, **101**, 513-520.

Lively, C.M., Dybdahl, M.F. (2000) Parasite adaptation to locally common host genotypes. *Nature*, **405(6787)**, 679-681.

Lively, C.M., Jokela, J. (1996) Clinal variation for local adaptation in a host-parasite interaction. *Proceedings of the Royal Society of Biological Sciences*, **263**, 891-897.

Louthan, A.M., Doak, D.F., Angert, A.L. (2015) Where and when do species interactions set range limits? *Trends in Ecology and Evolution*, **30(12)**, 780-792.

Mallet, J. (2012) The struggle for existence: how the notion of carrying capacity, *K*, obcures the links between demography, Darwinian evolution, and speciation. *Evolutionary Ecology Research*, **14**, 627-665.

Morran, L.T., Schmidt, O.G., Gelarden, I.A., Parrish II, R.C., Lively, C.M. (2011) Running with the red queen: host-parasite coevolution selects for biparental sex. *Science*, **333(6039),** 216-218.

Mueller, U.G., Mikheyev, A.S., Hong, E., Sen, R., Warren, D.L., Solomon, S.E. Ishak, H.D., Cooper, M., Miler, J.L., Shaffer, K.A., Juenger, T.E. (2011) Evolutionof cold-tolerant fungal symbionts

permits winter fungiculture by leafcutter ants at the northern frontier of tropical ant-fungus symbiosis. *Proceedings of the National Academy of Sciences*, **108(10)**, 4053-4056.

Newbold, T. (2010) Applications and limitations of museum data for conservation and ecology, with particular attention to species distribution models. *Progress in Physical Geography*, **34(1)**, 3-22.

Nuismer, S.L. (2006) Parasite local adaptation in a geographic mosaic. *Evolution*, **60(1)**, 24-30.

Pearman, P.B., Guisan, A., Broennimann, O., Randin, C.F. (2007) Niche dynamics in space and time. *Trends in Ecology & Evolution*, **23(3)**, 149-158.

Peters, A.D., Lively, C.M. (1999) The red queen and fluctuating epistasis: a population genetic analysis of antagonistic coevolution. *The American Naturalist*, **154(4)**, 393-405.

Peterson, A.T. (2003) Predicting the geography of species' invasions via ecological niche modelling. *The Quarterly Review of Biology*, **78(4)**, 419-433.

Petitpierre, B., Kueffer, C., Broenniman, O., Randin, C., Daehler, C., Guisan, A. (2012) Climatic niche shifts are rare among terrestrial plant invaders. *Science*, **335**, 1344-1347.

Quinn, J.M., Hickey, C.W. (1990) Magnitude of effects of substrate particle size, recent flooding, and catchment development on benthic invertebrates in 88 New Zealand rivers. *New Zealand Journal of Marine and Freshwater Research*, **24(3)**, 411-427.

Richards, D. C. (2004). Competition between the threatened Bliss Rapids snail, *Taylorconcha serpenticola* (Hershler et al.) and the invasive, aquatic snail, *Potamopyrgus antipodarum* (Gray).

Ricklefs, R.E. (2010) Evolutionary disversification, coevolution between populations and their antagonists, and the filling of niche space. *Proceedings of the National Academy of Sciences*, **107(4)**, 1265-1272.

Riis, T., Biggs, B.J.F. (2003) Hydrological and hydraulic control of macrophyte establishment and performance in streams. *Limology and oceanography*, **48(4)**, 1488-1497.

Riley, L.A., Dybdahl, M.F. (2015) The roles of resource availability and competition in mediating growth rates of invasive and native freshwater snails. *Freshwater Biology*, **60**, 1308-1315.

Riley, L.A., Dybdahl, M.F., Hall, R.O. (2008) Invasive species impact: asymmetric interactions between invasive and endemic freshwater snails. *Journal of the North American Benthological Society*, **27(3)**, 509-520.

Scarsbrook, M.R., Townsend, C.R. (1993) Stream community structure in relation to spatial and temporal variation: a habitat templet study of two contrasting New Zealand streams. *Freshwater Biology*, **29**, 395-410.

Schemske, D.W., Mittelbach, G.G., Cornell, H.V., Sobel, J.M., Roy, K. (2009) Is there a latitudinal gradient in the importance of biotic interactions. *Annual Review of Ecology, Evolution, and Systematics*, **40**, 245-269.

Schreiber, E.S.G., Quinn, G.P., Lake, P.S. (2003) Distribution of an alien aquatic snail in relation to flow variability, human activities and water quality. *Freshwater Biology*, **48**, 951-961.

Sexton, J.P., McIntyre, P.J., Angert, A.L., Rice, K.J. (2009) Evolution and ecology of species range limits. *Annual Review of Ecology, Evolution, and Systematics*, **40**, 415-436.

Short, T.M., Black, J.A. Birge, W.J. (1991) Ecology of a saline stream: community responses to spatial gradients of environmental conditions. *Hydrobiologia*, **226**, 167-178.

Smith, D.L., Ericson, L., Burdon, J.J. (2011) Co-evolutionary hot and cold spots of selective pressure move in space and time. *Journal of Ecology*, **99**, 634-641.

Smith, J.M., Maynard-Smith, J. (1978) The Evolution of Sex. Cambridge: *Cambridge University Press.*

Sponseler, R.A., Benfield, E.F., Valett, H.M. (2001) Relationships between land use, spatial scae and stream macroinvertebrate communities. *Freshwater Biology*, **46**, 1409-1424.

Stockwell, D.R.B., Peterson, A.T. (2002) Effects of sample size on accuracy of species distribution models. *Ecological Modelling*, **148(1)**, 1-13.

Thompson J.N. (1998) Rapid evolution as an ecological process. *Trends in Ecology and Evolution*, **13(8)**, 329-332.

Thompson, J.N. (2005) *The geographic mosaic of selection*. University of Chicago Press.

Thuiller, W., Munkemuller, T., Lavergne, S., Mouillot, D., Mouquet, N., Schiffers, K., Gravel, D. (2013) A road map for integrating eco-evolutionary processes into biodiversity models. *Ecology Letters*, **16(1)**, 94-105.

Tibbets, T.M., Krist, A.C., Hall, R.O., Riley, L.A. (2010) Phosphorus-mediated changes in life history traits of the invasive New Zealand mudsnail (*Potamopyrgus antipodarum*). *Oecologia*, **163(3)**, 549-559.

Tsoularis, A. (2001) Analysis of logistic growth models. *Mathematical Biosciences*, **179(1)**, 21-55.

VanDerWal, J., Shoo, L.P., Graham, C., Williams, S.E. (2009) Selecting pseudo-absence data for presence-only distribution modelling How far should you stray from what you know? *Ecological Modelling*, **220(4)**, 589-594.

Verhulst, P.F. (1838) Notice sur la loi que la population suit dans son accroissement. Correspondance Mathématique et Physique Publiée par A. *Quetelet*, **10,** 113-121.

Vinson, M., Harju, T., & Dinger, E. (2007). Status of New Zealand Mud snails (*Potamopyrgus antipodarum*) in the Green River downstream from Flaming Gorge Dam: current distribution; habitat preference and invertebrate changes; food web and fish effects; and predicted distributions. *Final Reports for Project Agreements: USFWS-601815G405, NPS-J1242050058. BLM-JSA041003*.

Zaniewski, A.E., Lehmann, A., Overton, J.M. (2002) Predicting species spatial distributions using presence-only data: a case study of native New Zealand ferns. *Ecological Modelling*, **157(2-3)**, 261-280.