Fast versus slow: differing life history strategies of two New Zealand damselfly (Odonata: Zygoptera) species.

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This thesis is dedicated to the memory of the first person to have utter faith in my scientific abilities, who truly believed that I was capable of more than I ever knew possible, the reason I have come this far, and the reason I will forever strive to be the best that I can be.

Professor Jules Kieser.
20 Dec 1950 - 10 Jun 2014
My mentor, my boss, my colleague and my friend.
Rest in peace.

Abstract

Life history strategies are important for all organisms and are studied in large part to understand how an individual, population or species reacts to/lives in/survives in its environment and how it/they adapt to changes within that environment. No single strategy is optimal because environmental, morphological and physiological constraints lead to trade-offs between different traits, and how a species responds to these constraints determines their life history. Two variations of life history strategies are slow and fast, which are characterised by differences in activity, development, metabolism, behaviour and their environment. These differences can result in species divergent preference for different habitats, influencing species distribution.

Around 90% of New Zealand's insects are endemic and most are not well represented in the literature. Their life histories often lack synchronicity, seasonality, and winter diapause, when compared to their Northern Hemisphere counterparts, traits which are often associated with a mild, maritime climate. Odonata are model insects for life history studies but their diversity in New Zealand is low. Two species of damselfly (Odonata: Zygoptera) are present in the South Island: *Austrolestes colensonis* and *Xanthocnemis zealandica*. Both of these species were selected to study because they are easy to locate, abundant and widely distributed. They are well described, taxonomically distinct, and are easy to collect, and maintain in the lab. These two species also permit the study of two closely related, cohabitating, predator species that potentially differ in their life history strategies.

The primary objective of this thesis was to determine if a fast-slow life history strategy dichotomy exists between *A. colensonis* and *X. zealandica* by investigating aspects of their life history and distribution. A long term (two year) field study was used to investigate differences in life history characteristics between both species in six different populations over an altitudinal gradient. A survey of the lower half of the country was conducted to create a distribution map for each species and investigate any species-specific habitat preferences. Laboratory studies were conducted to investigate differences in metabolism, by measuring movement behaviour and ability to withstand starvation, as well as the likelihood of winter diapause occurring.

A. colensonis naiads were found to grow larger, move more, have a decreased starvation tolerance, and a preference for lower altitude. These characteristics are consistent with a life history at the fast end of the continuum. *X. zealandica*, on the other hand, display characteristics more in alignment with a slow life history, because naiads of this species are smaller, move less, and can survive longer periods of starvation. *X. zealandica* require permanent habitats; however, they can take advantage of low quality habitats, particularly those at high altitudes, which don't suit *A. colensonis*. Therefore, a fast/slow life history strategy dichotomy is confirmed to be present and may influence how these species interact with the environment and each other. Additionally, like many other endemic New Zealand invertebrates, *A. colensonis* and *X. zealandica* undergo quiescence rather than diapause when overwintering. This allows these species to opportunistically take advantage of a mild changeable climate and hence the periods when suitable conditions for growth prevail.

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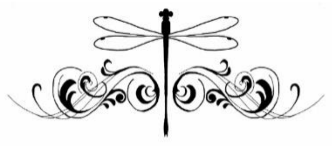
General introduction



1.1 Life history strategies

Life history strategies are important for all organisms and are studied in large part to understand how an individual, population or species reacts to/lives in/survives in its environment and how it/they adapt to changes within that environment (Stearns 1992). No single strategy is optimal because environmental, morphological and physiological constraints lead to trade-offs between different traits (Stearns 1989, Zera and Harshman 2001), and how a species responds to these constraints determines their life history. Fitness is maximised, via these trade-offs, through the allocation of different amounts of resources (such as energy or time) to a given trait (Zera and Harshman 2001). Not all species will allocate the same amount of resources to the same trait (or suite of traits), and given that resources are ultimately finite, increased resource allocation to one trait reduces allocation to an alternate trait. This can result in multiple variations in life histories between species living in the same environment (Tallamy and Denno 1981). Insects are a model group of organisms with which to investigate life history strategies because they are small, have short life cycles, develop quickly, live in most available habitats and exhibit many different life history strategies (Vogler and Kelley 1995, Keller and Jemielity 2006).

1.1.1 Fast vs. slow life history strategies

Two variations of life history strategies are slow and fast, which are characterised by differences in activity, development, metabolism, behaviour and their environment (Pianka 1970, Southwood 1977, Werner and Anholt 1993, Johansson 2000, Reznick, Bryant et al. 2002, McCauley 2008), as outlined in Table 1.1. Slow life styles are associated with reduced activity and restricted habitat use which reduces exposure to predators; this in turn results in lower metabolic, feeding and growth/development rates (Johansson 2000, McCauley 2008). The opposite is a life style where individuals are active, consume more energy and grow faster, and hence are given the term fast life histories (Johansson 2000, McCauley 2008). The disadvantage of this strategy is an increased risk of being seen by a predator, resulting in increased predation and reduced survival (Johansson 2000, McCauley 2008). Fast life styles (particularly in the case of freshwater invertebrates) therefore, evolve in habitats where predators are absent, such as ephemeral environments (Johansson 2000, Galatowitsch and McIntosh 2016). Animals in these habitats can disregard the threat of predation and maintain high activity and metabolic rates which allows them to grow and develop quickly

Table 1.1 Comparison of generalisations of fast and slow life history strategies (adapted from Johansson 2000, Pianka 1970, Reznick, Bryant et al. 2002 and Southwood 1977).

Fast	Slow
Highly active	Low activity
Rapid development	Slower development
High metabolic rate	Low metabolic rate
Short life span	Long life span
Early reproduction	Delayed reproduction
Small body size	Large body size
High level of dispersal	Low level of dispersal
Lower competitive ability (low investment in defence)	Greater competitive ability (high investment in defence)
Sensitive to predators	Predator avoidance behaviour
Variable population size (usually well below carrying capacity)	Stable population size (at or around carrying capacity)
Environment resource rich but variable or unpredictable (e.g. ephemeral habitats)	Environment resource poor but constant or predictable (e.g. permanent habitats)
Time efficient	Food and space resource efficient

enough to complete their life cycle before the habitat dries out. These are the two extremes of this scale - the reality is likely more of a continuum, where species may fall at either end, or anywhere in between (Johansson 2000). These differences in life history strategies can result in species preference for different habitats (which will influence species distribution) (Blank, Tedesco et al. 2007).

1.2 Climate and its impact on insects

Insects, as poikilotherms, have a limited ability to regulate their own internal temperature and rely on their environment for temperature control (Bale and Hayward 2010). Some insects may display thermoregulatory behaviours, such as basking in sunlight (for example dragonflies, grasshoppers and butterflies), with their bodies orientated to maximise temperature increase (May 1979), but unlike mammals and birds, they are generally unable to actively generate their own body heat. Therefore, insects are restricted in their distributions to environments that allow them to maintain bodily function (Harrison, Woods et al. 2012). This isn't so much of an issue in tropical regions, where temperatures fluctuate very little year-round. However, animals living in temperate regions must be able to survive fluctuations in temperature on a daily basis, and even larger fluctuations between seasons. For example, in Winnipeg, Canada, average daily maximum and minimum temperatures for the period 1981-2010 were -11.3 to -21.4°C in January (winter) and 23.2 to 10.7°C in July (summer), with extremes of -45 to 40.6°C[1].

1.2.1 Overwintering mechanisms

Winter is known for the onset of cold, harsh environmental conditions in temperate climates. Fortunately, insects have evolved a great diversity of different strategies with which to cope with these adverse conditions (Turnock and Fields 2005, Danks 2006, Leather 2008, Bel-Venner, Mondy et al. 2009), for example: migration, cold hardiness, dormancy, etc. (Leather 2008). Migration is a behavioural and physiological response whereby the organism physically removes themselves from the environment for the duration of the adverse conditions, returning once they have passed (Dingle 1972, Allaby 1999). The most well known insect migration is that of the monarch butterfly, *Danus plexippusi,* which travels over 3000 km south across North America in the autumn to escape the harsh winters at the higher latitudes (Dingle 1972). Cold hardy insects are either freeze tolerant or intolerant (Leather 2008). Freeze intolerant insects reduce their body temperature via supercooling to prevent the formation of ice crystals (Sinclair 1999, Sinclair, Addo-Bediakom et al. 2003). This requires the build up of antifreeze protein and sugars, such as glycerol and fructose, which maintain the body fluids in a liquid form without freezing (Leather, Walters et al. 1993, Leather 2008). In contrast, freeze tolerant species can survive freezing by using ice nucleating peptides or proteins to instigate the formation of small ice crystals in extracellular spaces to

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[1] www.climate.weather.gc.ca accessed 7th December 2016

minimise damage (Leather, Walters et al. 1993). The two most well defined forms of dormancy are quiescence and diapause (Kostal 2006). Quiescence is a period of interrupted growth, initiated as a direct result of unfavourable conditions that ends when those conditions have passed, and its effects are reversible (Denlinger 1986, Tauber, Tauber et al. 1986, Kostal 2006, Hahn and Denlinger 2007, Gordh and Headrick 2011). Diapause is a pre-programmed physiological response initiated prior to the onset of winter (usually as a response to decreasing day length), where development is suppressed (Roberts 1977, Denlinger 1986, Denlinger 2002, Kostal 2006, Hahn and Denlinger 2007, Gordh and Headrick 2011). It is controlled by environmental, hormonal and molecular regulators and consequently cannot be broken by (nor is it associated with) the return of favourable conditions (Tauber and Tauber 1981, Denlinger 1986, Denlinger 2002, Kostal 2006). Diapause may occur at any stage of an insects life, but for any given species, it usually only occurs during a single developmental stage (Bel-Venner, Mondy et al. 2009). An advantage of diapause is that it allows for synchronisation of the life cycle with all members of that year's cohort coming out of diapause at the same time (Bel-Venner, Mondy et al. 2009).

The habitat in which the insect chooses to overwinter in also plays an important role in determining its method of overwintering (Danks 2006). Habitats which are covered by snow, ice or soil are more stable as conditions are less variable and often warmer than exposed habitats (Danks 1978). For example, aquatic lentic habitats often maintain temperatures around 4°C below the ice layer (Danks 1978). Soil also provides similar protection, although temperature levels are linked to particle size and the amount of trapped air to provide insulation (Danks 1978, Danks 2006).

1.2.2 Influences of altitudinal and latitudinal gradients

Species with wide geographical ranges often show variation in life history characteristics (such as body size, development time etc.) across latitudinal or elevational gradients (Danks 2007). Many abiotic factors have been shown to have correlations with changes in altitude and latitude, such as: light (solar radiation), air pressure, CO_2/O_2 content and most importantly for insects, temperature (Körner 2007). As altitude increases, temperature decreases at approximately 6°C per kilometre (Barry 2008). Because many of an insect's life history characteristics are influenced by temperature, many features of an insect's life history strategy can show trends across elevation or latitude gradients. For example; reduced growth rate and larger body size at maturity can be associated with higher latitudes and elevations, which is consistent with Bergmann's rule (species grow larger in cooler environments) (Angilletta, Steury et al. 2004). Similar patterns can be seen for habitat productivity and species diversity, which both decrease with increasing distance away from the equator and along an increasing altitudinal gradient (Pianka 1966, Huston 1994, Rahbek 1995).

1.2.3 Northern vs. Southern Hemispheres

Large scale climatic differences exist between Northern and Southern Hemispheres. Northern Hemisphere climates are influenced by large continental land masses (Leather, Walters et al. 1993). Air over land heats and cools more rapidly than air over water, resulting in greater variability in day/night fluctuations and more extreme summer highs and winter lows (Leather, Walters et al. 1993). Smaller landmasses in the Southern Hemisphere (such as New Zealand) have a large coastline compared to landmass, which influences the climate. The more stable air masses of a large ocean systems produce less difference between daily and seasonal extremes, but increased fluctuations in weather patterns make them less predictable over short temporal scales (Leather, Walters et al. 1993, Sinclair, Addo-Bediakom et al. 2003). Due to these contrasting climatic regimes, it is appropriate to assume there would be different responses in the distribution of life history strategies and characteristics between Northern and Southern Hemispheres due to the importance of temperature (Lancaster and Downes 2013, Singh, Mishra et al. 2014).

1.2.4 Implications of climate change on insects

There is no denying that global temperatures are on the increase (e.g. Walther, Post et al. 2002, Thomas, Cameron et al. 2004, Solomon, Plattner et al. 2009, Bestion, Teyssier et al. 2015, Seebacher, White et al. 2015, Urban 2015). Increases in average global temperature of 0.6°C over the past three decades have been recorded and further increases are predicted (Hansen, Sato et al. 2006). This could have a significant influence on insects. Insects are particularly susceptible to climate change as they rely on environmental conditions to mediate body temperature which affects physiological responses (Bestion, Teyssier et al. 2015). This could be detrimental to species which, a) have limited ranges with no space to expand, and b) have little plasticity (Bale, Masters et al. 2002), as climate change can affect the distribution of a species (Thomas, Cameron et al. 2004) and may ultimately lead to mass species extinctions (Seebacher, White et al. 2015, Urban 2015). Poleward shifts in species distributions linked to climate change have already been reported, for example butterflies (Lepidoptera) in Australia (Beaumont and Hughes 2002, Thomas, Cameron et al. 2004), America (Parmesan 1996) and Europe (Parmesan, Ryrholm et al. 1999, Wilson, Gutierrez et al. 2005, Wallisdevries and Van Swaay 2006), and dragonflies (Odonata) in Britain (Hansen, Sato et al. 2006), Europe (Ott 2001, Flenner and Sahlen 2008, Flenner, Richter et al. 2010) and Japan (Aoki 1997). It is unclear if Southern Hemisphere species follow the same patterns of distributional change as the literature is heavily biased towards Europe and North America (Seebacher, White et al. 2015), therefore, more information about geographical distributions of insects in the Southern Hemisphere is required.

1.3 The New Zealand situation

New Zealand is situated in the South Pacific and has a land mass that covers approximately 270 000 km^2 over two main islands and a multitude of offshore islands (Cranston 2009). These fragmented environments support a much lower biodiversity that other areas of the same size (Cranston 2009). New Zealand broke away from Gondwanaland 82 million years ago (McCulloch, Wallis et al. 2010) and subsequent isolation and tectonic activities have shaped the evolution of New Zealand insects and their distributions. As a result, many of New Zealand's insects (more than 90%) are endemic to the country (Gibbs 2007).

1.3.1 New Zealand climate

New Zealand's climate is complex and highly variable (Wissinger, Greig et al. 2009), and with 15,000-18,000 km of coastline (Walrond 2005), has a strong maritime influence. The northernmost part of the country has a warm temperate climate, while the bottom of the South Island has a predominantly cool temperate climate (Walrond 2005). The South Island, which is the focus of this thesis, is divided by a mountain range (the Southern Alps) which runs the length of the western side of the island. The highest peak (Mt Cook/Aoraki) reaches 3724 m, and has a permanent cover of snow. The amount of rainfall throughout the country is unpredictable; storms or dry periods may occur at any time of the year (Wissinger, Greig et al. 2009). Warm, moist, tropical air mixes with cold, dry, Antarctic air, creating a series of high and low pressure systems which move over the country (Walrond 2005). This creates highly variable short term weather patterns. However, despite the variability, weather extremes are not as severe as those experienced in a continental climate, such as those in North America or Europe (Sinclair, Addo-Bediakom et al. 2003). The West Coast region has a high annual rainfall, compared to the rest of the country, resulting from prevailing westerly-driven water-laden air coming across the Tasman Sea being pushed up over the Southern Alps (Scarsbrook and Pearson 2008). Areas to the east of the Southern Alps (Central Otago and Canterbury) have the lowest rainfall in the country, as well as the most variable seasonal temperatures (Walrond 2005). For example, in Queenstown (in Central Otago) the average daily maximum and minimum temperatures for the period 1969-1998 were 8.1 to 0.1°C in July (winter) and 22.5 to 8.1°C in January (summer), with extremes of 34.1 to -8.4°C. In comparison, Dunedin (Otago), on the eastern coast, for the same period recorded average daily maximum and minimum temperatures of 9.9 to 3.1°C in July and 18.9 to 11.5°C in January, with extremes of 35.7 to -8.0°C[2].

1.3.2 New Zealand Insects

New Zealand houses an estimated 20 000 insect species, representing 25 different orders (Gibbs 2007), although some orders are represented by a single species e.g. scorpionflies (Mecoptera) and

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[2] www.metservice.co.nz accessed 16th December 2016

dobsonflies (Megaloptera) (Gibbs 2007). New Zealand's high rainfall and geological history has created numerous isolated streams which contribute to, a greater than expected diversity of stream invertebrates such as: mayflies (Ephemeroptera); stoneflies (Plecoptera); caddisflies (Trichoptera) (Gibbs 2007). Not all aquatic freshwater invertebrates are well represented however, with damselflies and dragonflies (Odonata) having only 16 species reported as having breeding populations throughout the country, plus an additional two species considered as infrequent visitors from Australia and the Pacific (Rowe 1987, Gibbs 2007, Rowe, Davies et al. 2011).

Insects endemic to New Zealand, are reported to lack synchronicity, seasonality, and winter diapause, when compared to their Northern Hemisphere counterparts (Dumbleton 1967, Roberts 1977, Roberts 1978, Winterbourn 1978, Towns 1981, Morris 1989). It is energy expensive to undergo processes such as diapause (Hahn and Denlinger 2007). Since New Zealand conditions are not as harsh (as Northern Hemisphere conditions), it is possible that insect species here have lost the ability (or never gained it) to undergo diapause. This would allow them to take advantage of favourable conditions when they arise at any time of year. In addition, New Zealand insects (especially aquatic species) appear to be largely generalists that can survive under a broad range of environmental and ecological conditions (Winterbourn, Rounick et al. 1981, Wissinger, Greig et al. 2009). However, little attention has been given to New Zealand species, particularly in comparison to overseas counterparts, and more knowledge is required about their distributions, limits, behaviours etc.

1.4 Odonata

Odonata is one of the oldest insect orders, dating to around 250 million years before present (Corbet 1999). In excess of 5000 species have been identified worldwide, across two main suborders: Epiprocta (dragonflies; previously Anisoptera) and Zygoptera (damselflies) (Corbet 1980, Corbet 1999). Due to their size, colouring and behaviour, they are easily spotted (Kalkman, Clausnitzer et al. 2008). Additionally, they are easy to maintain in the lab, making them regular subjects in scientific studies (Hardersen and Wratten 1996). Some recent examples are Chavez, Mabry et al. (2015), Elo, Pennttinen et al. (2015), Oliveira-Junior, Shimano et al. (2015), Thornton and Switzer (2015), Andersen, Nilsson et al. (2016), Bybee, Cordoba-Aguilar et al. (2016), Callahan and McPeek (2016), Hesse, Falk et al. (2016), Marinov, Amaya-Perilla et al. (2016), and Palacino-Rodriguez, Munguia-Steyer et al. (2016). Odonata are widespread across the globe, inhabiting most environments with the exception of the polar regions (Corbet 1999), making them useful biological indicators of the health of aquatic systems worldwide (Bulankova 1997, Foote and Rice Hornung 2005, Kalkman, Clausnitzer et al. 2008). Temperature strongly influences Odonate distribution, with greater diversity occurring in tropical climates (Corbet 1999, Kalkman, Clausnitzer et al. 2008). Because low temperatures are associated with increasing altitude, Odonate distribution is also limited by altitude in much the same way as latitude with an increase in both resulting in a decrease in diversity (Corbet 1999).

1.4.1 The life cycle of Odonata

Odonata are hemimetabolous (having only three life stages: egg, naiad and adult) (Figure 1.1) with eggs and naiads usually being aquatic, and found in both lentic and lotic systems (generally species will restrict themselves to one habitat type, although this is not always the case) (Morse 2009). Eggs may be laid in or on plant tissue or directly on the water's surface, and will undergo either direct or delayed development (Corbet 1980, Corbet 1999). In direct development, eggs hatch shortly after laying, usually around 5-40 days (although exact development time is dependent on temperature), whereas in delayed development, eggs will undergo a diapause period (hatching in around 80-230 days) (Corbet 1980). The naiad stage is typically much longer than any other stage, lasting from several weeks to many years. During this time, naiads will moult through a number of different instars as they grow (typically 9-15) (Corbet 1999). The length of time spent as naiads and the number of instars can be highly variable within an individual species (even more so between species) and is primarily influenced by environmental conditions, particularly temperature (Corbet 1999). Odonata overwinter in their naiad or egg stages, with adults surviving for an average of four to six weeks (Corbet 1999).

1.4.2 New Zealand species

Since its release in 1987, Rowe's book on New Zealand Odonates has been the authoritative text in this country. Despite the earlier claim of Odonata being well studied, New Zealand species have not been given the same level of importance or study as their Northern Hemisphere counterparts. The diversity of New Zealand's Odonata is low, with a maximum of 16 species reported (10 Epiprocta and 6 Zygoptera: Table 1.2) (Rowe 1987, Rowe, Davies et al. 2011). The focus of this study is solely on Zygoptera, therefore, New Zealand Epiprocta shall not be considered further here.

The New Zealand damselflies are represented by three genera, *Austrolestes* (family Lestidae), *Ischnura* and *Xanthocnemis* (family Coenagrionidae). *Ischnura aurora* is an airborne migrant and the only species in the genus located in New Zealand (Rowe 1987). Its current distribution is restricted to the North Island. As the focus of this thesis is species commonly found in South Island, it shall not be considered further. *Austrolestes* is also represented by a single species *A. colensonis*, an endemic species common throughout the country (including the Chatham islands, Stewart Island and other offshore islands) (Rowe 1987). *Xanthocnemis* is an endemic genus, reported to be represented by four species: *X. zealandica, X. sobrina, X. tuanuii* and *X. sinclairi* (Rowe 1987). *X. zealandica* is common throughout the entire country (similar to *A. colensonis*), the other three species have small geographic ranges; *X. sobrina* the far north of the North Island (including Northland,

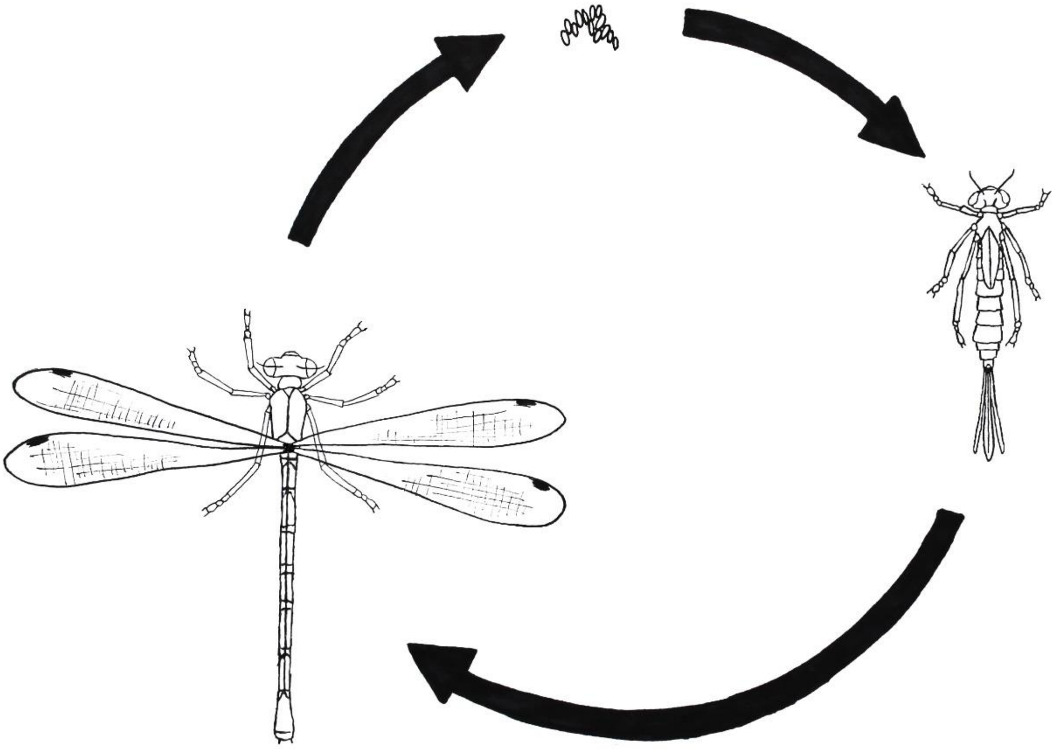

Figure 1.1 Generalised life cycle of Odonata.

Table 1.2 List of Odonata species with breeding populations in New Zealand (Rowe 1987).

Suborder	Family	Species	Location	Status[3]
Epiprocta	Petaluridae	*Uropetala carovei* (White)	North Is. and South Is.	Not common but widespread, endemic
		U. chiltoni (Tillyard)	South Is.	Not common but widespread, endemic
	Aeshnidae	*Aeshna brevistyla* (Rambur)	Australia, New Zealand, New Caledonia, and Vanuatu	Widespread, native
		Anax papuensis (Burmeister) (*Hemianax papuensis*)	Indonesia, Papua New Guinea, Australia, North Is. New Zealand	Common and widespread
	Corduliidae	*Antipodochlora braueri* (Selys)	North Is.	Locally common, widespread, endemic
		Procordulia grayi (Selys)	Southern North Is. and South Is.	Stable population, endemic
		P. smithii（White）	North, South and offshore Islands	Common, potentially in decline, endemic
		Hemicordulia australiae	Australia, New Zealand, Indonesia	Widespread, native
	Libelluidae	*Diplacodes bipunctata* (Brauer)	Within Australasia and Oceania	Not common but widespread, native
		Tramea loewii (Brauer) (Rowe et al. 2011)	Western Pacific, Australia, North Is. New Zealand	Widespread, native
Zygoptera	Coenagrionidae	*Ischnura aurora* (Brauer)	Asia, Indonesia, Australasia, North Is. New Zealand	Widespread, range expanding
		Xanthocnemis zealandica (McLachlan)	North, South and Stewart Islands	Widespread, common, endemic
		X. sobrina (McLachlan)[4]	Northern half of North Is.	Habitat and population unknown, endemic
		X.tuanuii (Rowe)	Chatham Is.	Limited population, endemic
		X. sinclairi (Rowe)[4]	South Is. - alpine region, Canterbury	Habitat unknown, population stable, endemic
	Lestidae	*Austrolestes colensonis* (White)	North, South and offshore Islands	Common and widespread, endemic

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[3] www.iucnredlist.org accessed 12th November 2016

[4] validity of species questioned (Amaya-Perilla, Marinov et al.2014, Marinov, Amaya-Perilla et al. 2016)

Auckland and Coromandel regions); *X. tuanuii* restricted to the Chatham Islands; *X. sinclairi* restricted to high altitude tarns in the mid Canterbury region. These species were originally described as separate species based on small differences in body size, colour, habitat, naiad behaviour and the shape of adult male appendages (Rowe 1987). Recent literature has called into question the validity of *X. sobrina* (Marinov, Amaya-Perilla et al. 2016) and *X. sinclairi* (Amaya-Perilla, Marinov et al. 2014) as individual species based on new geometric morphometric and molecular analysis. *X. sobrina* and *X. sinclairi* were grouped with *X. zealandica*, while *X. tuanuii* differed in both types of analysis and subsequent recommendations are that *Xanthocnemis* is represented by two species *X. zealandica* and *X. tuanuii* (Marinov, Amaya-Perilla et al. 2016). Since the Chatham Islands are outside the scope of this thesis, all occurrences of *Xanthocnemis* throughout this thesis will be considered to be *X. zealandica*.

This thesis focuses on the two most common and widespread species of damselfly *Austrolestes colensonis* and *Xanthocnemis zealandica* (Table 1.3). They are the only two damselfly species reported to be found in Otago, New Zealand (Rowe 1987), where this work was conducted. Both species were selected because they are easy to locate, abundant and widely distributed, are well described and taxonomically distinct, and are easy to collect and maintain in the lab (Hardersen and Wratten 1996). These two species also allow for the study of a model system of two closely related, cohabitating, predator species that potentially differ in their life history strategies. Both species are found in and around aquatic habitats that range from brackish waters near the ocean to small tarns in the Southern Alps (Rowe 1987). Crumpton (1979) reported that both species are generalist feeders, feeding on multiple different species of prey. While they appear to have slightly different diet preferences (eating roughly the same species, but in differing quantities), this is based on the stomach contents of populations from two separate ponds over two consecutive years. Some variation in prey may be possible due to their activity and feeding method, for example, *A. colensonis* is faster and more active and can therefore, capture prey which is in turn more active (Crumpton 1979).

The species descriptions below, unless otherwise stated are based on Rowe (1987).

Austrolestes colensonis

A. colensonis is the larger of the two species considered in this thesis, with adults growing to around 40-47 mm and naiads reach around 17-21 mm in body length before emerging as adults. Adult males are blue with black markings while females are pale yellow/green with dark green/black markings. Naiads are more elongated than *Xanthocnemis spp.* and are more active with fluid/streamlined movements, they are known to actively pursue prey and have a flight response to predators (Rowe 1985). The overwintering stage is as an egg, although Deacon (1979) reports late stage larval diapause also occurring in this species. Eggs may develop and hatch directly (in around

Table 1.3 Life history characteristics of *Austrolestes* and *Xanthocnemis* from Rowe (1987).

	Austrolestes colensonis	***Xanthocnemis zealandica***
Adult (Adult photos supplied by Edward Ramirez)		
Naiad		
Status	Endemic species, genus found throughout Australasia	Endemic genus
Habitat preference	Lentic freshwater habitats with rushes or sedges	Ubiquitous, freshwater
Egg development	Direct (no diapause), 3-4 weeks or diapause, 4+ months	Direct (no diapause), 3-4 weeks
Overwinter as	Egg[5]	Late stage naiad
Naiad size	17-21 mm	15-18 mm
Time spent as naiad	Auckland: 5 months	Most of NZ: 2 years
	South Island high altitude: > 1 year	Foothills of Southern Alps: 3 years
Swimming behaviour	"Active and mobile"	"Slow and laborious"
Adult flight season	October to June	August to March
Adult size	40–47 mm	30–35 mm

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[5] Deacon (1979) suggests additional naiad diapause

20 days) or development may be halted (if diapause occurs) prior to hatching until suitable conditions return in spring. No literature was identified that reported the number of naiad instars for *A. colensonis.* Studies such as Deacon (1979) and Crumpton (1979) grouped instars together, identifying only the penultimate and final instars. *A. colensonis* spends between five months (in Auckland in the North Island) to over one year (at high altitude, South Island sites) as a naiad.

Xanthocnemis zealandica

The adult males of *X. zealandica* are brilliant red in colour with black markings, and while most females are a light yellowish brown with black markings, a small portion (around 16% of the population) are similar in colour to the males. Adults measure around 30-35 mm and naiads 15-18 mm in body length. All eggs develop directly, in around 21 days, with overwintering in *X. zealandica* occurring as naiads. Naiads of *X. zealandica* have a sit and wait strategy for feeding (Crumpton 1979). Scott (1971) reported 13 instars for *X. zealandica,* while Rowe (1985) reported between 12 and 14 instars, which can be extended by two to three instars when stressed, such as when surviving periods of desiccation by burying themselves in mud. *X. zealandica* lives as a naiad for one to three years (Crumpton 1979, Rowe 1985, Rowe 1987).

1.5 Terminology

There are numerous instances in the literature where different words are used to mean the same thing (or the same word to have different meanings). To avoid confusion, there are a few words, or terms that have been specifically selected for use in this thesis and the reasons for this are discussed here.

As there are only two species considered in this thesis, from differing genera, from here on, each species will be referred to by genus only i.e. *Austrolestes* and *Xanthocnemis*.

The use of the terms larva, nymph or naiad for juvenile insect stages has been hotly contested in the literature in recent years. While all three are used interchangeably in Odonate literature, the words themselves do not actually mean the same thing. Bybee and colleagues (2015) attempted to clarify the use of these terms in literature and suggested a universal approach to terminology, however it met with resistance from the scientific community (Muzon and Lozano 2016, Redei and Stys 2016, Sahlen, Suhling et al. 2016). The term larva is commonly used in key texts (e.g. Rowe 1987, Corbet 1999) and recent literature (Dayaram, Galatowitsch et al. 2014, Chavez, Mabry et al. 2015, Brown and Robinson 2016, Cantania and McCauley 2016, Duong and McCauley 2016) and is the preferred term for many researchers. Corbet (2002) dismissed the use of any term other than larva as not having any contemporary merit and Muzon and Lozano (2016) suggested it should be used as it was most accepted in the literature. However, a larva is visually different from the adult form and precedes a pupa stage (Gordh and Headrick 2011), which Odonata lack. Like the term larva, nymph is common in recent literature (for example: Pokhrel and Dubey 2012, Busse, Genet et al. 2013, Busse and Hornschemeyer 2013, Faithpraise, Idung et al. 2014, Younes, El-Sherif et al. 2015). However, nymph is used to describe immature insects that resemble adults in shape and appearance, and live in the same habitat as the adult form but lack fully formed wings and genitalia (Gordh and Headrick 2011, Bybee, Hansen et al. 2015). Naiad was originally proposed by Comstock (1918) to differentiate between the aquatic stage of Ephemeroptera, Odonata and Plecoptera (which exhibit gills that are lost once metamorphosis to adulthood is complete) to that of terrestrial nymphs (such as those of Hemiptera and Orthoptera) (Gordh and Headrick 2011). And while the term is used in recent literature (for example Collier, Nair et al. 2010, Schmit, Martens et al. 2012, Din, Zia et al. 2013, Buckland-Nicks, Hiller et al. 2014, Weterings, Umponstira et al. 2015), it is certainly not widely accepted (Bybee, Hansen et al. 2015). As the definition for naiad is quite specific and refers to the juvenile life stage of Odonata, it will be used throughout this thesis instead of larva or nymph.

Odonates are hemimetabolous, and as such, do not undergo true complete metamorphosis. However, metamorphosis is an accepted term in the literature when referring to the transformation between naiad and adult forms in aquatic insects (e.g. Truman and Riddiford 1999, Nijhout and Callier 2015, Redei and Stys 2016). Metamorphosis and adult emergence are used interchangeably throughout this thesis.

Dragonfly is commonly used in older literature and by the general public to refer to all members of the order Odonata (Johnson 1991). In this thesis, where the term dragonfly is used, it pertains only to those species in the suborder Epiprocta, while damselfly is used for species in the suborder Zygoptera. When referring to all members of the order simultaneously, Odonata or Odonates is used.

1.6 Thesis structure

The purpose of this thesis is to investigate differences in the life history strategy, distribution and behaviour of two cohabitating species of damselflies found in Otago, New Zealand. Chapters two to five have been written as individual stand alone chapters prepared and intended for submission to different journals. Therefore, similar content may be covered by multiple chapters. An indication of the progress on each chapter manuscript at point of submission can be found in Appendix A, along with a list of conference attendances, including abstracts, where work based on (or is an extension of) this thesis has been presented and other forms of publication/presentation.

Chapter 2 - Life history strategies

Chapter two investigates the life histories strategies of *Austrolestes* and *Xanthocnemis*. A long term (two year) field study was conducted looking at changes to naiad populations along an altitudinal gradient over time to determine if any species-specific patterns could be identified. It is predicted that naiads will live longer at higher altitudes and average naiad body length will increase through the warmest months and be followed by a drop (signifying metamorphosis occurring); patterns should differ between species. Additionally, *Xanthocnemis* is expected to be found at higher altitudes more frequently than *Austrolestes*.

Chapter 3 – Distribution and habitat preferences

Chapter three investigates the distribution of damselflies throughout the South Island (and additionally Stewart and Codfish Islands), and investigates any species-specific habitat preferences. This chapter looks to build on species differences over an altitudinal gradient identified in chapter two, and investigates the likelihood of this pattern being part of a larger scale. It is predicted that distribution is influenced by altitude, vegetation type and habitat type (lentic or lotic).

Chapter 4 - Movement behaviour and starvation tolerance

Differences in activity and metabolic rates are routinely linked to fast and slow life history extremes (as previously discussed). Chapter four is a laboratory based study investigating the differences in the amount of movement exhibited by both species as they starve. It also investigates the length of time each species is able to survive starvation. It is predicted that *Austrolestes* will be more active and movement will increase as starvation occurs, while *Xanthocnemis* will be more sedentary and will decrease its movements as starvation occurs. Additionally, *Xanthocnemis* will have a higher starvation tolerance than *Austrolestes.*

Chapter 5 - Diapause

Literature (Deacon 1979, Rowe 1987) suggests both *Austrolestes* and *Xanthocnemis* use diapause as their method for overwintering as naiads. However, the results of the investigation into the life history of both species (in chapter two) suggest this might not be the case. Therefore, chapter five is a laboratory based study investigating the plausibility of winter diapause occurring in naiads of both species. It is predicted that diapause does not occur in these species and metamorphosis will occur in 'diapausing' naiads when placed in warmer temperatures under a winter light regime.

Chapter 6 - General conclusions

The final chapter summarises the key findings of each of the data chapters and provides an overall general comparison between the life histories of *Austrolestes* and *Xanthocnemis,* and discusses the likelihood of these species conforming to the fast/slow life history dichotomy. Suggestions for future directions that Odonata research (both in New Zealand and overseas) could take are made (with particular focus on the two species studied here).

Chapter 2

Life history strategies

2.1 Introduction

An organism's life history is characterised by factors such as development rate, life cycle, reproductive success, life span, dispersal (Stearns 1976, Orians and Wittenberger 1991, Verberk, Siepel et al. 2008). The fitness consequences of any particular life history trait can vary across ecological time and space, with no one life history strategy being universally successful (Charlesworth 1990, Verberk, Siepel et al. 2008, Lancaster and Downes 2013). Life history strategies are usually described as being one extreme or another, but in reality, individuals tend to fall along a continuum between the two extremes; for example, the fast to slow life history strategy continuum (Promislow and Harvey 1990, Johansson 2000, Haag 2013). Species exhibiting fast life history strategies tend to be more active and maintain higher metabolisms, both of which require increased food consumption and result in larger body size (Werner and Anholt 1993, Careau, Bininda-Emonds et al. 2009, Stoffels 2015). Species with slow life history strategies exhibit cryptic behaviours that minimise energy expenditure. Their reduced feeding and low metabolic rates result in smaller body size, and often a longer life-span (Careau, Bininda-Emonds et al. 2009, Humphries and McCann 2014, Stoffels 2015).

Ambient temperature can influence development rate, particularly for ectotherms (including many invertebrates) which have a limited ability to regulate their internal body temperature (Bale and Hayward 2010). For example, in insects, growth rate increases with temperature at close to a linear rate (Gilbert and Raworth 1996) and lower temperatures are associated with slower growth rate but larger body size at maturity (Angilletta, Steury et al. 2004). Because temperature tends to vary predictably along altitudinal and latitudinal gradients, with lower temperatures being associated with higher altitudes and latitudes (a decrease of approximately 6°C per kilometre of increasing altitude (Barry 2008)), geographic species distribution likely correlates with variation in ectotherm species' life history traits, such as growth rate or body size (Atkinson and Sibly 1997, Chown and Gaston 1999, Chown and Klok 2003, Ashton 2004).

The Odonates are a model group of organisms with which to compare geographic species distribution with differences in life history traits. Odonates are hemimetabolous; they undergo incomplete metamorphosis, transitioning from an aquatic juvenile (naiad) directly to a terrestrial adult without a pupal stage (Figure 1.1) (Corbet 1999). Odonates spend most of their lives as naiads. Adults are usually only seen during the summer months when they mate and lay eggs on plants in streams or standing water, and survive an average of four to six weeks (Corbet 1999). In warmer climates, Odonates are predominantly univoltine (a generation takes one year to mature), whereas in colder climates they are more often semivoltine (each generation takes longer than one year to reach adulthood) (Corbet 1980, Lancaster and Downes 2013). In regions where species have semivoltine developmental strategies, multiple generations of naiad may be present at any one time. Each cohort (i.e. a single generation of same-age naiads), can be identified by distinct size differences (i.e., first instar naiads are significantly smaller than second instar, etc.) (Hale, Margham et al. 1995).

Odonates that live in temperate climates are exposed to variable or extreme conditions over the winter months that can inhibit growth, reproduction or metabolic functions (Leather, Walters et al. 1993). Odonate naiads (or eggs) may avoid the effects of those conditions by undergoing diapause (Corbet 1980, Corbet 1999), a period of arrested growth and development initiated prior to the onset of adverse conditions (Hale, Margham et al. 1995, Allaby 1999, Hahn and Denlinger 2007, Lancaster and Downes 2013). It is important to note this is a genetically programmed response, controlled by environmental, hormonal, and molecular regulators, that cannot be broken by the brief return of favourable conditions (e.g. warmer days) (Denlinger 2002, Hahn and Denlinger 2007, Lancaster and Downes 2013), instead requiring a series of favourable conditions to occur (Tauber and Tauber 1981, Denlinger 1986, Denlinger 2002, Kostal 2006). An alternative strategy of avoiding harsh conditions is to undergo quiescence, also a period of arrested growth initiated at the onset of adverse conditions (such as cool temperatures), but one that ends when those conditions cease (Denlinger 1986, Tauber, Tauber et al. 1986, Kostal 2006, Hahn and Denlinger 2007). Diapause is one way insects can establish synchronicity in growth or reproductive development (Scarsbrook 2000, Bel-Venner, Mondy et al. 2009). This is important where many Odonate species coexist and temporal separation of key life history stages (e.g. emergence) can be timed to avoid other species and reduce competition for resources (Grant and Mackay 1969, Benke and Benke 1975, Johannsson 1978, Crowley and Johnson 1982).

Unlike the Northern Hemisphere where large assemblages of many Odonate species coexist (for examples refer to Kormondy and Gower 1965, Wissinger 1988, Wissinger 1988, Johansson 2000, McCauley 2008), New Zealand has a very low Odonate diversity, particularly with respect to damselflies (Odonata: Zygoptera). Only two species of damselfly (*Austrolestes* and *Xanthocnemis*) are commonly found throughout the entire country (Rowe 1987). The majority of what is known about the life histories of these two species is from studies conducted in inland Canterbury in the late 1970s to mid-1980s (see Crumpton 1975, Crumpton 1977, Crumpton 1978, Deacon 1978, Crumpton 1979, Rowe 1981, Rowe and Winterbourn 1981, Rowe 1985), aided by unpublished student research (from Canterbury University) and observations/field notes from Rowe (1987). Life history characteristics as provided by Rowe (1987) have been collated in Table 1.3. *Austrolestes* is the larger of the two species. Naiads of *Austrolestes* are good swimmers that have a conspicuous flight response to predators (that avoids invertebrate predators, but presumably would expose them to visual-hunting predatory fish) and actively hunt their prey (Rowe 1987). Life cycles for this species range from five months in Auckland (in the northern part of the country) to 12-24 months further south, with overwintering completed as either an egg (Rowe 1987) or a naiad (Deacon 1979). These characteristics are synonymous with a fast life history strategy. *Xanthocnemis* on the other hand are smaller, and are slow swimmers with laborious movements. *Xanthocnemis* naiads exhibit a cryptic response to predators (i.e. freeze in place when a predator is near), and employ a sit-and-wait strategy for prey capture. *Xanthocnemis* live for two to three years, and overwinter as a naiad (Rowe 1987). These characteristics represent a slow life history strategy for this species. While some life history characteristics of these two species have been previously described (for example see Crumpton 1975, Crumpton 1977, Crumpton 1978, Deacon 1978, Crumpton 1979, Rowe 1981, Rowe and Winterbourn 1981, Rowe 1985), no literature has examined how life history strategies of these species vary across geographic clines.

The purpose of this chapter is to investigate the life histories of two endemic New Zealand dragonflies, and to determine if these species exhibit consistently faster or slower life history strategies across environmental gradients. Since these two sympatric species occupy similar prey and environmental niches (Rowe 1987), having differing life history strategies may allow these species to successfully coexist. Six populations of naiads, at different altitudes throughout the Otago region of southern New Zealand, were monitored periodically for two years. The following hypotheses were tested:

1) The number of cohorts present at a site (gauged through monitoring naiad body sizes present) can be used as an indication of uni- or semi-voltinism. Based on previous observations, it is predicted *Austrolestes* to have a single cohort present, and *Xanthocnemis* to have multiple cohorts present at low altitudes. At higher altitudes (with cooler climates), it is predicted that the length of the life cycles of these aquatic ectotherms should increase, and therefore, the number of cohorts present per species should increase as well.

2) Growth rates of insects are linked to temperature (Gilbert and Raworth 1996). It is predicted that as temperatures increase, so too will the growth of naiads followed by adult emergence over a short period of time (Huey and Kingsolver 1989, Angilletta, Steury et al. 2004). This should be represented by increasing average body length during the spring and summer months (September to January) followed by a sharp drop in average body length after peak warm periods in February.

3) *Xanthocnemis* exhibits cryptic behaviours and has a longer life cycle than *Austrolestes* (which is highly active). It is predicted that this difference in life history strategy will result in a greater

number of *Xanthocnemis* present at higher altitudes, where temperature and primary productivity is generally reduced.

2.2 Methods

2.2.1 Site selection

Six sites were chosen throughout the Otago region (Figure 2.1) over an altitude gradient of 0 to 1000 metres above sea level (m.a.s.l) (Barry 2008). Potential sites at a variety of different altitudes were located using a topographical map of New Zealand (www.topomaps.co.nz). Sites were then investigated to assess their suitability. To reduce the amount of variation between sites, each site was required to contain a permanent water body with little or no water movement. Descriptions of each site are given in Table 2.1. The following three-letter codes were assigned to each site (identified in Figure 2.1), which they shall henceforth be referred to as: SCW - Sinclair Wetlands; SUT – Sutton; SUL - Sullivan's Dam; ODR - Old Dunstan Road; CPD - Coalpit Dam; MKS - McKeller Saddle and will be reported in order of altitude from lowest to highest.

2.2.2 Frequency of site visitation

Since environmental conditions change from year to year, to measure changes within naiad populations, sites were repeatedly visited between September 2012 and December 2014. Due to the isolated nature of some of the sites, the number and frequency of visits differed, from every two weeks to once every three months. Because of access issues at some sites (e.g. snow/ice cover, mammal pest control, lambing and duck shooting seasons), sites were not measured between July and October. Access to the SCW site was by walking over floating rafts of Raupō (*Typha orientalis*), but due to the degradation of the Raupō rafts, monitoring of the SCW site ceased eight months earlier than on the remaining sites.

2.2.3 Data collection

To determine morphological differences between naiads of both species, individuals were collected from overhanging and aquatic vegetation along a 5 m section along the water's edge of each site using an aquarium fish net with an opening of 125 x 150 mm and a depth of 120 mm. Once collected, damselfly naiads were identified to species and measured from the tip of the head to the end of the abdomen using Vernier callipers to the nearest 0.5 mm (similar to methods used in Galatowitsch (2014)). Measurement of body length is not as accurate as head width (Deacon 1979) because the body can be flattened inadvertently during measurement, adding some more variation to the values obtained. However, measuring body length has the advantage of being easily and quickly conducted in the field, allowing for individuals to be released unharmed after

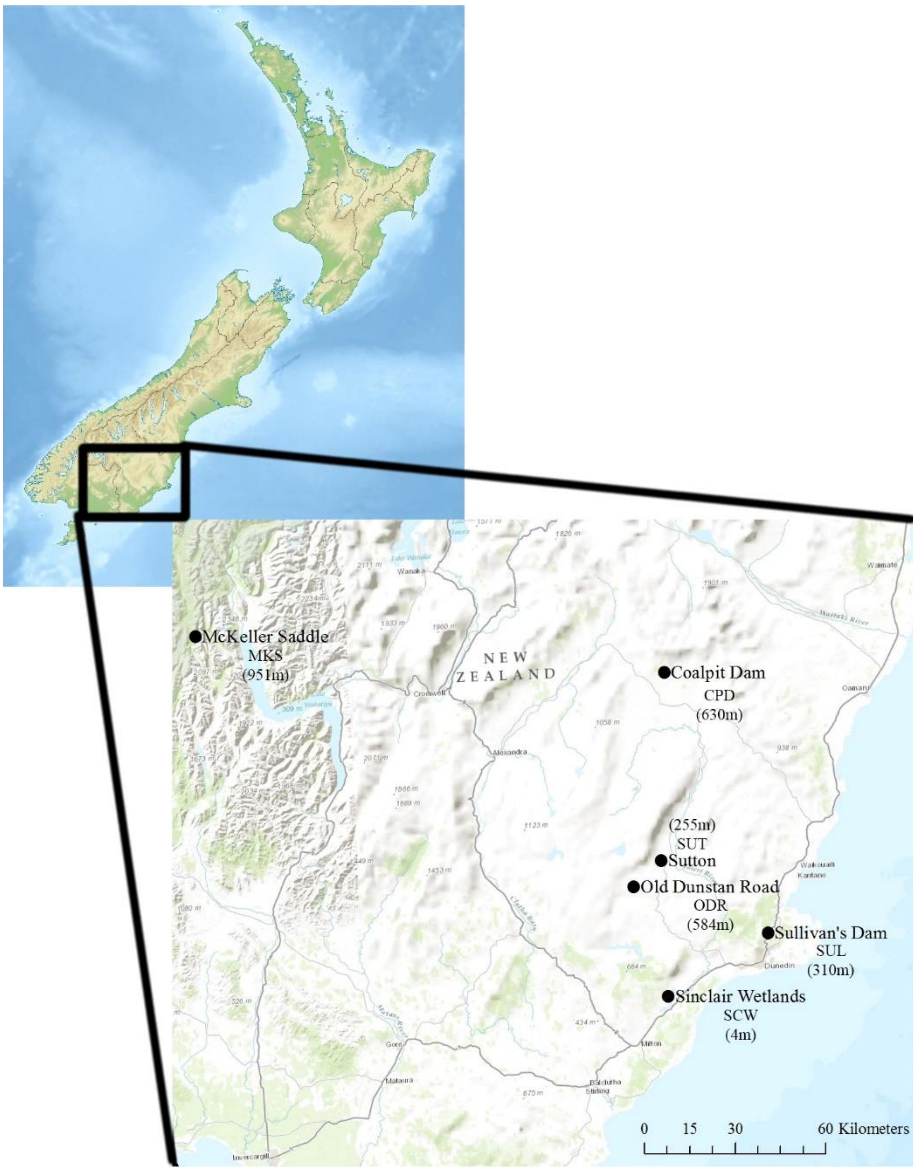

Figure 2.1 Locations of the six field sites within Otago, New Zealand.

Table 2.1 List of field sites and their general descriptions.

Site	Altitude (m)	GPS	Approx size (m^2)[6]	Image	Site description
SCW	4	45°58'59"S 170°5'13"E	81000		Larger pond in a series of connecting wetlands Public access limited High avian disturbance
SUT	255	45°34′46″S 170°4′41″E	6100		Small pond Stock access (cattle/sheep) Private farmland Highly exposed Restricted access during lambing season
SUL	310	45°48'21"S 170°31'18"E	58000		Town (back up) water reservoir. Public access (fishing). Surrounded by native bush.
ODR	584	45°39'24"S 169°57'27"E	1800		Small pond next to road Stock access (cattle/sheep) Farmland Highly exposed Restricted access during lambing season
CPD	630	45°1'13"S 170°7'4"E	36000		Town water reservoir Public access (fishing) Surrounded by pines Restricted access due to shooting seasons (mammal pests and ducks)
MKS	951	44°50'52"S 168°9'48"E	1200		Small tarn next to back country walking track Above tree line Conservation land Highly exposed Restricted access in winter due to snow

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[6] Size estimations are approximations of area from topographical maps; actual size may vary from this value. As all areas were approximated the same way, the size of each site relative to each other is expected to be true.

measurement. To reduce operator-induced variation as much as possible, all measurements were carried out by a single person. Caudal lamellae were excluded from body length measurements as these can break off. Handling of larvae was kept to a minimum and done with care.

To establish the proportion of each species within the community, naiad collection continued until 50 of one species had been captured. When conditions did not allow collecting 50 individuals of any one species, collection was halted after two hours.

HOBO Pendant® Temperature/Light 64K Data Loggers (www.onsetcomp.com) were placed at each site to record water temperature at hourly intervals over the entire duration of the study. Data are missing for several time periods (between one and three months) at two different sites due to loss of one logger and cessation of recording between downloads (for unknown reasons). However, all sites had a minimum of one year of continual temperature data; therefore, this minor data loss was considered to be inconsequential for the purposes of this study.

2.2.4 Visual analysis

To identify if cohorts were present, visual analysis of body length measurements for each site visit across time was conducted. Cohorts should present as groupings of individuals of the same or similar size followed by voids without naiads present. Species were considered separately. To establish if emergence patterns are linked to temperature, changes in mean body length across time were graphed to establish if drops in mean size were visually detectable within a population. Comparisons were made with temperature graphs. To determine which species was more prevalent at each site, the percentage of individuals of each species measured from the total of individuals measured at each site visit was graphed and differences between sites was visually examined.

2.3 Results

Naiad size distributions varied between site, year and species (Figures 2.2a and 2.2b). Single cohorts could not be determined for either species as there were times of the year when naiads of all sizes were present. For *Xanthocnemis*, voids appeared between two different size groups around the start of summer (December) for SCW, SUT, SUL and ODR (Figure 2.2b), although these voids were not consistent across all sites or years. For example, three of the sites (SCW, SUT and ODR) showed a more pronounced void in the 2012/13 season than in the 2013/14 season. Voids culminated in the disappearance of the largest individuals during mid to late summer (January - February) (Figure 2.2b SCW, SUT, SUL and ODR), although adults were still seen emerging at these sites in March

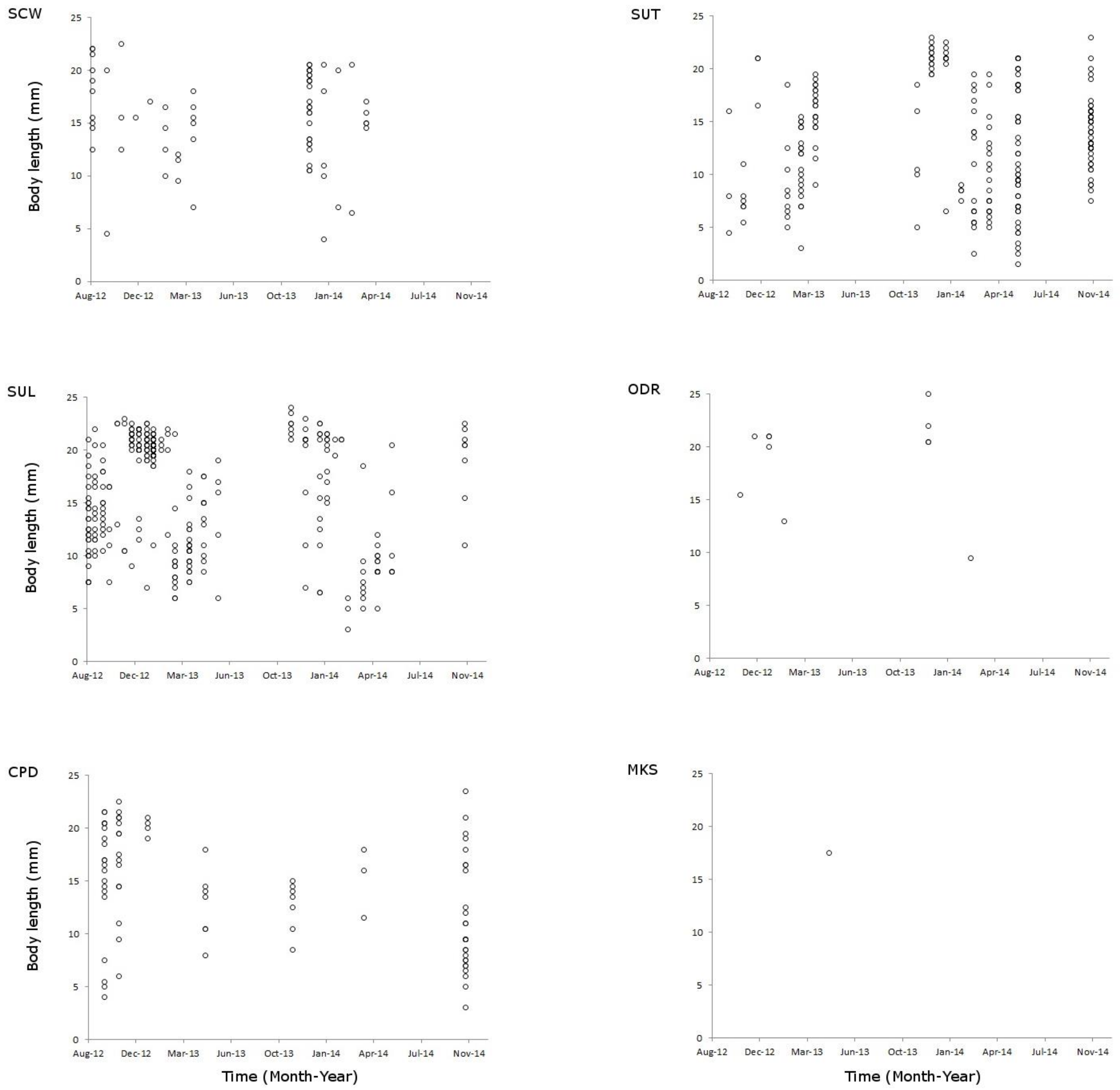


Figure 2.2a Body length (mm) of every individual *Austrolestes* naiad measured at every visit to each site for the duration of the study (two years). Sites are ordered L-R, top-bottom from lowest altitude (m.a.s.l) to highest. Sampling did not occur during cooler months (July to Oct).

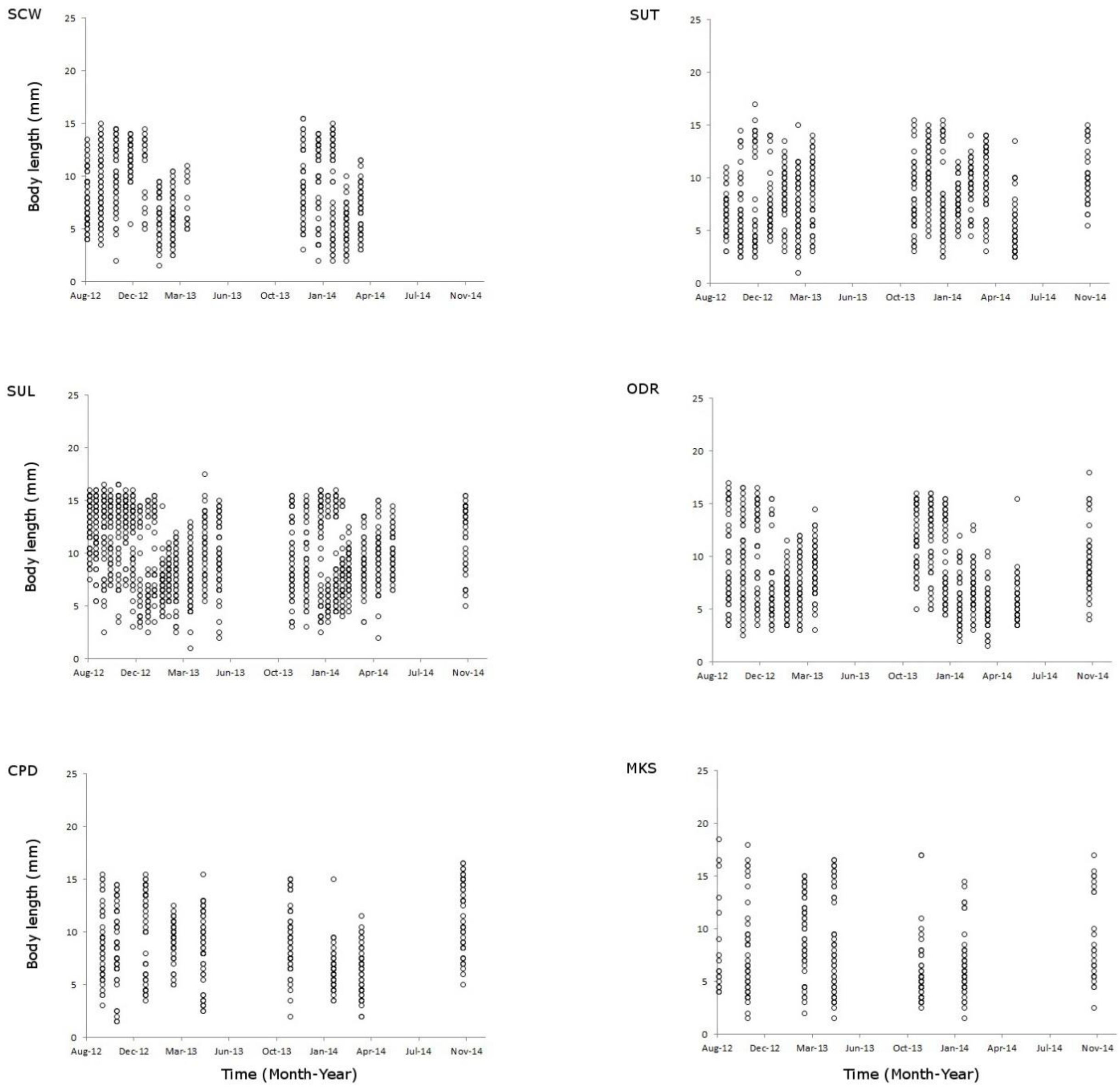


Figure 2.2b Body length (mm) of every individual *Xanthocnemis* naiad measured at every visit to each site for the duration of the study (two years). Sites are ordered L-R, top-bottom from lowest altitude (m.a.s.l) to highest. Sampling did not occur during cooler months (July to Oct).

(personal observation). *Austrolestes* naiads ready to metamorphose were generally larger, with a maximum size of 25 mm compared with 18.5 mm for *Xanthocnemis*.

In 2013, there was a single peak in temperatures during February, while in 2014, there was an earlier peak in December, followed by a cooler month (January) and a second peak in February (Figure 2.3). Temperature did not decrease with increasing altitude, the highest site (MKS) did have the lowest temperatures overall, however, the lowest site (SCW) did not have the highest.
Xanthocnemis showed steady increase in growth over the spring and summer months at the lowest site (SCW) during 2012-13, but did not show any other steady patterns of growth at any other site or year (Figure 2.4). *Austrolestes* did not show any patterns of steady growth at any site during either year (Figure 2.4) Large drops in mean body length were seen but varied in month, site and year for both species (Figure 2.4). Mean body length increased over the winter months between site visits for both species over both years, although this varied between sites (Figure 2.4).

There were more *Xanthocnemis* than *Austrolestes* across all six sites on all but three visits (once at SUL, twice at SUT) (Figure 2.5). The percentage of *Austrolestes* found at each site was greater at lower altitude sites (SCW, SUT and SUL) than higher sites (ODR, CPD and MKS). Only one individual *Austrolestes* naiad was located on one visit at MKS (no *Austrolestes* adults were ever observed during any visit). The percentage of *Austrolestes* observed during any visit never reached more than 30% for any of the sites above 500 m a.s.l. (CPD, MKS and ODR) (Figure 2.5).

2.4 Discussion

The purpose of this chapter was to investigate and compare the life histories of two species of damselfly: *Austrolestes* and *Xanthocnemis,* from sites throughout the Otago region of the South Island of New Zealand that varied in altitude, to determine the extent to which life history strategy correlated with geography. To understand how life history is affected by temperature, three hypotheses were investigated:

1) If *Austrolestes* is univoltine, then only a single cohort should be present, and if *Xanthocnemis* is semi-voltine, then multiple cohorts would be present. The current data is indeterminant for both species and therefore, the voltinism of either species in Otago cannot be confirmed.

2) If growth rates of insects are linked to temperature, then naiad size and adult emergence will increase with temperature. The data shows that patterns varied between species and years over all sites and showed no consistency. Temperature did not decrease with an increase in altitude. This is important because factors other than temperature may be influencing altitudinal gradients. This is discussed further in chapter three.

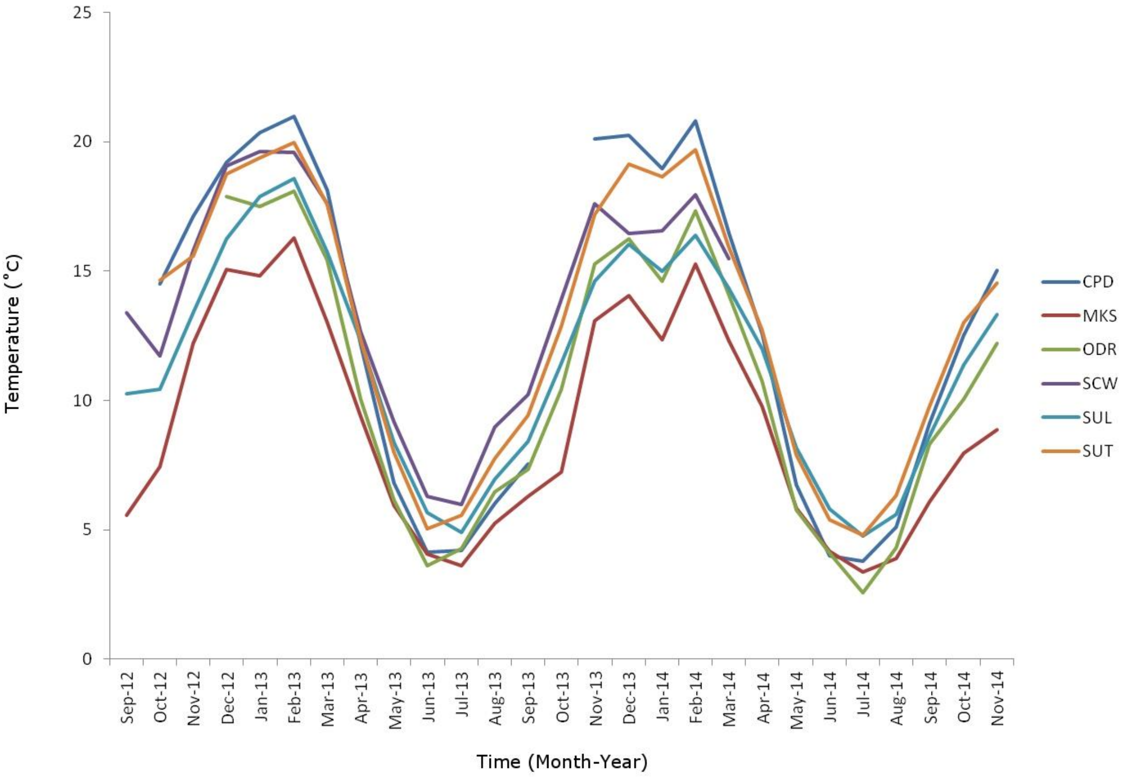


Figure 2.3 Seasonal variation in average monthly temperature (˚C) across all six sites for the duration of the two year study period.

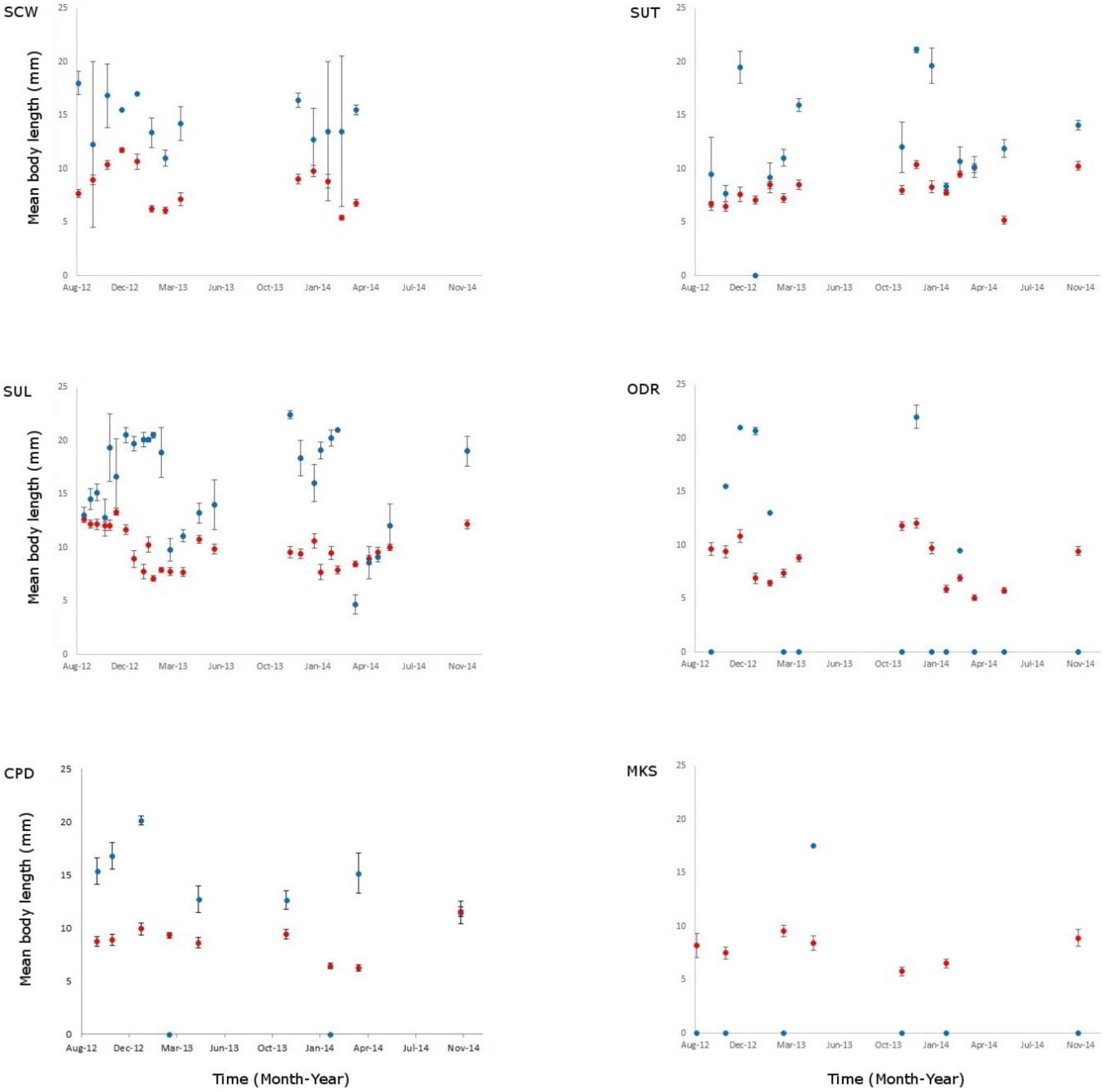


Figure 2.4 Variation in mean body length (mm) for *Austrolestes* (blue dots) and *Xanthocnemis* (red dots) naiads measured at every visit to each site for the duration of the study (two years). Sites are ordered L-R, top-bottom from lowest altitude (m.a.s.l) to highest. Error bars ± 1 S.E.

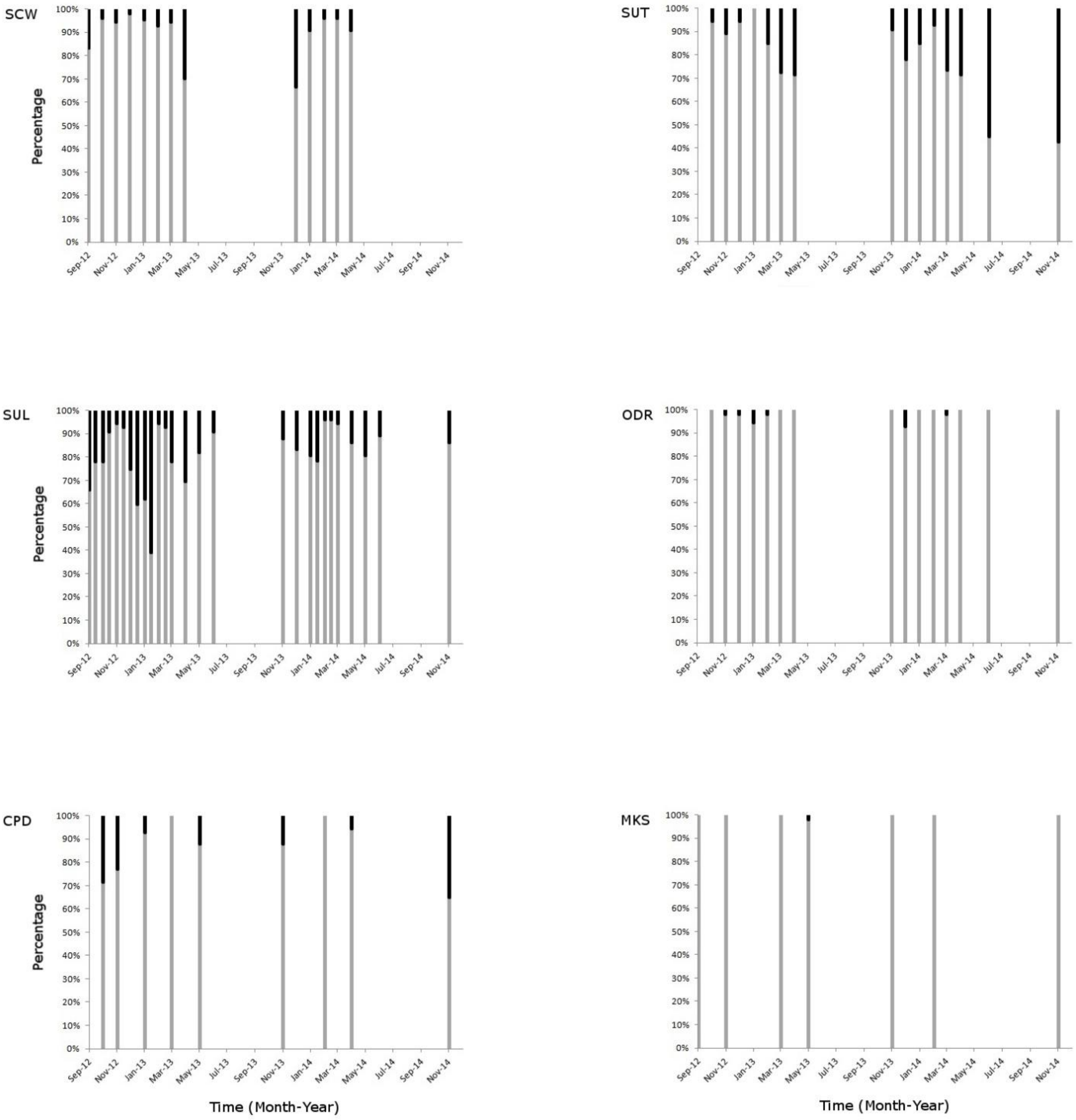


Figure 2.5 Percentage of *Austrolestes* (black) and *Xanthocnemis* (grey) naiads from the total number of naiads measured at every visit to each site for the duration of the study (two years). Sites are ordered L-R, top-bottom from lowest altitude (m.a.s.l) to highest.

3) If the cryptic behaviour and longer life cycle of *Xanthocnemis* (compared to the highly active *Austrolestes*) make them better adapted to cooler temperatures, then they should be present at greater numbers at higher altitudes. The data shows that the percentage of *Austrolestes* present at each site decreased with increasing altitude. This is significant because it indicates that higher altitude sites (with lower productivity) do not support the life history strategy employed by *Austrolestes*.

The number of cohorts present at any one time would have given an indication of how many years were spent as a naiad (which was expected to be influenced by altitude/temperature). The current data set precludes the identification of clearly separate cohorts. This is likely to be due to the continual input of new individuals over a long reproductive season, and as a result, multiple cohorts are likely to be present that cannot be distinguished from one another. Partial voids that appeared in some *Xanthocnemis* populations could not be attributed to cohorts with any certainty because they developed part way through a growth season (i.e. were not present from the time of hatching) and could be due to predation or cannibalism (which both species do; personal observation).

Naiads of both species were present across the entire year at all sites (except at the highest altitude for *Austrolestes*), although naiad sizes for both species were highly variable throughout the course of a year, and differed between years. The presence of naiads during winter for *Austrolestes* does indicate that at least some of the individuals in any of the populations studied were semivoltine. *Austrolestes* has been reported as being semivoltine only at "high altitude South Island" (i.e. from Canterbury sites) (Rowe, 1987). The cooler Otago climate possibly increases the life-span of *Austrolestes*, even at sea level, making a semi-voltine life cycle more prevalent. Other damselflies (e.g. *Coengarion resolutum* from Canada) have been recorded as having a mixture of univoltine and semivoltine individuals across temperature gradients (Krishnaraj and Pritchard 1995). *Austrolestes* naiads found throughout Otago were larger than previously reported (Rowe 1987). However, previously reported measurements for this species were taken from more northern populations than those reported here (Rowe 1987). Individuals within a species often (although not always) grow larger in cooler climates (Atkinson and Sibly 1997, Chown and Gaston 1999, Chown and Klok 2003), such as those at higher latitudes and altitudes. Generalisations across a species should therefore, be based on information from individuals covering the entire species' range, something that has been previously lacking for Odonates.

A mix of uni- and semivoltine individuals within a population, as well as having naiads of all sizes present throughout the year, suggests that the life histories of *Austrolestes* and *Xanthocnemis* are more closely aligned with those of other invertebrate species endemic to New Zealand as opposed to their Northern Hemisphere counterparts. Insects endemic to New Zealand have been reported to have poorly synchronised, flexible, generalist life histories with long hatching and emergence periods (Winterbourn 1978, Towns 1981, Winterbourn, Rounick et al. 1981, Towns 1983). For example, the mayfly *Austroclima jollyae* along with a number of species of *Deleatidium,* show constant recruitment of early instars and long emergence periods with little evidence of temporal segregation while maintaining a large amount of habitat and life history overlap (Towns 1983). This has been linked to differences in climate. Insects living in New Zealand's relatively mild maritime climate do not incur the same selection pressures that occur in continental Northern Hemisphere climates (such as North America and Europe) which are more seasonally extreme with greater daily variability but also more seasonally predictable (Roberts 1978, Leather, Walters et al. 1993).

Changes in the size of naiads through the winter season was not expected. Rowe (1987) and Deacon (1979) both stressed that these species diapause over winter: *Austrolestes* as an egg (Rowe 1987) or naiad (Deacon 1979), and *Xanthocnemis* as a late stage naiad (Rowe 1987). During diapause, development is halted (Hale, Margham et al. 1995, Allaby 1999, Hahn and Denlinger 2007, Lancaster and Downes 2013), therefore, growth was not expected to occur over this period. Growth was estimated as the increase in mean body size among those naiads collected at different times of the year. In these populations, for both species, increase in body size was slow during the winter. Therefore, it is more likely these naiads are undergoing a quiescent phase, rather than diapause (see chapter five).

In progressively cooler environments (i.e. with increasing altitudes) the encounter rate and proportion of *Austrolestes* decreased. It is unclear if a population of *Austrolestes* is established at MKS, adults were never witnessed at that altitude, but were seen (as well as naiads) in both valleys either side of the saddle (personal observation). Therefore, it is possible that occasionally an adult female is caught in air currents and transported to higher altitudes where she lays eggs without an established breeding population existing. It is likely that productivity limitations due to cooler temperatures at high altitudes restrict the range of *Austrolestes* (McCoy 1990). Fast life histories require more productive environments to support more active life styles, increased growth rate and larger body sizes, while slow life histories can survive in less productive habitats because their life styles minimise energy consumption (Promislow and Harvey 1990, Werner and Anholt 1993, Johansson 2000, Careau, Bininda-Emonds et al. 2009, Haag 2013, Humphries and McCann 2014, Stoffels 2015). Therefore, *Austrolestes* fits with a fast life history strategy and *Xanthocnemis* a slow life history strategy. Differences in distribution between the two species with regards to altitude is discussed further in chapter three.

Chapter 3

Distribution and habitat preference

3.1 Introduction

Species have different geographical ranges depending on their tolerances to a set of environmental factors, including (but not limited to) climate, food abundance, predation, and intra- and inter-specific competition (Lawton, MacGarvin et al. 1987). Temperature is repeatedly reported as the dominant factor influencing distribution of poikiliotherms, i.e., organisms that cannot precisely regulate their own body temperature by direct metabolic mechanisms (Ward and Stanford 1982, Cossins and Bowler 1987, Bale, Masters et al. 2002). Still, other factors such as altitude and latitude (Ward and Stanford 1982, Bale, Masters et al. 2002), though they might correlate with temperature (e.g., increase in altitude is associated with a decrease in air temperature of approximately 6˚C per kilometre (Barry 2008)), can also correspond to changes in species diversity and habitat productivity (Rahbek 1995). Understanding how abiotic factors affect species distribution provides insights into how organisms respond (or adapt) to changes within their environment (e.g. climate change, pollution).

Differences in life history strategy, in combination with adaptations to changing conditions across geographic ranges, are also expected to influence species distribution. Variations in life history strategies lie on a continuum that is usually described as being fast to slow (Promislow and Harvey 1990, Johansson 2000, Haag 2013). Species at the fast end of the scale are more active, and have higher metabolic and growth rates (Johansson 2000, Johansson and Suhling 2004, McCauley 2008, Careau, Bininda-Emonds et al. 2009, Stoffels 2015). Species with fast life histories, then, require productive habitats, often ephemeral and lacking predators (for example, shallow ponds that dry in late summer for aquatic insects) to be successful (Wissinger, Whiteman et al. 1999, Johansson 2000, Johansson and Suhling 2004, McCauley 2008, Galatowitsch and McIntosh 2016). On the other hand, slow species have much longer life cycles owing to slower metabolisms and growth rates (Johansson 2000, Careau, Bininda-Emonds et al. 2009, Stoffels 2015). These species are unable to complete their life cycle before ephemeral habitats change (e.g., ponds dry) and are therefore restricted to habitats that are permanent (Johansson 2000, McCauley 2008).

Changes to the environment will likely lead to changes in species development and distribution (Porter, Parry et al. 1991), but changes can only be detected if there is a starting reference with which to compare, and unfortunately, long-term monitoring data are lacking worldwide (Smol and

Douglas 2007). Where good historic data are available, climate change has been shown to affect the timing of life cycles (Parmesan and Yohe 2003, Root, MacMynowski et al. 2005, Thackeray, Sparks et al. 2010) and distributions (Parmesan, Ryrholm et al. 1999, Parmesan and Yohe 2003, Hickling, Roy et al. 2005, Hickling, Roy et al. 2006, Chen, Hill et al. 2011, VanDerWal, Murphy et al. 2013) of many species. Chen et. al. (2011) reported mean range shifts of 17.6 km/decade in latitude towards the poles and 12.2 m/decade increase in altitude in their meta-analysis of multiple taxonomic groups, which they attributed to changes in global temperature increase. Poleward shifts have specifically been recorded for a group of aquatic invertebrates, the Odonates, in the United Kingdom (Hickling, Roy et al. 2005), Japan (Aoki 1997), and parts of Europe (Ott 2001, Flenner and Sahlen 2008, Flenner, Richter et al. 2010). To date, there is little historic data on the distribution of Odonates in the Southern Hemisphere.

Rowe (1987) created distribution maps of all Odonate species in New Zealand from historical museum collections (prior to 1976), private collections and a nationwide survey conducted in 1980, details about which, were not provided. Distributions of the two damselflies *Austrolestes* and *Xanthocnemis* have not been updated for over 30 years. Crumpton (1977) reported *Austrolestes* being found at sites in the Canterbury region up to 610m, and *Xanthocnemis* up to 924m, but did not investigate higher altitudes for the presence of either species. In fact, no studies have specifically investigated habitat preferences for either species and anecdotal observations of species distributions seem to contradict one another. For example, Rowe (1987) reported finding *Austrolestes* naiads in streams (where water movement is present) that had suitable oviposition sites (i.e. vegetation such as reeds and sedges) on the banks. Crumpton (1977), on the other hand, suggested *Austrolestes* should not be found in habitat with significant water movement or wave action (such as streams, or large lakes). *Austrolestes* naiads do not cling tightly to vegetation and are more active (Crumpton 1977, Rowe 1987), therefore, it is possible that water movement may dislodge them more easily. Unlike *Austrolestes*, wave action or water movement does not appear to affect *Xanthocnemis* naiads at all, as they are described as excellent clingers, holding onto vegetation securely (Rowe 1987). What is generally agreed upon is that sites must have suitable vegetation for both species to allow oviposition to occur. *Austrolestes* seem to have a possible preference for reed-like plants with strong stems, while *Xanthocnemis* show no preference and will oviposit on any floating, aquatic, or overhanging vegetation (both dead or alive) (Crumpton 1977, Deacon 1978, Crumpton 1979, Rowe 1987).

Since little is known about New Zealand damselflies, and long term data are unavailable, this chapter will investigate the current distribution and habitat preferences of *Austrolestes* and *Xanthocnemis*, specifically throughout the South Island at various latitudes and altitudes. Distribution patterns are expected to follow those outlined in Rowe (1987) with both species being found throughout the South Island. Due to differences in life histories (*Austrolestes* being fast and requiring high energy systems, while *Xanthocnemis* being slow can survive in habitats that are less productive, as discussed in chapter two), it is expected that *Austrolestes* will be more likely to be found at lower, warmer altitudes that are more productive, whereas *Xanthocnemis* will be more likely to be found at higher altitudes with cooler temperatures and generally lower productivity. Because of behavioural differences between the two species (*Xanthocnemis* clinging tightly to vegetation, while *Austrolestes* potentially being disturbed by water movement), it is expected that *Austrolestes* naiads will be found in lentic (standing) rather than lotic (moving) aquatic systems, and *Xanthocnemis* will show no preference for one over the other. Multiple literature sources discuss *Austrolestes* ovipositioning in reed-like vegetation, therefore, it is expected that *Austrolestes* will show a preference for sites that have reeds as the predominant vegetation and *Xanthocnemis* will again show no preference as it is reported to utilise many types of vegetation for oviposition.

3.2 Methods

Fieldwork was conducted between September 2012 and November 2014. To investigate the distribution of *Austrolestes* and *Xanthocnemis* across the lower half of New Zealand, sites were sampled across both South and Stewart Islands. A site survey was conducted at each site where sampling took place using the survey form (Table 3.1). Latitude, longitude, and altitude were measured using a Garmin etrex 10 GPS (www.garmin.com). One option for each factor (species, habitat, vegetation, and substrate) was circled. Where more than one vegetation type was present, the predominant type was chosen. Substrate categories were selected per the grain size criteria described in NZ Geotechnical Society Inc (2005) where rocks > 60 mm; gravel = 2-60 mm; sand = 0.06-2 mm; silt < 0.06 mm.

The presence of naiads was determined by sampling with an aquarium fish net with an opening of 125 x 150 mm and a depth of 120 mm, sweeping through aquatic vegetation close to the edge and overhanging vegetation at lentic and lotic water bodies. For a species to be marked as present, a single larva or adult needed to be identified at a site. A minimum of three sweeps of the net at five points (0.5 m apart) along the edge of a water body were made before a species was recorded as being absent. During the flight season, adults were identified visually without being captured. If their presence was noted away from a water body, a GPS and altitude reading was taken to be included in the relevant habitat preference analysis. A full list of data points is provided in Table B.1.

Additional data points were collected from www.naturewatch.org.nz (referred to from here on as Nature Watch). To be included, entries on Nature Watch had to have been made during the fieldwork period (Sept 2012 to Nov 2014), have a photograph from which identification could be verified and GPS coordinates accurate to 1 km. A full list of additional data points included in the distribution analysis and the relevant attribution are provided in Table B.2.

Table 3.1 Copy of recording sheet for distribution survey. Each site where larvae were sampled for or an adult was sighted was recorded on a separate sheet.

<table>
<tr><td colspan="4">Latitude:</td><td colspan="5">Longitude:</td></tr>
<tr><td colspan="9">Altitude:</td></tr>
<tr><td>Species</td><td colspan="2">None</td><td colspan="2">*Austrolestes* only</td><td colspan="2">*Xanthocnemis* only</td><td colspan="2">Both</td></tr>
<tr><td>Habitat</td><td colspan="4">Lentic (still)</td><td colspan="4">Lotic (moving)</td></tr>
<tr><td>Vegetation</td><td>Grass/reeds</td><td colspan="2">Low-growing / overhanging</td><td colspan="2">Moss</td><td colspan="2">Aquatic</td><td>None</td></tr>
<tr><td>Substrate</td><td colspan="2">Silt</td><td colspan="2">Sand</td><td colspan="2">Gravel</td><td colspan="2">Rocks</td></tr>
</table>

All GPS readings from confirmed sightings of adults or naiads (from both fieldwork and additional data) were mapped using ArcGIS 10.0 (www.esri.com). Altitude values for additional data points were extrapolated from GPS readings using topomap.co.nz. Additional data points were used in altitude analysis, but were unable to be used in other analyses as details pertaining to habitat features were not recorded. To detect any difference in altitudinal range between species present, an ANOVA was conducted and to investigate the likelihood of any species group being found at any given altitude, a multinomial logistic regression (MLR) was conducted. Statistical analysis was done in R version 3.2.3 (R Core Team 2015). For the MLR, the nnet, ggplot2 and reshape2 packages were used, altitude was the independent variable and species present the dependent variable (reference = none). To investigate other factors influencing species distribution, a second MLR was conducted using habitat, vegetation and substrate types as independent variables, and species present as the dependent variable (reference = none).

3.3 Results

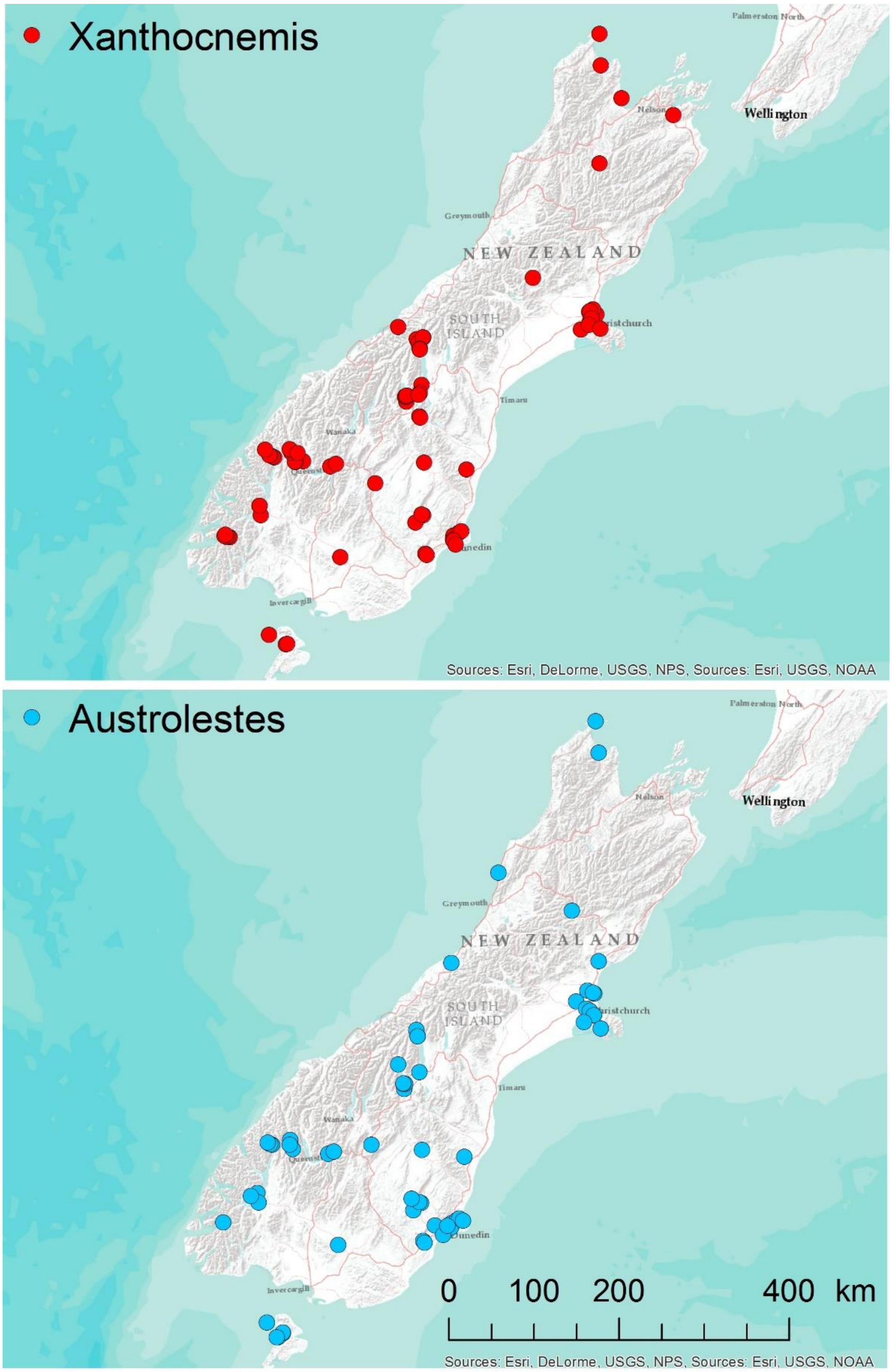
The distribution of locations where *Austrolestes* and *Xanthocnemis* were present covered most of the South Island, as well as locations on Codfish Island and Stewart Island (Figure 3.1).

Altitude ranged from sea level to 1600 m.a.s.l. There were significant differences in altitudes between each group of species present (ANOVA, $F_{3,148} = 4.838$, $p = 0.003$). *Xanthocnemis* were found at higher altitudes than *Austrolestes*. The probability of finding *Xanthocnemis* on its own increased as altitude increased (from 0.17 to 0.55), while the probability of finding *Austrolestes* on its own, or in combination with *Xanthocnemis* decreased (0.27 to 0.01, 0.30 to 0.08 respectively) (Figure 3.2).

A summary of the data set used in habitat analysis is provided in Table 3.2. Habitat type influenced the species present, but vegetation and substrate types did not (z values and p values are provided in Table 3.3). *Austrolestes* are more likely to be found on their own in lotic systems (probability 0.10, compared to 0.04 in lentic). While *Xanthocnemis* on its own, or together with *Austrolestes*, are more likely to occur in lentic systems (0.37 and 0.31 respectively) than lotic (0.12 and 0.14 respectively) (Figure 3.3).

3.4 Discussion

This chapter investigated the distribution and habitat preferences for the two species of damselfly present in the South Island of New Zealand: *Austrolestes* and *Xanthocnemis*. Distribution patterns were, as expected, similar to historical data provided by Rowe (1987). *Austrolestes* and *Xanthocnemis* appear to have similar distributions across the lower half of New Zealand, with both



Sources: Esri, DeLorme, USGS, NPS, Sources: Esri, USGS, NOAA

Sources: Esri, DeLorme, USGS, NPS, Sources: Esri, USGS, NOAA

Figure 3.1 Locations of confirmed sightings of *Austrolestes* (blue; n = 65) and *Xanthocnemis* (red; n = 79), naiads or adults, within the southern half of New Zealand. Data were collected between September 2012 and November 2014 by way of a field study, supplemented by additional points gathered from sightings reported on www.naturewatch.org.nz.

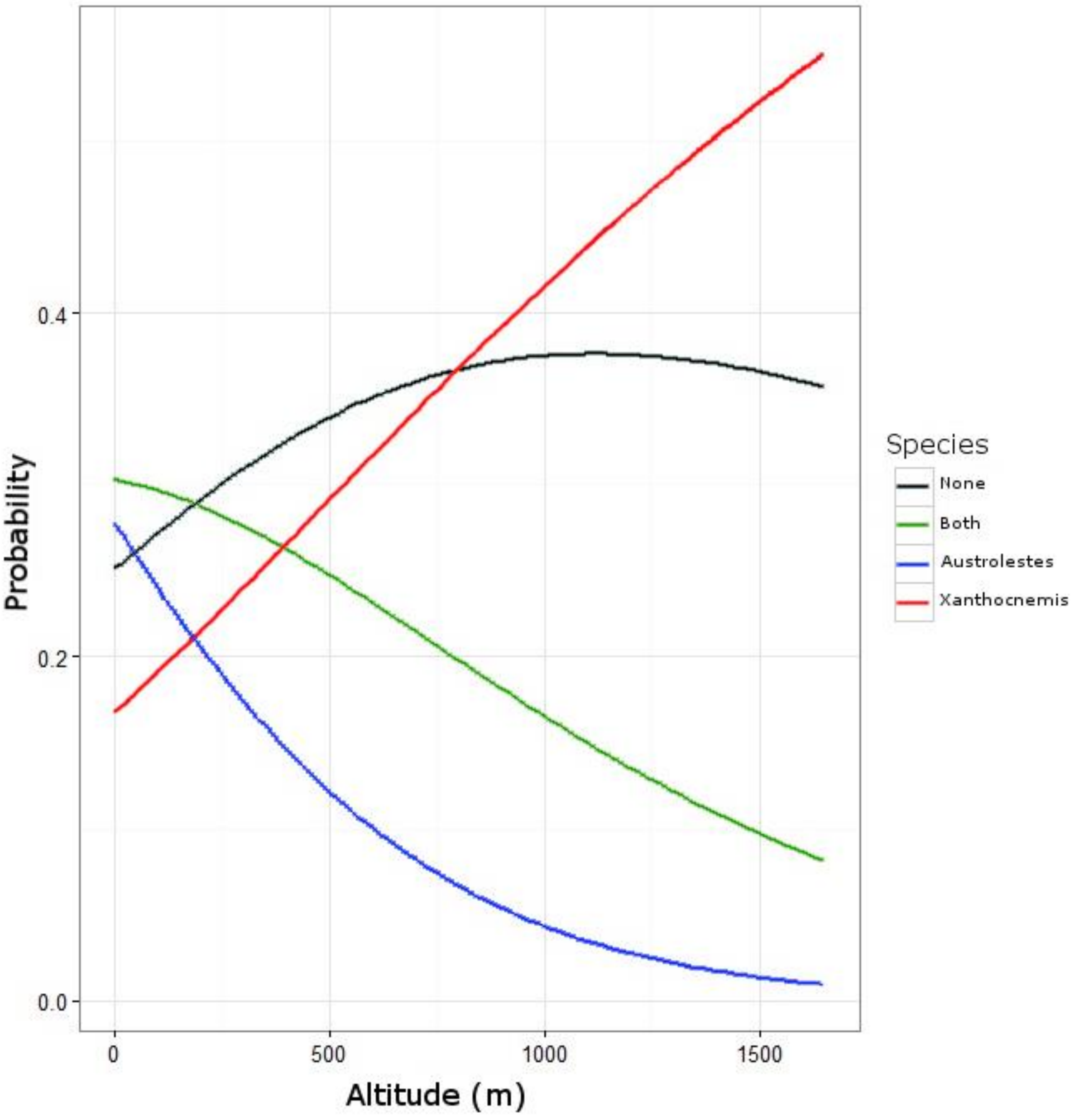


Figure 3.2 Probability of finding either *Austrolestes* only (blue; n = 26), *Xanthocnemis* only (red; n = 40), both species (green; n = 39) or neither species (black; n = 47) at a site at any given altitude (m.a.s.l, up to 1600m). Derived from the multinomial logistic regression.

Table 3.2 The number of sites containing neither species, *Austrolestes* only, *Xanthocnemis* only, or both species for each habitat type (lentic or lotic).

	None	*Austrolestes*	*Xanthocnemis*	Both	Total
Lentic	20	3	26	22	71
Lotic	27	4	5	6	42
Total	47	7	31	28	113

Table 3.3 Z values (a) and p values (b) of the multinomial logistic regression for site factors, where independent variables are habitat, vegetation and substrate, the dependent variable is species present and the reference = none. Statistically significant results marked with *.

a

	(Intercept)	habitat	vegetation	substrate
Austrolestes	-1.545	0.062	1.268	-0.841
Xanthocnemis	1.685	-3.434	1.735	0.319
both	1.734	-2.354	1.496	-1.931

b

	(Intercept)	habitat	vegetation	substrate
Austrolestes	0.122	0.951	0.205	0.400
Xanthocnemis	0.092	0.0006*	0.083	0.750
both	0.083	0.019*	0.135	0.054

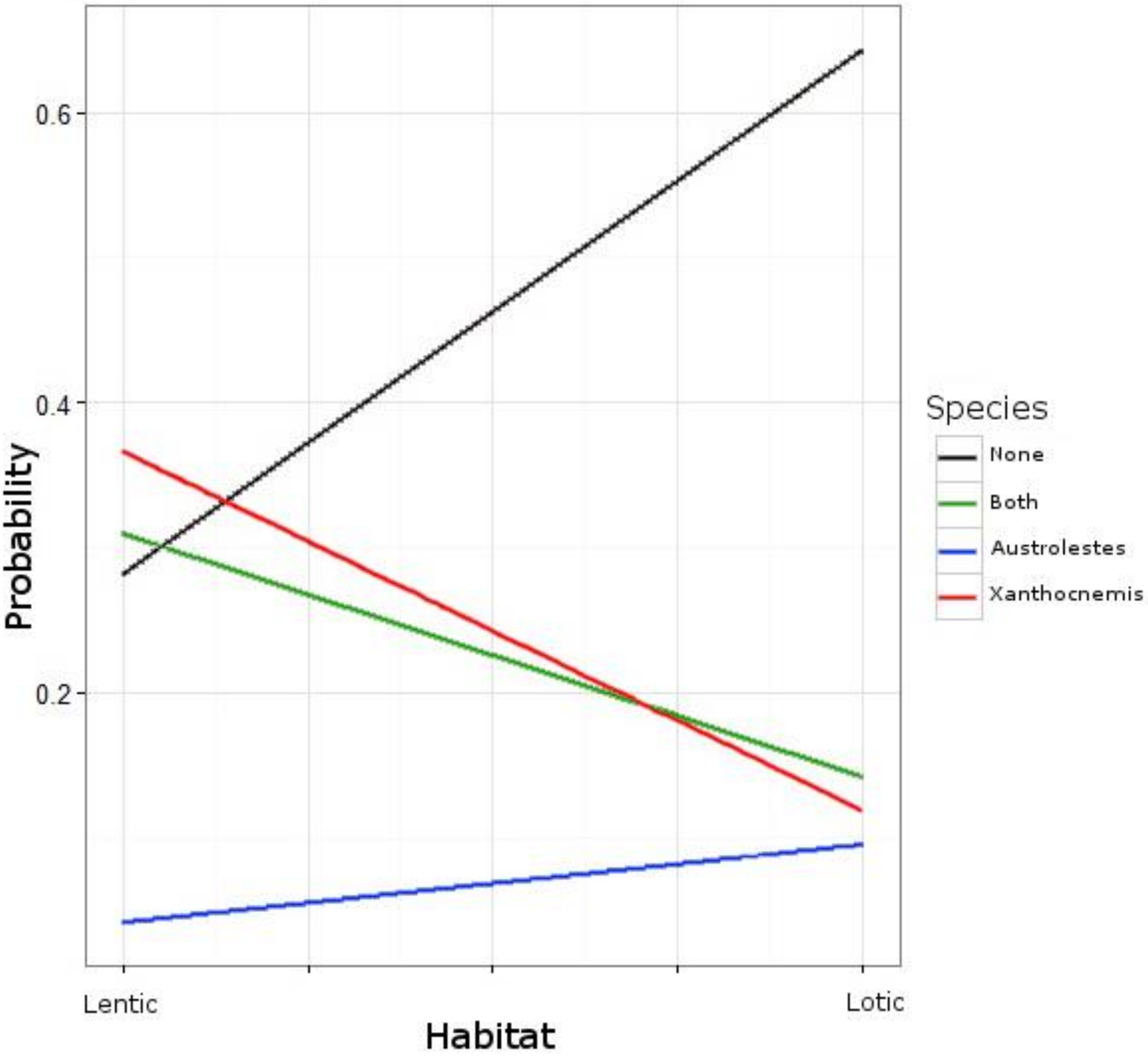


Figure 3.3 Probability of finding either *Austrolestes* only (blue), *Xanthocnemis* only (red), both species (green) or neither species (black) in lentic (still water) verses lotic (moving water) habitats. Derived from the multinomial logistic regression.

species being found throughout the South Island, as well as on Stewart and Codfish Islands[7]. However, since Rowe (1987) did not provide a list of data points (just a list of obscure or hard to obtain references), it was not possible to revisit those sites to check if either species was still present. Additionally, no previous studies have investigated distribution over an altitudinal gradient. Many invertebrates, including those in the order Odonata, have been shown to have significant shifts in distribution by expanding their ranges into higher altitudes and latitudes in response to climate change, for example, in Britain (Hickling, Roy et al. 2005, Hickling, Roy et al. 2006, Hassall and Thompson 2008). The two species considered here already have a geographical range covering the entire country so there is no opportunity (or landmass available) for any southern latitudinal advance towards the poles (southern shifts in latitude could occur at the northern edge of the species range). However, changes to altitudinal ranges could occur, with distributions potentially expanding into higher altitudes. Investigations in to changes in distribution require long term species data, which are lacking for most New Zealand invertebrates (including damselflies). This study provides a starting point for distributional surveying of two ecologically important damselfly species; further work is required to investigate the influence of climate change on the distribution of New Zealand damselflies and the implications for these species. Reporting websites, such as Nature Watch, will provide increasingly useful information on species distributions over time.

Increasing altitude was expected to influence the distribution of each species, and this was shown to be the case. *Xanthocnemis* was found as high as 1600 m.a.s.l. Sites above this altitude were not investigated as they are extremely difficult and potentially dangerous to access. Therefore, *Xanthocnemis* could potentially be found higher if suitable habitats exist. *Austrolestes* distribution, on the other hand, only reached 1040 m.a.s.l. While there is significant overlap between the distributions of the two species, there is habitat segregation at the extremes of their geographical ranges. Increases in altitude is known to be linked with decreases in temperature and dissolved oxygen content, as well as species richness and productivity (Rahbek 1995, Jacobsen 2008). Jacobsen (2008) suggested a decrease in species richness associated with increasing altitude was more likely due to the decrease in oxygen content, rather than temperature, as even sub-lethal levels can have long term effects on invertebrates. Since *Austrolestes* is known to be more active that *Xanthocnemis* (discussed in chapter four), it would be expected to have higher oxygen requirements. If oxygen was a limiting factor in high altitude sites, this could account for why *Austrolestes* is not commonly found at higher altitudes. Still, *Austrolestes* is reported to grow faster and have a shorter life cycle (Crumpton 1977, Crumpton 1979, Rowe 1987), which allow it to complete a full naiad cycle in one growing season and take advantage of ephemeral habitats. *Xanthocnemis* is restricted to habitats that are permanent although they can survive short term desiccation; Galatowitsch and McIntosh

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[7] Both species are also found in the North Island and other offshore islands, however, this was outside the geographical range of this study.

(2016) reported 80-90% survival of *Xanthocnemis* naiads after eight days without water, and 10-20% survival after 16 days in moist sediment.

Habitat type, vegetation, and substrate were all expected to influence distribution, however, only habitat type (lentic or lotic) showed a significant correlation. Previous literature indicated *Austrolestes* showed a preference for habitats with reed/sedge type vegetation, but this was not the case here. This could potentially be due to a simplified assessment 'vegetation type' for the broad scale survey completed in this study. If *Austrolestes* prefers only one vegetation type (reeds/sedges, as Rowe (1987) suggests), then future studies may need to quantify this vegetation type at each site more precisely. *Austrolestes* may utilise more types of vegetation than just reeds, although this is not supported by the literature (Crumpton 1977, Deacon 1978, Crumpton 1979, Rowe 1987). *Xanthocnemis* showed no preference for any specific vegetation type which is consistent with the literature (Rowe 1987).

It was expected that *Austrolestes* would show preferences for lentic rather than lotic systems and *Xanthocnemis* would show no preference for either habitat. *Austrolestes* when on its own didn't show a preference for either habitat (potentially due to a low number of sites containing only *Austrolestes*). However, *Austrolestes* was also found at sites containing *Xanthocnemis*. At these sites, they were more likely to be found in lentic rather than lotic systems. There were a high number of lentic sites which had both species present (compared to lotic sites), which indicates that despite *Austrolestes* not showing a preference when found on its own, they most likely do have a preference for lotic systems, although they are not completely excluded from lotic habitats. *Xanthocnemis* shows a preference for lentic systems either on its own, or with *Austrolestes*. There may be other requirements of a habitat which are more important to distribution than water movement, such as food availability and suitable sites for oviposition and metamorphosis (Rowe 1987). The generalist nature of New Zealand species contrasts with Odonata overseas which are usually habitat specific and found in either still or moving water, not both (Corbet 1999, Hawking and New 2002, Hof, Brandle et al. 2006).

Of the factors studied in this chapter, the primary predictor of South Island damselfly distribution is altitude. *Austrolestes* and *Xanthocnemis* are more often found together, except at the extremes of their habitat ranges where the differences in their life histories become apparent. *Xanthocnemis* has the ability to survive in the low productivity habitats found at higher altitudes. *Austrolestes* requires more energy to sustain growth and is restricted from surviving in those environments, but is able to take advantage of temporary habitats due to its shorter life cycle. Habitat type may also prove to be a useful predictor in species distribution, with lentic systems being preferred to lotic.

Chapter 4

Movement behaviour and starvation tolerance

4.1 Introduction

Differences in the life history strategy of predatory animals are reflected in contrasting activity and developmental rates (Werner and Anholt 1993, McCauley 2008). Those species considered to have fast life histories actively hunt prey and subsequently have higher metabolisms which allows them to grow more rapidly, as well as being larger compared to those with slow life histories (Werner and Anholt 1993, Careau, Bininda-Emonds et al. 2009, Stoffels 2015). Slow species minimise energy expenditure by reducing activity, which is advantageous during periods of low food availability (Careau, Bininda-Emonds et al. 2009, Humphries and McCann 2014). Therefore, movement behaviour can be used to assess an individual's response to abiotic and biotic factors in their environment (Anholt and Werner 1995, Humphries and McCann 2014). Fast species are primarily considered to have higher activity, but the trade-off is an increase in vulnerability to predation (Wissinger, Whiteman et al. 1999, Johansson 2000, Johansson and Suhling 2004, McCauley 2008). Slow species exhibit cryptic behaviours such as predator avoidance or sit-and-wait feeding strategies, which reduce feeding and metabolic rates, growth and size, and generally leads to a longer life cycle (Stoffels 2015). Slow species are likely to perform better in habitats with predators present (Wissinger, Whiteman et al. 1999, McCauley 2008) or in low productivity habitats, such as those at high altitudes (Bears, Martin et al. 2009). By contrast, fast species generally do better in highly productive habitats with reduced permanence gradients (e.g. temporary ponds which dry in summer) as they grow and mature quicker (Johansson 2000, Johansson and Suhling 2004). Because increased activity uses more energy, requiring a greater metabolic rate, larger individuals have greater reserves of stored energy allowing them to survive longer when starving (Gergs and Jager 2014, Humphries and McCann 2014). Since an individual's ability to resist starvation is also linked to its metabolism (Harshman, Hoffmann et al. 1999, Sinclair, Bretman et al. 2011), metabolism should also be considered when investigating differences in life history strategies.

Such fast-slow life history dichotomies may facilitate species coexistence in assemblages of odonates (Kormondy and Gower 1965, Wissinger 1988, Johansson 2000, McCauley 2008). However, little work has been done on such assemblages in New Zealand. Of the six species of damselfly that have been identified in New Zealand, only two species commonly coexist (Rowe 1985, Rowe 1987), *Austrolestes* and *Xanthocnemis*. These species are common and widely distributed throughout the North, South and Stewart Islands; both are endemic and often found to inhabit the same locations (Rowe 1987). *Austrolestes,* the larger of the two species, has naiads that are active and mobile, with a marked flight response to predators (Rowe 1987). *Xanthocnemis* naiads on the other hand, are sedentary with laborious movement and cryptic behaviour (Rowe 1987). *Austrolestes* requires from five months to over 12 months (but less than 24) to complete development, depending on the local climate (Rowe 1987). *Xanthocnemis* exhibits a much longer life cycle, requiring two to three years to complete development (Rowe 1987).

This model system, comprising two species that frequently coexist, represents an excellent opportunity to examine if species with different life history strategies exhibit varying behaviours and starvation tolerance, which could give them an advantage under certain environmental conditions. In this laboratory experiment, it is hypothesised that there will be differences between *Austrolestes* and *Xanthocnemis* naiads with regards to movement behaviour and their ability to resist starvation. *Austrolestes*, which are considered to have fast life histories, are predicted to move more than *Xanthocnemis*, which are considered to have slow life histories. Changes in movement patterns are expected as the naiads start to starve. *Austrolestes,* being more active, will become more frantic and their movement will increase as they attempt to hunt for prey, while *Xanthocnemis,* which are sit-and-wait predators, will reduce their movements to save energy. Since *Austrolestes* are expected to move more overall, they should use up their energy stores quicker than *Xanthocnemis,* and take less time to die of starvation.

4.2 Methods

4.2.1 Experimental set up

Naiads of both species were collected using fine mesh aquarium fish nets, from aquatic vegetation along the edge of a pond on private farmland in Sutton, Otago, New Zealand (45˚34′46″S, 170˚4′41″E). To account for potential effects due to size differences among naiads, all individuals were weighed to the nearest 0.01 mg prior to testing and body mass was included as a predictor in the statistical analysis (see below). During weighing, time out of water was kept to a minimum to avoid undue stress. As Odonata naiads are known to be cannibalistic, individuals were placed in separate 200 mL clear plastic containers (Figure 4.1). Environmental factors such as temperature and light are known to influence damselfly naiad behaviour and growth (Johansson, Stoks et al. 2001, De Block and Stoks 2004) as is the presence of predators (Johansson, Stoks et al. 2001, Brodin and Johansson 2002, Brodin, Mikolajewski et al. 2006). Therefore, temperature and light were kept constant throughout the experiment using a climate-controlled laboratory room. Containers were filled with locally sourced spring water (Speights spring, Dunedin) which was free from fish odour to ensure that any changes in naiad movement could be attributed only to being deprived of food. To reduce the likelihood of larger individuals and naiads in the control treatments metamorphosing or going into quiescence/diapause, a temperature/light regime of 15°C and 12:12 hour (day:night)

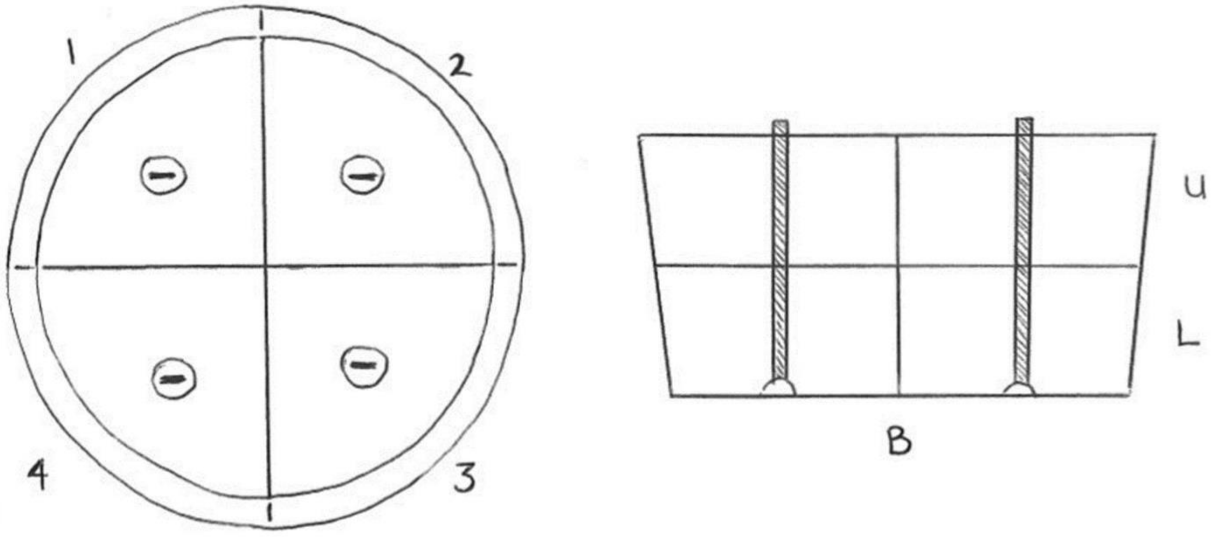

Figure 4.1 Above and side views of the arrangement of container sections for recording movement behaviour of damselfly naiads.

cycle was chosen (based on average temperatures recorded in chapter two). Stratified random sampling was used to assign containers to blocks on separate shelves, and an even number of each species were assigned to each shelf.

To ensure laboratory conditions were not influencing naiad death, fed controls (20 individuals of each species) were included in the experiment, but were not included in any analysis. Control individuals were fed every second day with 2 mL of spring water containing a high density of *Artemia* nauplii (Johansson and Suhling 2004, Corbet and Brooks 2008, De Block and Stoks 2008). Water quality was maintained by completely changing the water in all containers every two weeks and topping up in between. Accumulated uneaten, dead *Artemia* in control containers were removed after every second feeding using a plastic transfer pipette, and care was taken to avoid disturbance of the naiads as much as possible.

4.2.2 Data collection

Naiad positions, determined by dividing containers into sections within the containers, were measured at least once a day. Lines were drawn in marker pen on the outside of the containers and plastic sticks were glued in place using a hot glue gun to provide an artificial vegetation for the naiads to cling to (Figure 4.1). Position was recorded as the section number (1-4) followed by a level (U = upper/above the mid line; L = lower/below the mid line; B = on the bottom) where the naiad was perched. Where naiads sat on a line, the section in which the majority of the body was located was recorded as the naiad position. If a naiad was deemed to be 50% in one section and 50% in another, the section containing the head was recorded as the naiad position. Naiad positions were then converted to movements (the difference between one recording and the next), and were either assigned as either having not moved (no difference between recordings) or moved (any difference). Movement behaviour data was collected until all individuals of one species (*Austrolestes*) had died.

The number of days it took each naiad to die was used as a measure of starvation tolerance. The experiment was stopped on day 127 when laboratory space became unavailable (seven *Xanthocnemis* naiads remained alive at this stage). Controls, individuals that had not died, and those which died non-natural deaths (e.g. sucked up a syringe) were excluded from statistical analysis. After exclusions, the sample size of *Austrolestes* was 136 and *Xanthocnemis* was 129.

4.2.3 Data analysis

Statistical and graphical analysis was carried out using the software R version 3.1.1 (R Core Team, 2013). To test if location within the room had an effect, an exploratory analysis using a Friedman test was conducted, but no significant difference among shelving blocks was identified. To assess if there was a difference in movement behaviour patterns between the two species over time, a generalised linear mixed effects model (GLMM) was used on the movement data using the lme4 package (R Core Team, 2013). Effect sizes (ES) are reported as coefficient estimates ± 1 SE. The influence of naiad body weight on time until death (starvation tolerance) was investigated between species using a general linear model (LM). For both the GLMM and the LM the fixed factors were species (two levels) and time (continuous), while individual was a random factor.

4.3 Results

4.3.1 Movement behaviour

Overall, *Xanthocnemis* moved significantly less often (54% of the time) than *Austrolestes* (79% of the time) (ES = -1.67 ± 0.10, z = -17.37, $p < 0.001$) (Figure 4.2). There was no change in the proportion of individuals moving as starvation period lengthened for *Austrolestes* (ES = <0.001 ± 0.002, z = 0.327, p = 0.744). However, the proportion of *Xanthocnemis* that moved increased from 46% to 68% (ES = 0.016 ± 0.002, z = 9.732, $p < 0.001$), and there was a significant difference in movement over time between the two species (ES 0.01 ± 0.003, z = 4.67, $p < 0.05$) (Figure 4.2).

4.3.2 Starvation tolerance

The mean number of days until death was 32 ± 1.03 (SE) for *Austrolestes* and 88 ± 1.99 (SE) for *Xanthocnemis.* All *Austrolestes* died within 60 days, whilst seven *Xanthocnemis* naiads (not included in the analysis) were still alive at the conclusion of the experiment on day 127. There was some overlap in the distribution of deaths over time between the two species, however, 64% (87/136) of the *Austrolestes* naiads died before a single *Xanthocnemis* naiad died (Figure 4.3). Body mass significantly influenced time to death in both species, with smaller individuals dying sooner than larger individuals ($F_{2,262} = 631$, $p < 0.001$), but the slope and fit of the relationships differed between species (Figure 4.3).

4.4 Discussion

Fed controls were used to establish that deaths in the experimental group were due to starvation and not laboratory conditions. A few deaths of control specimens did occur for both *Austrolestes* and *Xanthocnemis* early on. These deaths were caused by suffocation, due to a build-up of organic matter (unconsumed food) in the bottom of the plastic containers. Growth occurred for all remaining control specimens of both species, and some *Xanthocnemis* naiads metamorphosed to adults. Because control specimens grew throughout the experiment, and only died from causes that could be attributed to being fed, assumptions that the deaths of treatment specimens were due to starvation are correct.

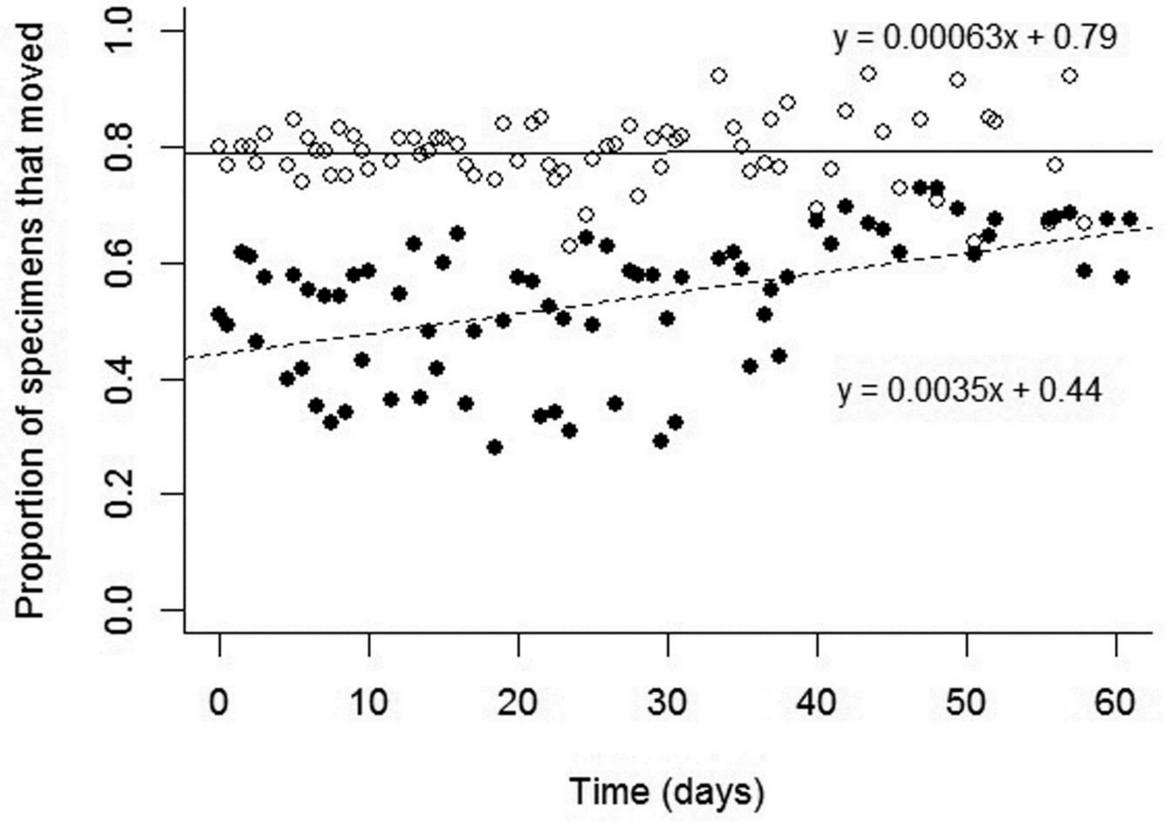

Figure 4.2 The proportion of individual naiads of each species which moved (changed position within their container between measurements) over time (hours) as starvation occurred. Starting sample size was n = 136 for *Austrolestes* (open circle, solid line) and n = 129 for *Xanthocnemis* (filled circle, dashed line), and sample size decreased over time as individuals died due to starvation for this analysis.

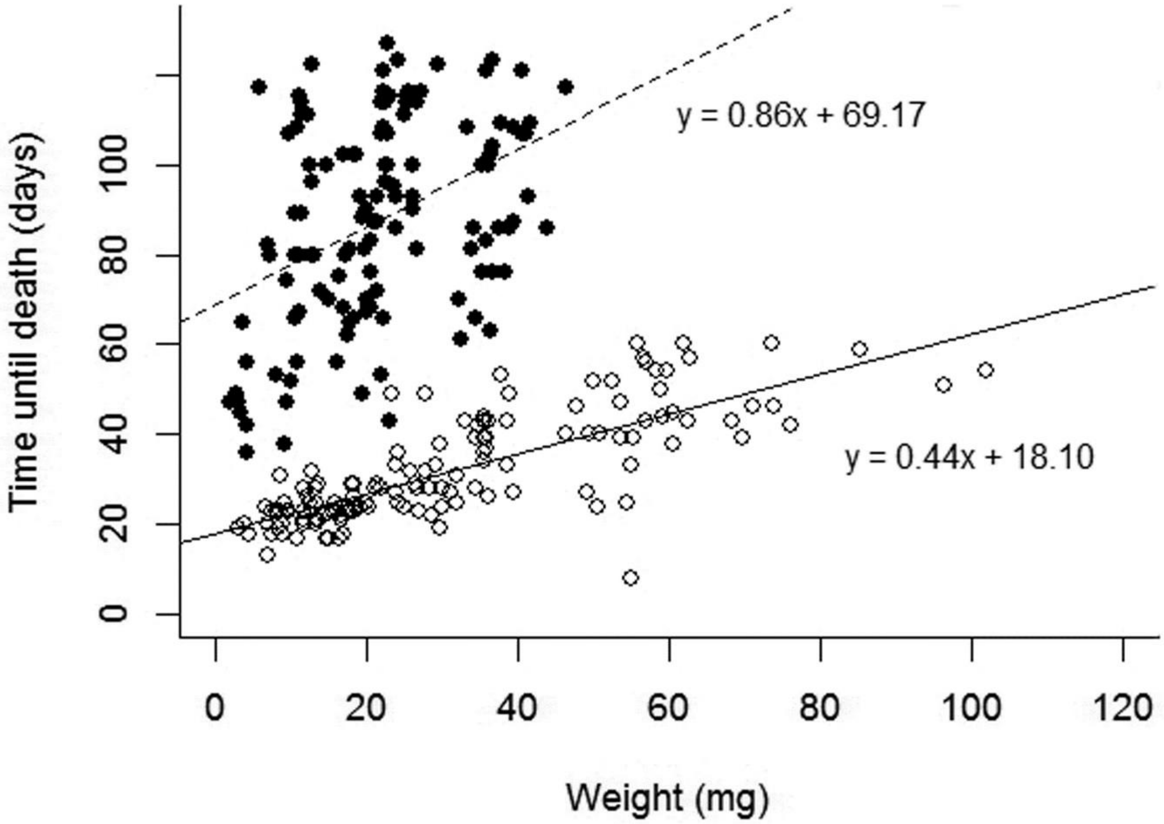

Figure 4.3 Relationships between body mass of an individual (mg) and the length of time (days) for death to occur due to starvation for naiad *Austrolestes* (open circle, solid line) (n = 136) and *Xanthocnemis* (filled circle, dashed line) (n = 129).

4.4.1 Movement behaviour

In agreement with the first hypothesis, it was found that overall the fast life history species, *Austrolestes,* moved more on average than the slow life history species, *Xanthocnemis*. This result supports earlier work by Johansson (2000) who found the same correlation between movement and life history in six different odonate species in Sweden. Changes in behaviour as starvation occurred were species-specific, but individual species responses differed from predictions. In the second hypothesis, *Austrolestes* movement was expected to increase as starvation progressed because fast species generally have relatively high metabolic rates which require food to be hunted actively (Humphries and McCann 2014, Stoffels 2015); therefore, individuals should increase their search efforts for prey as they starved. However, this was not the case as movement behaviour by *Austrolestes* remained broadly constant throughout the experiment, suggesting *Austrolestes* have limited behavioural plasticity in their life histories and, hence, are more likely to be vulnerable to adverse environmental conditions. Similar dynamics to those displayed by *Austrolestes* may be seen in active fish species from Australia challenged by hypoxia; such species have limited scope to reduce activity even under adverse hypoxic conditions, resulting in rapid suffocation (McNeil and Closs 2007). The third hypothesis predicted *Xanthocnemis* movement to decrease during starvation, in contrast to *Austrolestes*, as this species employs a sit-and-wait feeding tactic (Rowe 1987) thus maximising energy conservation (Johansson 2000). However, a significant increase in movement by *Xanthocnemis* as starvation progressed was observed, highlighting their scope to actively respond to challenging environmental conditions.

A trade-off must exist between the need for food and the desire to conserve energy (Sogard and Olla 1996); therefore, at some point it becomes advantageous to abandon the sit-and-wait tactic and actively seek out a food source, resulting in an increase in movement. *Xanthocnemis* takes longer to respond to starvation due to the initial lower movement, and has the ability to change its behaviour/feeding tactic when environmental conditions require. This is likely due to their slow life histories, reserving energy that can be made available to switch to searching for food during periods of low food availability (e.g. winter). If this is the case, then there are potential implications for starvation or food deprivation studies in which the individuals are not starved to death (for example (De Block and Stoks 2008, Scharf, Filin et al. 2009). The total length of time taken for any species to starve to death needs to be considered because starving individuals for a few hours or days may not be long enough to elicit a significant or representative response. Also, larger individuals (i.e. those in later instars) have more energy stores available, resulting in longer survival times (Speakman 2005, Gergs and Jager 2014). Whilst late instar naiads would be storing energy for metamorphosis and reproduction, such energy could be diverted to survival under stressful conditions, but likely after an initial delay to ensure no other option is available as this strategy will be at the cost of fecundity.

4.4.2 Starvation tolerance

When starved, *Xanthocnemis,* with its slow life history, survived significantly longer than the fast life history species, *Austrolestes.* This fitted with the final hypothesis that fast life history species are more active and therefore, expend their energy supplies faster and die earlier than slow life history species when challenged by starvation. Finiguerra et. al. (2013) found similar patterns when investigating the starvation tolerances of male and female copepods (*Acartia tonsa*). Males had a lower starvation tolerance than females (i.e. they took less time to die), which was attributed to greater energy expenditure through increased activity (in this instance due to searching for mates). Rowe (1987) noted that *Austrolestes* adults carried over less fat reserves from their naiad stage than *Xanthocnemis*. It is likely, however, given the results of this experiment, that *Austrolestes* naiads never retain fat reserves in the same way as *Xanthocnemis* do. Stoks et. al. (2005) found differences in the ability to store triglycerides between *Enallagma aspersum* and *Ischnura verticalis* damselfly naiads in North America. Potentially, *Austrolestes and Xanthocnemis* exhibit similar differences, which would influence their distribution by dictating which habitats can support their metabolic needs. More work investigating underlying metabolic differences between the two species is warranted and should consider how this influences changes in behaviour.

If starvation tolerance was purely based on size, then one would expect *Austrolestes* to survive longer than *Xanthocnemis*, as the former are larger. This clearly did not happen in this experiment; however, larger individuals of each species survived longer under starvation conditions. Similar patterns were also found for a number of different species, for example, ant lion larvae (Griffiths 1991, Arnett and Gotelli 2003), backswimmers (Gergs and Jager 2014), *Drosophila* flies (Chippindale, Chu et al. 1996, Harshman, Hoffmann et al. 1999), ground beetles (Knapp and Saska 2012), and larval fish (Miller, Crowder et al. 1988). Increased body size has been attributed to increased survival when starving, primarily due to the ability to store greater quantities of fat, which is the primary fuel used during starvation in insects (Gilmore 1965, Caloin 2004, Gibbs and Reynolds 2012, Gergs and Jager 2014). While body size can be used to determine starvation tolerance of individuals of the same species, activity and metabolic rate are likely to be more important factors when comparing starvation tolerance between species.

When food is abundant, there is probably little competition between the naiads of the two damselfly species because most of the habitats shared by these two species appear to be productive enough to support both life histories. Therefore, the driving factor for the difference in life histories can most likely be found in the extremes of their environmental range. Differences in patterns of movement behaviour and starvation tolerance between the two life histories were identified in this experiment. *Austrolestes* was found to move more and can only sustain much shorter periods without food. These behaviours, coupled with their known flight response to predators and shorter life cycle (Rowe 1987), indicates that one would expect to find *Austrolestes* naiads in highly productive habitats, particularly ones free from predators, such as shallow, warm temporary ponds which dry out in late summer. *Xanthocnemis*, by contrast, cannot survive in these habitats as they need permanent ponds to complete their longer life cycle. However, their reduced movement exhibited in this experiment and their known freeze response to predators (Rowe 1987), probably allow *Xanthocnemis* to survive in habitats in which predators are present. Although naiads may rarely encounter conditions where they would starve to death in the field, *Xanthocnemis* can clearly survive for extended periods without food, which indicates they are capable of surviving in low productivity environments, such as high alpine tarns.

Chapter 5

Diapause

5.1 Introduction

Invertebrates are sensitive to climatic changes in their environments (Hance, van Baaren et al. 2007, Robinet and Roques 2010). In temperate regions, this is more pronounced during exposure to adverse cold conditions in winter (Lee Jr 1989). Some insects, for example monarch butterflies, use migration as a way of avoiding these conditions (Rankin and Burchsted 1992); however, most insects do not migrate and must evolve to survive unfavourable conditions. In the Northern Hemisphere, where winters are generally less variable with greater extremes for extended periods (Sinclair, Addo-Bediakom et al. 2003), diapause is a common method of overwintering in insects (Morris 1989). In New Zealand, diapause in insects has been reported to be greatly reduced due to the relatively mild, maritime winter climate experienced both now, and in the Pleistocene period, when diapause is believed to have developed (Dumbleton 1967, Roberts 1977, Roberts 1978, Morris 1989). For example, alpine grasshoppers (of multiple genera) are active all winter on suitably warm days (in contrast to their North American counterparts that diapause as eggs), indicating quiescence rather than diapause (Ramsay 1978). Quiescence also occurs in the stick insect *Niveaphasma annulata* as nymphs and adults of both sexes are active throughout the year, suggesting they are capable of continuous reproduction (Dennis, Dunning et al. 2014).

Diapause is a form of developmental arrest which occurs (usually) during one stage of an insect's life history (Roberts 1977, Denlinger 1986, Denlinger 2002, Kostal 2006, Hahn and Denlinger 2007). Diapause is common in Odonata (for example: Corbet 1956, Lawton 1970, Lawton 1971, Lutz 1974, Ingram and Jenner 1976, Corbet 1980, Wissinger 1988, Pritchard 1989, Johnson 1991, Ferreras-Romero 1997, Corbet, Suhling et al. 2006, May 2013), with diapause occurring at either the egg or naiad stage. It is a physiological response initiated prior to the onset of adverse conditions (most often triggered by decreasing day length) to ensure avoidance of these conditions and, therefore, survival (Roberts 1977). Diapause is controlled by environmental, hormonal and molecular regulators (Denlinger 2002) and consequently cannot be broken until sometime after favourable conditions return (Tauber and Tauber 1981, Denlinger 1986, Denlinger 2002, Kostal 2006). Quiescence is also a halt in development; however, unlike diapause, it is initiated as a result of adverse conditions and ends when those conditions have passed providing some flexibility in response to changing conditions (Denlinger 1986, Tauber, Tauber et al. 1986, Kostal 2006, Hahn and Denlinger 2007). In the field, it is often difficult to distinguish between the two (Morris 1989), but it is important to do so when considering a species' life history (Denlinger 2008) as there are physiological differences between insects that diapause and those which are quiescent (e.g. metabolic rate) (Hodek 1996). Since climate plays such an important role in insect life histories, the current global climate change crisis is likely to influence developmental rates, flight periods and the ability to survive winter in many species of insect (Robinet and Roques 2010).

Current thinking regarding the overwintering of the two New Zealand damselflies commonly found in the South Island is that both species (*Austrolestes* and *Xanthocnemis*) undergo diapause (Deacon 1979, Rowe 1987), with the onset of diapause being linked to changes in photoperiod (Deacon (1979). Most of the previous literature on *Austrolestes* and *Xanthocnemis* cites Rowe (1987) on diapause (for example Morris 1989), opinions which are based on his own observations plus one doctoral thesis (Deacon 1979) containing data from sites in Canterbury and over 30 years old. *Xanthocnemis* is reported to diapause as a late stage naiad, and *Austrolestes* as an egg (Deacon 1978, Rowe 1987). In addition, Deacon (1979), also discusses the ability of *Austrolestes* to diapause as a late stage naiad. Diapause is usually restricted to a single life history stage (Denlinger 2002), so while possible, it seems unlikely that *Austrolestes* would undergo diapause at both an egg and naiad stage. Given that quiescent behaviour has been mistaken for diapause in previous studies (Roberts 1977), it is possible that South Island damselflies, like many species adapted to the New Zealand climate, do not undergo diapause, but instead engage in period(s) of quiescence during unfavourable conditions. Since it is proposed that both species undergo quiescence (instead of diapause), it is expected that naiads collected during winter will experience growth, moulting and/or metamorphosis when placed in a warm environment while remaining under winter light conditions.

5.2 Methods

At the beginning of winter (10 June 2013), 12 naiads of each species were collected from a pond on private farmland at Sutton, Otago, New Zealand (45˚34′46″S, 170˚4′41″E. Naiads were patted dry, weighed (to the nearest 0.01 mg) and measured (whole body length to the nearest 0.5 mm), using Vernier callipers. Caudal lamellae were excluded from body measurements as they can fall off during handling). Naiads were randomly assigned to one of two different temperature treatments; 5˚C or 25˚C (temperatures were selected from the high and low end of those recorded by data loggers placed at sites in chapter two), and placed into individual 200 mL containers filled with locally sourced spring water (Speights spring, Dunedin) in an incubator set to the required temperature. Water had been left for six hours to equilibrate prior to the start of the experiment. Containers had four plastic sticks glued vertically to the base to act as an artificial emergence platform if metamorphosis did occur (containers were set up as per the experiment in chapter four, see Figure 4.1). To prevent food being a limiting factor for growth, naiads were fed daily with 2 mL of spring water containing a high density of live *Artemia* (Johansson and Suhling 2004, Corbet and

Brooks 2008, De Block and Stoks 2008). As per the previous experiment, accumulated uneaten, dead *Artemia* were removed every second day using a plastic transfer pipette. Incubators were situated next to windows and natural lighting was used for this experiment. The timing of the experiment was designed to be during the middle of winter and include the shortest day. The number of daylight hours per day for the duration of the experiment, which was stopped on 8 July 2013 after 28 days, was 8 hours 45 mins ± 5 mins.

To investigate the influence of temperature on change in weight, a general linear model was conducted in R (R Core Team 2015) using species and temperature as independent variables and weight change (final weight minus starting weight) as the continuous response variable.

5.3 Results

Metamorphosis occurred for both species at 25˚C, but not at 5˚C. Moulting occurred in both species at 25˚C, while only one naiad (*Austrolestes)* moulted at 5˚C (Table 5.1). For both species (that did not metamorphose (or die) during the experiment), naiads grew more when reared at 25˚C compared to 5˚C ($F_{1,13} = 64.34$, $p < 0.001$). *Austrolestes* grew more than *Xanthocnemis* ($F_{1,13} = 14.69$, $p = 0.002$) (Figure 5.1). Although not measured, an increase in movement / activity among individuals of both species at 25˚C compared to those at 5˚C was evident.

5.4 Discussion

It was expected that even when winter light conditions were maintained, growth and metamorphosis of both *Austrolestes* and *Xanthocnemis* would occur in warmer temperatures. Insects in diapause should not be able to break out of diapause until well after adverse conditions have passed, when sensitivity to the token stimuli has reduced (Tauber and Tauber 1981, Kostal 2006). Deacon (1979) reported that photoperiod is the token stimulus inducing and controlling diapause in *Austrolestes* and *Xanthocnemis* damselflies. The results of this study support the hypothesis that *Austrolestes* and *Xanthocnemis* are undergoing quiescence rather than diapause when overwintering, and are therefore responsive to changes in temperature, rather than light regime. Like many other New Zealand invertebrates, quiescence may allow *Austrolestes* and *Xanthocnemis* naiads to opportunistically take advantage of a changeable climate and hence the periods when suitable conditions for growth prevail (Dumbleton 1967, Watt 1975, Roberts 1977, Roberts 1978, Morris 1989). Inferences regarding different rates of growth based on naiad instar or size could not be made due to a) the small sample size and b) the fact that final weights could not be obtained for individuals that metamorphosed in the 25˚C treatment. However, this study confirms that naiad growth (of naiads at any instar/size) is reduced in cooler environments, suggesting temperature is

Table 5.1 Number of individuals of each species (n = 12) that moulted or metamorphosed during the experiment.

Species	Temperature (˚C)	Number of individuals that moulted	Number of individuals that metamorphosed	Number of individuals that died
Austrolestes	5	1	0	1
	25	5	1	2
Xanthocnemis	5	0	0	0
	25	3	3	0

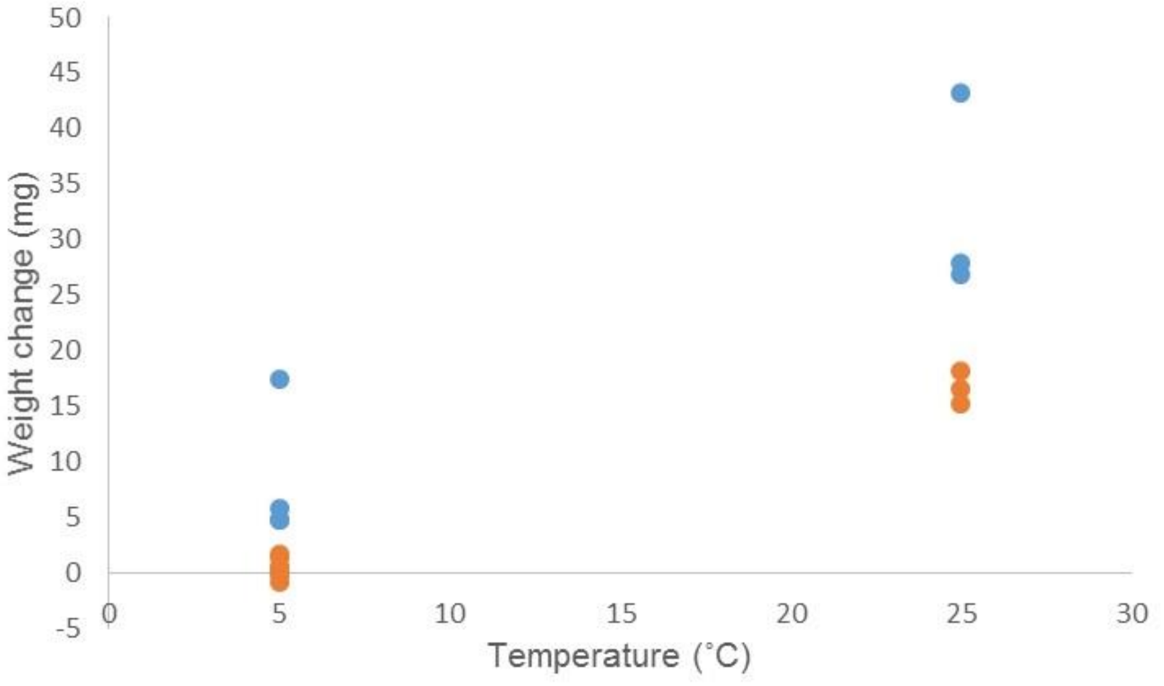

Figure 5.1 The weight change (final weight minus starting weight in mg) of *Austrolestes* (blue) and *Xanthocnemis* (red) naiads at each experimental temperature (˚C); n = 6 for each treatment group.

the primary variable growth. While this chapter does not investigate the possibility of *Austrolestes* egg diapause, similar arguments may hold true for eggs as well as naiads.

Diapause as a late stage naiad is advantageous for insect species with highly synchronised and short flight seasons in spring/early summer as it allows all adults to metamorphose at the same time. However, both *Austrolestes* and *Xanthocnemis* have extended emergence and flight seasons (Rowe 1987, personal observation), traits that are likely to be advantageous in a variable maritime climate. Since temperature affects life histories (Robinet and Roques 2010), and there is substantial climate variation between regions within New Zealand (strongly influenced by topography and directionality of prevailing weather systems which fluctuate seasonally) (Coulter 1975), comparative studies of individuals across the country should be made before we can infer the universality of any of these patterns. Further investigation into the effects of temperature and photoperiod on overwintering in these two species from multiple sites around the country is warranted.

Chapter 6

General conclusions

6.1 Chapter summaries

This thesis investigated the life history strategies of two species of coexisting damselfly common across the South Island of New Zealand: *Austrolestes* and *Xanthocnemis*. The four data chapters are briefly recapped here:

6.1.1 Life history strategies

This chapter investigated and compared differences between the life histories of both species. *Austrolestes* and *Xanthocnemis* are both generalist species with long hatching, emergence and flight seasons which contrasts with most Northern Hemisphere species which exhibit high levels of synchronicity with short emergence seasons and diapause (Dumbleton 1967, Roberts 1977, Roberts 1978, Winterbourn 1978, Towns 1981, Morris 1989). Naiad growth over a two year period at six sites across a 1000m altitude gradient was monitored. It was difficult to identify individual cohorts for either species as individuals of all sizes were present at all times of year due to the long recruitment season. The long recruitment season also meant that predicted patterns in mean body length were not seen. Larger body sizes were expected at higher temperatures; however, this was not seen. This result is likely an artefact of the sampling method rather than confirmation that the hypothesis was not supported. This theory was supported by drops in mean body length associated with peak warm periods. *Xanthocnemis* was more prevalent in the cooler, less productive, higher altitude sites than *Austrolestes*, which was predicted as they are believed to have a slow life history, with reduced movement and energy requirements.

6.1.2 Distribution and habitat preference

The focus of this chapter was broad scale species distribution and habitat preference. Current distribution maps matched historical distribution data (Rowe 1987). A lack of extensive and detailed information prevented any changes in distribution from being identified (if any occurred). This highlighted the need to encourage the use of new technologies and reporting websites, such as Nature Watch (www.naturewatch.org.nz) or its international counterpart(s) (iNaturalist.org network), which are available for anyone to access and use for free.

Altitude was the best predictor of distribution, with *Austrolestes* more frequently found at lower altitudes than *Xanthocnemis*. This is likely due to differences in their life histories. *Xanthocnemis* is predicted to have a slow life history, which allows it to survive in the generally lower productivity habitats found at higher altitudes. *Austrolestes* is largely excluded from those environments; with a predicted fast life history, it requires more productive habitats, but can take advantage of temporary habitats due to its shorter life cycle. Both species showed preferences for lentic rather than lotic habitats, although neither exclusively used one habitat over the other. Neither vegetation nor substrate type influenced the distribution of either species.

6.1.3 Movement behaviour and starvation tolerance

In this chapter, differences in the amount of movement and levels of starvation tolerance exhibited by both species were examined. *Austrolestes* and *Xanthocnemis* did show differences in movement behaviours, and as predicted, overall *Austrolestes* moved more than *Xanthocnemis*. However, changes to this behaviour caused by starvation did not follow original predictions. It was predicted that *Austrolestes* movement would increase with starvation because it was expected that as active hunters, they would become more frantic looking for food and increase their movements to keep up with their higher metabolic needs. But what was seen was neither an increase nor a decrease, but a fairly constant rate of movement, which was attributed to limited behavioural plasticity in their life histories, making them more vulnerable to adverse changes in environmental conditions. *Xanthocnemis* were predicted to decrease their movement as they reduced their metabolic needs to maximise energy consumption. Instead the opposite was seen, after an initial period of low activity an increase in movement was observed (although this increase was still below the activity rate of *Austrolestes*), and suggests that *Xanthocnemis* have greater behavioural plasticity which allows them to actively respond to changes in their environment.

In addition to being less active, *Xanthocnemis* was expected to survive starvation longer than *Austrolestes* by not consuming energy by excess movement. This proved to be true with *Xanthocnemis* naiads out-surviving *Austrolestes* naiads by an average of 56 days. This result has implications for the types of habitats each species can survive in, meaning *Xanthocnemis* can access low productivity environments or those with reduced growing season, such as high altitude tarns, and *Austrolestes* is restricted to productive habitats.

6.1.4 Diapause

This chapter investigated the plausibility of winter diapause occurring in naiads of both species. Naiads of both *Austrolestes* and *Xanthocnemis* were reported to undergo winter diapause that was controlled by day length (Deacon 1979). However, in chapter two, naiads showed growth and development during winter months, despite supposedly being in diapause (even in the colder, higher altitude sites). When day light hours were kept at winter levels that would have been experienced in the field, individuals that were placed in warmer environments grew and/or metamorphosed (depending on their size at the start of the experiment), while those in cooler environments remained static, even when provided with adequate food. This indicates that it is unlikely that these species undergo winter diapause, and more likely they experience a quiescence controlled by ambient temperatures. This is consistent with patterns seen in other endemic New Zealand insect species as opposed to overseas counterparts.

6.2 General conclusions

The overall primary objective of this thesis was to determine if a fast-slow life history dichotomy exists between *Austrolestes* and *Xanthocnemis* by investigating aspects of life history and distribution. *Austrolestes* displays characteristics which are consistent with the theory that *Austrolestes* has a life history at the fast end of the continuum. Evidence for this inference includes growing larger (chapter two), having shorter life cycles (Deacon 1978, Crumpton 1979, Rowe 1987), moving more (chapter four), which results in a decrease in starvation tolerance (chapter four), having a preference for lower altitude habitats (chapters two and three), and being able to take advantage of ephemeral habitats (Barclay 1966, Crumpton 1977). *Xanthocnemis*, on the other hand, display characteristics more in alignment with a slow life history. Evidence for this inference includes individuals being smaller (chapter two), moving less (chapter four), living longer than one year (and potentially up to three) (Deacon 1978, Crumpton 1979, Rowe 1987), requiring permanent habitats (chapter three), however, they can take advantage of low quality habitats, particularly those at high altitudes (chapters two and three). Therefore, the dichotomy is confirmed to be present and may influence how these species interact with the environment and each other. This thesis has focused solely on the two species of damselfly which are commonly found in Otago, however, there are other species of Odonata, ten species of Epiprocta (Rowe 1987, Rowe, Davies et al. 2011) and at least two additional species of Zygoptera (Rowe (1987) describes four, however two species of the *Xanthocnemis* genus are currently being debated; see (Amaya-Perilla, Marinov et al. 2014, Marinov, Amaya-Perilla et al. 2016). How do other species compare and where do they fit on the fast/slow continuum? And how do they compare to species found elsewhere?

Differences in life history strategy cannot be confirmed as the reason *Austrolestes* and *Xanthocnemis* successfully coexist, as those mechanisms are likely to be far more complex. However, the differences indicate these species have different energy requirements throughout their life cycles, which allow them to take advantage of extreme environments that the other species cannot survive in. Habitats in which these two species coexist are likely to be more productive as both species appear to be able to successfully coexist in low to mid altitude habitats that are permanent in nature. If resources were limited, one species would likely out competing the other. Segregation does start to occur at the extremes of their environmental ranges.

New Zealand damselfly species exhibit different life histories to their Northern Hemisphere counterparts. The life histories of *Austrolestes* and *Xanthocnemis* are influenced by New Zealand's mild maritime climate which is seasonally unpredictable (Wissinger, Greig et al. 2009). Both species lack clear cohort division due to long flight seasons and continual recruitment of individuals, and are more likely undergoing a temperature induced quiescence rather than true diapause. However, there is a lack of Odonate research conducted in variable maritime climates in both hemispheres (e.g. Ireland and New Zealand; for examples, see: Fox and Cham 1994, Nolan, Hogg et al. 2007) and in continental southern hemisphere climates (e.g. Southern Africa and South America; for examples, see: Clark and Samways 1996, Groeneveld, Clausnitzer et al. 2007, von Ellenrieder 2009), with a bias in the literature towards studies conducted in continental northern hemisphere climates (e.g. Europe and North America; for examples, see: Willigalla and Fartmann 2012, May 2013, Corser, White et al. 2014, Kohli, Schneider et al. 2014, Andersen, Nilsson et al. 2016, Callahan and McPeek 2016, Pinkert, Brandl et al. 2016). Comparative studies into those regions underrepresented in the literature (i.e. maritime and continental southern hemisphere) warrant further attention.

Much of insect life history is linked to changes in temperature, however, thermal tolerances (maximum and minimum) are not known for either *Austrolestes* or *Xanthocnemis*. Given differences in the distribution between the species over an altitudinal gradient, it is possible they have different thermal limits which potentially could restrict habitat selection. This could have implications for susceptibility and being able to adapt to environmental changes associated with climate change. It would be advantageous to conduct studies into shifts in distribution over time using museum collections and databases such as Nature Watch. Changes in distribution linked to climate change have been reported in Odonates from the UK (Hickling, Roy et al. 2005, Hickling, Roy et al. 2006, Hassall and Thompson 2008), Europe (Ott 2001, Flenner and Sahlen 2008, Flenner, Richter et al. 2010) and Japan (Aoki 1997). While both species studied here are present throughout the country (and unable to move further poleward), changes in range may still occur with the northern range receding southward or increases in altitude. Additionally, the ability of *Austrolestes* to take advantage of temporary habitats in cooler southern climates was not investigated in this thesis. Wissinger et al (2009) suggest both *Austrolestes* and *Xanthocnemis* are rarely found in temporary habitats. However, they only investigated 15 temporary habitats from one small area in the central Canterbury region. This is unlikely to represent the full range of temporary habitat conditions throughout the country or a species' likelihood to survive in temporary habitats. Research into the likelihood of *Austrolestes* inhabiting temporary habitats throughout the entire country should be investigated. Since *Austrolestes* appears to be semivoltine in the cooler Otago conditions than suggested by the literature, does this affect its ability to excel in these habitats where it should have an advantage over *Xanthocnemis*?

Austrolestes and *Xanthocnemis* exhibit differences in activity levels and starvation tolerance and attempts were made to measure the respiration rates of each species for this thesis. Unfortunately, the equipment available wasn't sufficiently sensitive to measure individual naiads, and when trials to determine respiration rates were attempted using multiple naiads in a single chamber, cannibalism prevented obtaining reliable reads. *Xanthocnemis* as a slow species exhibiting reduced activity, a sit and wait predation strategy, longer starvation time and reportedly longer life cycle, should have a much lower respiratory rate than *Austrolestes* which could be linked to distribution/habitat selection and predict how they would likely respond to hypoxic environments. Metabolic profiles can be measured in terms of lipid, protein, and carbohydrate levels. *Xanthocnemis* survived starvation much longer than *Austrolestes*, but how? Storage of different compounds (or different levels/ratios of the same compounds) could explain this. Earlier literature (Rowe 1987) suggests that *Xanthocnemis* carried over more fat reserves during metamorphosis (although these assumptions have not been tested), and that the study in chapter four shows marked differences between survival rates of the species under starvation conditions. This has begun to be investigated in these two species as an extension of this thesis. Preliminary reports were presented at the 2016 ICE/ESA conference in Orlando, FL in September 2016 (see Appendix A.2.4). This research involved combining two different test methods and does require further method development, but once perfected, this could potentially open up a whole new method of testing metabolic profiles of lipid, carbohydrate and proteins on single individuals for all insects, not just Odonates.

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Appendix A

Publication information

A.1 Manuscripts

This section contains a list of intended publications from each chapter, including additional work done as an extension of this thesis, and the progress of each intended publication at time of submission. Where manuscripts are still in the progress of being written, intended titles, co-authors and journals (where known) have been included.

Table A.1 List of intended publications.

Chapter	Title	Co-authors	Journal	Progress
Two	Fast verses slow: differing life history strategies of two species of New Zealand damselfly (Odonata: Zygoptera).	J M Jandt G P Closs		First draft in progress
Three	Distribution and habitat preferences of two species of damselfly (Odonata: Zygoptera) found in the South Island of New Zealand.	J M Jandt G P Closs	Freshwater Ecology	First draft in progress
Four	The influence of life history strategy on movement behaviour of damselflies (Odonata: Zygoptera) during starvation.	G R W Humpries C D Matthaei G P Closs		Edits required from peer review process. Submission to new journal intended shortly
Five	Do New Zealand damselflies really diapause? An argument for temperature induced quiescence in *Austrolestes colensonis* and *Xanthocnemis zealandica* (Odonata: Zygoptera).	G P Closs J M Jandt	NZ Journal of Entomology	First draft complete, ready to send to co-authors for edits/suggestions

A.2 Conference abstracts

Provided in this section are abstracts of presentations given at conferences (or accepted to be given at time of submission) for work associated with this thesis, as well as work done as an extension of this thesis.

A.2.1 International Symposium on the Environmental Physiology of Ectotherms and Plants (ISEPEP) 5 - London, Ontario, Canada - August 2013

Physiological responses underpinning fast/slow life histories and species interactions.
Dann, Tanya J.

Multiple species of damselfly coexist in the same habitats accessing the same resources; therefore, to successfully coexist they require different life history strategies. Experiments will be conducted to evaluate the relationship between physiological responses (i.e. metabolic rate, thermal sensitivity, starvation tolerance and behaviour) and life history strategies. Species with fast life-styles are predicted to have faster rate processes, greater thermal sensitivity and reduced starvation tolerance. Species with slow life-styles are predicted to have a slower metabolic rate to take advantage of low productivity habitats, thus avoiding competition with fast life-style species.

A.2.2 New Zealand Entomological Society - Queenstown, New Zealand - April 2014

Do New Zealand damselflies exhibit a fast/slow life history dichotomy?
Dann, Tanya J.

Multiple species of Odonata can co-exist in the same habitat while feeding on the same prey; therefore, to successfully co-exist they require different life history (LH) strategies. One comparative strategy is the fast-slow dichotomy, which has been attributed to the development of predator avoidance or flight response behaviour. A species with a slow LH should have a slower metabolism and differing behavioural responses, it is expected that they will be able to survive longer without food than a species with a fast LH, by reducing movement and energy expenditure. Two species of New Zealand damselfly (*Austrolestes colensonis* and *Xanthocnemis zealandica*) are being used to investigate this life history dichotomy. Larvae of both species were starved to identify the time required for death to occur. Larvae position was recorded daily and notes were made about behavioural responses witnessed. *X. zealandica* survived an average of 87 days and had a preference for sitting on vertical sticks placed in the enclosures. *A. colensonis* preferred resting on the bottom of the enclosures and survived for a significantly shorter period of time (average 31 days). It was observed that when the surface of the water was disturbed, *A. colensonis* move away from the disturbance while *X. zealandica* flattened its body to the surface it was attached to. This suggests that *A. colensonis* can be considered to have a fast LH and *X. zealandica* to have a slow LH.

A.2.3 ISEPEP 6 - Aarhus, Denmark - August 2015

The dance of the damselflies: Does starvation affect movement behaviour?

Dann, Tanya J.[1], Humphries, Grant R.W.[2], and Closs, Gerry P[1].

[1] University of Otago, Dunedin, New Zealand.

[2] University of California Davis and Farallon Institute for Advanced Ecosystem Research, California, USA

An organism’s activity is often linked to differences in their life histories. Previous studies have shown that fast-slow life history strategy dichotomies exist between multiple organisms and within communities of Odonate assemblages. Slow species display a sit and wait behaviour, waiting for prey to come to them, while fast species actively hunt. It is expected that during periods of starvation, the movement behaviour of slow species will decrease to allow survival through the lean times until food becomes available. On the other hand, when fast species are starved, individuals are expected to increase their movements with the aim of increasing their rate of encounters with sparsely distributed prey as they have higher net energetic demand that cannot be reduced. Larvae of two species of damselflies (Odonata: Zygoptera) were collected from a single site in rural Otago, New Zealand. Movement behaviour was recorded for each individual as they starved. *Xanthocnemis zealandica* (a slow species) took longer to starve and moved less than *Austrolestes colensonis* (a fast species). Differences in starvation tolerance and movement behaviour between the two species are consistent for species exhibiting a fast-slow life history dichotomy. However, contrary to expectations, as starvation occurred *Xanthocnemis* movement increased and *Austrolestes* decreased. The increase in movement of *Xanthocnemis* is likely to be due to plasticity in behavioural responses. It becomes advantageous for individuals to abandon the sit and wait behaviour and increase their chances of encountering prey. The higher movement rate of *Austrolestes* uses up valuable resources foraging for non-existent prey, once energy is used up, there is no more available and movement decreases before death occurs.

A.2.4 Joint International Congress of Entomology (ICE) / Entomological Society of America (ESA) - Orlando, FL, USA - Sept 2016

Metabolic differences between fast/slow life histories of damselflies (Odonata: Zygoptera)

Dann, Tanya J.[1], Ferguson, Laura V.[2], Jakobs, Ruth[3], Closs, Gerry P.[1] and Sinclair, Brent J.[2]

[1] University of Otago, Dunedin, New Zealand.

[2] University of Western Ontario, London, ON, Canada

[3] Bielefeld University, Bielefeld, Germany

Differences in life histories are commonly reported between related species, particularly fast/slow dichotomies. Compared to their slow counterparts, fast species grow quicker, move more, die quicker, often have a reduced starvation tolerance and actively hunt prey (slow species sit and wait for prey). These variations in life history traits lead to differences in energy input/output requirements and are likely to result in variation in energy storage. Carbohydrate, lipid and protein levels were examined using two damselfly species found throughout New Zealand. *Austrolestes colensonis* is considered to have a fast life history and *Xanthocnemis zealandica* a slow life history. *X. zealandica* has been reported to carry greater fat stores through to adulthood than *A. colensonis,* although, this has not been tested. It is expected that metabolic profiles will differ between species. Larvae of each species were randomly assigned to one of 5 treatment groups, plus a control group. All of the treatment groups were starved until 10 individuals remained. Remaining individuals, plus 10 freshly collected and 10 controls were tested for lipids present using thin layer chromatography coupled to a flame ionisation detector. Additional larvae were collected and fed or starved for 1 to 4 weeks and tested for carbohydrate, glycogen and protein levels using the anthrone assay and the Bradford assay extraction methods. Both species showed different lipid profiles, and variation in the lipid profile patterns as they starved. Carbohydrate and protein levels also differed between species. These differences are likely to be linked to life history strategies.

A.3 Radio interview

An interview was given to Alison Ballance from Radio New Zealand, the interview aired on Thursday 17th Dec 2015, with a run time 11 min 54 seconds. The subsequent article and aired interview may be found on the following website:
www.radionz.co.nz/national/programmes/ourchangingworld/audio/201782907/damselflies-fast-blue-and-slow-red

Appendix B

Supplementary data for chapter three

B.1 Distribution data points from field survey

Table B.1 is a list of all raw data points collected in the field survey from the South, Stewart, and Codfish Islands between September 2012 and November 2014.

B.2 Additional data points from Nature Watch NZ

Nature Watch NZ is a community nature observation website, where the public can upload images of any living organism they see along with relevant details. This website is subject to creative commons copyright laws, and as such, the following record of data obtained from the site has been compiled in accordance with those laws. Table B.2 is a collection of all data points collected from www.naturewatch.org.nz used in chapter three. Observations from this site may be viewed by typing www.naturewatch.org.nz/observations/ followed by the ID# of the observation into an internet browser. All usernames and observation numbers were correct at the time of data collation (July 5, 2015). Data points collected from Nature Watch were used for the distribution map and altitude analysis only as they did not contain enough detail to be included in the habitat analysis.

Table B.1 Raw data for distribution map in chapter three. Coordinates are given in New Zealand Geodetic Datum 1949.

Easting	Northing	Altitude
2317206	5486230	310
2281912	5510190	255
2272717	5501511	584
2284180	5465293	4
2282824	5572430	630
2127860	5584395	951
2125857	5584436	644
2125857	5584436	632
2140748	5573800	465
2222879	5540021	300
2089302	5521693	1018
2088682	5521897	1082
2090676	5510421	218
2089683	5510393	184
2277471	5522153	1245
2261804	5644324	579
2262096	5644129	584
2262235	5643707	586
2263749	5650491	574
2263479	5650583	572
2262948	5650365	581
2262249	5650502	589
2260449	5649328	610
2260970	5650283	589
2261267	5650795	585
2260561	5652205	561
2262317	5651228	580
2262174	5651240	580
2113592	5352120	49
2113654	5352256	42
2113676	5352277	44
2113850	5352391	44
2114077	5352615	51
2114089	5352652	49
2114144	5352703	52
2114614	5353114	60
2117230	5354477	34
2117312	5354545	35
2119241	5356855	26
2119429	5357676	20

Easting	Northing	Altitude
2120062	5358366	17
2120441	5358621	12
2122012	5359147	12
2285164	5527806	640
2279762	5511212	315
2270906	5515055	838
2274288	5717436	1305
2276352	5713707	1040
2281615	5719649	758
2281539	5719777	763
2281518	5719802	759
2277680	5706337	625
2277695	5706343	620
2277567	5705246	606
2280010	5663889	520
2277782	5653825	425
2276174	5651921	459
2277092	5626454	362
2278444	5625330	369
2290566	5617526	274
2308482	5607273	215
2133124	5570932	498
2132728	5571423	504
2131390	5572921	540
2131304	5573076	536
2130877	5573498	543
2127569	5578770	587
2126950	5583989	985
2132519	5585098	469
2332694	5564406	103
2307570	5553621	521
2323494	5489625	322
2100399	5369453	1
2509624	6042110	17
2504566	6029876	983
2125430	5587767	691
2316788	5481136	130
2286002	5463425	3
2265008	5436403	3
2136517	5570247	526

Easting	Northing	Altitude
2124840	5587888	919
2320729	5476713	125
2326702	5491719	2
2106677	5578616	244
2104399	5579310	300
2103038	5580012	303
2101346	5581145	320
2101200	5581134	318
2096171	5587348	1056
2096170	5587469	1072
2096714	5587465	1129
2098614	5594870	82

Easting	Northing	Altitude
2096897	5518337	208
2089302	5521693	1018
2087402	5521936	1180
2082307	5521375	1237
2086084	5519880	464
2081494	5519002	413
2081494	5519002	413
2081940	5518353	400
2317150	5480412	25
2133885	5583234	440
2225442	5548152	226
2252517	5731994	40

Table B.1 List of data points obtained from www.naturewatch.org.nz. Observations from this site may be viewed by typing http://naturewatch.org.nz/observations/ followed by the ID# of the observation into an internet browser. All usernames and observation numbers were correct at the time of data collation (July 5, 2015).

Username	Observation ID#	Username	Observation ID#
absoluteandy	1163804	majo00	992062
caddisflyguy	1244708	maxbuxton	1228938
ecotype	985620	muerkc	1367105
felixcollins	973968	msomerville	947484
grahame	987648	nzwide	1006573
joepb	1189735	parkecology	954910
john_barkla	990681	philip-howe	949988
jon_sullivan	950250	rileyj	964824
	951197	sea-kangaroo	1459206
	983460		1482923
	988576		1483128
	1033021	steveattwood	947156
	1066343		957405
	1267847	steve_kerr	966135
	1518076		966136
	1523658		984332
keuda	1049362	suemcgaw	987272
	1057084		1150164
majo00	977657	thomasjwalsh	947054
	977658	zanejg	940986
	992053		

Appendix C

Supplementary data for chapter five

Table C.1 Raw data for diapause experiment in chapter five.

Species	Temp (˚C)	Start weight (mg)	Start length (mm)	Moult (days until occurrence)	Metamorphosis (days until occurrence)	Final weight (mg)	Final length (mm)	Weight change (mg)
Austrolestes	5	88.60	20.5			94.47	22.0	5.87
		34.08	15.5			38.97	17.5	4.89
		70.54	20.5	21		88.05	20.5	17.51
		80.34	21.5		died on day 20	n/a	n/a	n/a
		72.40	21.0			72.45	20.0	0.05
		81.94	20.0			86.80	21.0	4.86
	25	70.03	20.0	2	22	n/a	n/a	n/a
		74.70	20.5	1		101.65	21.5	26.95
		58.46	18.5	8	died on day 23	n/a	n/a	n/a
		60.87	18.5	10		88.87	21.0	28.00
		102.50	22.5		died on day 21	n/a	n/a	n/a
		28.45	14.5	13 & 21		71.75	20.0	43.3
Xanthocnemis	5	17.00	10.0			17.51	10.5	0.50
		18.80	10.5			19.35	10.5	0.55
		38.75	13.5			40.27	14.0	1.52
		35.04	13.0			35.00	13.0	-0.04
		31.05	13.0			32.73	12.5	1.68
		23.35	11.0			22.65	11.0	-0.70
	25	40.55	15.0		18	n/a	n/a	n/a
		21.01	11.5	16		36.34	14.0	15.33
		33.09	13.5		27	n/a	n/a	n/a
		19.31	11.5	20		37.47	14.0	18.16
		37.10	14.0		21	n/a	n/a	n/a
		24.06	12.0	18		40.73	14.5	16.67