The role of flow regime and movement in stream shrimp assemblages

By

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ABSTRACT

Researchers have long sought to understand what governs the distribution of organisms. For riverine animals and plants, there is often a strong relationship between hydrology (flow) and distribution and assemblage patterns. The dispersal behaviour and “inherent mobility” of organisms is thought to play a role in this relationship. This study examined the distribution patterns and movement behaviour of three Caridean shrimp species in the south-eastern region of the Murray-Darling Basin in the southeast of Australia, and related those patterns to flow. To do this, I applied multiple methods, including: basin scale occupancy modelling; monitoring of spatiotemporal distribution and abundance patterns; directional trapping to detect dispersal events; and laboratory experiments that compared the ability of the three species to maintain position and resist displacement.

The results demonstrated that flow regime seems to play a substantial role in the distribution and composition of shrimp communities throughout the Murray-Darling Basin, and dispersal and “inherent mobility” is likely to play strong roles in this relationship. *Caridina mccullochi* was found to be restricted to lowland rivers that experience relatively few high flow events in summer, which is typical of the natural flow regime in the southern Murray-Darling Basin. *Macrobrachium australiense* and *Paratya australiensis*, on the other hand, seem to be more tolerant of the more frequent summer high flow events in many of the more heavily regulated rivers.

*Caridina mccullochi* seems to be restricted to lowland river habitats for its entire life history, whereas *Paratya australiensis* can complete their life history in both lowland and upland river reaches. *Macrobrachium australiense* occurs further upstream than *Caridina mccullochi*, but it appears that this species cannot complete
its life cycle in upland reaches, and it is likely that individuals that occur in the upper reaches were spawned further downstream. *Macrobrachium australiense* was found to undertake upstream movements during early-to-mid summer. In contrast, there was no evidence to suggest that *Paratya australiensis* and *Caridina mccullochi* undertake significant movements, and are likely to be restricted to the relatively small area for their entire life history. Key to these findings was the discovery that *Caridina mccullochi* has a more limited ability to maintain position in flow compared to *Paratya australiensis* and *Macrobrachium australiense*, and also lacks a strong rheotactic response to flow.

These results have highlighted the importance of recognising both dispersal behaviour and “inherent mobility” of shrimp to understanding distribution and assemblage patterns. In the past, it has been hypothesised that differences in both habitat preferences and spawning and recruitment strategies could also result in different distribution and assemblage patterns under different flow regime conditions. Consequently, any useful framework for understanding freshwater shrimp populations should incorporate their movement and life histories, as well as their large-scale habitat relationships. This study has also highlighted the potential importance that flow regime management plays in the future conservation of not just shrimp but also the broader ecological community in the Murray-Darling Basin.
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CHAPTER 1
GENERAL INTRODUCTION

Background

The role of flow and flow regime in the distribution of riverine organisms

Compared to other ecosystems, rivers are extremely dynamic, often complex, networks of channels and floodplains, connected and disconnected through the action of flow. It is this mostly unidirectional flow of water downstream that is the single most defining feature of rivers and streams. River and stream flows are highly variable both temporally and spatially, and it is because of this variation that flow plays a significant role in ecosystem patterns and processes (Humphries et al. 2014).

The flow regime of a river can be described as a combination of the timing, magnitude and duration of flow events in river systems. Under natural conditions, the flow regime of a river is determined by the size and nature of the upstream catchment, the elevation, permeability of its underlying rocks, and the rainfall, slope and vegetation cover (Jowett and Duncan 1990, Humphries et al. 2014). In general, rivers are prone to disturbance (i.e., flooding, seasonal drying), causing a frequently changing ‘riverscape’ (Fausch et al. 2002). The dynamic nature of river flow, together with gradient, and geomorphology, determines water velocity and depth; two of the main constituents of habitat for riverine organisms. As a result, flow is a primary driver of riverine ecosystem patterns and processes (Vannote et al. 1980, Frissell et al. 1986, Junk et al. 1989, Calow and Petts 1992, Thorp and Delong 1994, Matthews 1998, Fausch et al. 2002).
In particular, flow has the potential to significantly influence the spatial and temporal patterns of stream organism assemblages at multiple scales (Schlosser 1985, Bain et al. 1988, Poff and Allan 1995). Stream organisms are distributed along velocity and depth gradients within a stream reach (Angermeier 1987, Aadland 1993) and longitudinally among stream reaches (Kuehne 1962, Evans and Noble 1979). The ever-changing, often unpredictable, flow environment results in the evolution of adaptations by organisms to cope with, ameliorate or exploit the conditions (Lytle and Poff 2004). Therefore, flow regimes can explain a range of biological features, including the distributions of individual fish species (Jowett 1990, Poff et al. 1997, Richter et al. 2003) and assemblage structure in fish (Poff and Allan 1995), invertebrates (Quinn and Hickey 1990, Death and Winterbourn 1995) and periphyton (Biggs 1995).

The role of movement and landscape connectivity in distribution patterns

The movement of an organism, defined as a change in the spatial location of the individual over time, is a fundamental characteristic of life, driven by processes that can act across multiple temporal and spatial scales (Nathan et al. 2008). Movement is an important ecological process that occurs at the individual level, but has ramifications for populations, communities, and evolution (Baker 1978, Dodson 1997, Nathan et al. 2008, Morales et al. 2010). There is a range of movement behaviours that animals undertake in their lifetime: individuals within populations often move little over long periods, punctuated by relatively brief, but important, periods of movement (Schlosser and Angermeier 1995, Vokoun and Rabeni 2005). Movements between habitat patches and breeding sites are now generally described as dispersal, and are considered to be different from movements within patches or foraging areas (Hawkes 2009).
To understand the importance of movement we have to understand the importance of landscape connectivity. Landscape connectivity is considered a vital element of landscape structure (Taylor et al. 1993) because it is so critical to population survival (Fahrig and Merriam 1985, Fahrig and Paloheimo 1988) and metapopulation dynamics (Levins 1970). Landscape connectivity can be defined as “the degree to which the landscape facilitates or impedes movement between resources patches” (Taylor et al. 1993). Connectivity is often divided into three categories, “structural”, “potential” and “actual” connectivity. Structural connectivity is based on the physical elements of the landscape that influence species distributions, which includes the size and arrangement of habitat patches in the landscape, the distances among habitats, and relative disturbance (Calabrese and Fagan 2004).

“Potential connectivity” considers whether a species can navigate the landscape to access suitable habitat patches. It does this by considering the mobility of an organism and the characteristic of the landscape that favour or limit movement. Species vary in their mobility and how they respond to the landscape. Individuals, of some species, usually vary in their mobility relative to other species. That variability is “inherent” and likely subject to isolation of some populations and the eventual development of genetic differences. Learning and behavioural adaptations are also likely involved. These differences in inherent mobility produce different rates, patterns and scales of biological connectivity in the landscape (Taylor et al. 1993).

Movement of riverine organisms

The movement of organisms in rivers is defined largely by the unidirectional flow of water. For many animals, this makes maintaining their position in rivers or streams a challenge, and can inevitably result in downstream displacement. This is particularly
the case during high flow events, but even during moderate to low flows, downstream losses may be substantial due to drift, particularly for macroinvertebrates (Brittain and Eikeland 1988). The ability of drift of macroinvertebrates has been well-documented, and is a common event for many species (Waters 1972, Brittain and Eikeland 1988). Because drift is so common, ecologists have been led to consider compensatory mechanisms for the maintenance of local populations (Elliott 1971, Benson and Pearson 1987, Williams and Williams 1993). For aquatic invertebrates that can fly as adults, upstream flight and oviposition are considered influential in compensating for downstream losses by drift (Elliott 1971, Hershey et al. 1993). For fully aquatic animals, however, swimming or crawling is the only way that these animals are able to move upstream. These upstream movements have been observed in freshwater crabs (Ryan and Choy 1990), crayfish (Momot 1966) and shrimp (Lee and Fielder 1979, Bauer and Delahoussaye 2008, Kikkert et al. 2009). In addition, many stream animals display positive rheotactic behaviour in response to elevated flows (Hultin et al. 1969, Hynes and Hynes 1970, Elliott 1971, Lee and Fielder 1984, Williams and Williams 1993, Hancock and Bunn 1999, Hancock and Hughes 1999). This behaviour is generally understood to be an adaptation to maintain populations in streams and rivers with variable flows which allows these species to recolonise dried-out or erosion-denuded river or stream reaches where local extinction has occurred (Minckley 1964, Bishop and Hynes 1969).

Upstream movement may require significant energy expenditure, can increase predation risk, and may necessitate physiological adjustments (Bernatchez and Dodson 1987, Gross et al. 1988, Jonsson et al. 1997, Hinch and Rand 1998). Many species minimize these costs by timing upstream movement with the most
favourable conditions (Gross et al. 1988, Jonsson et al. 1997, Rivinoja et al. 2001, Dahl et al. 2004). The factors that affect the timing of these movements are often unknown, but movement is commonly stimulated by one or more proximate environmental cues, including flow (Dahl et al. 2004, Lytle and Poff 2004).

The flow of water in rivers also acts as a vector for the dispersal of many riverine organisms. For example, flow often facilitates longitudinal connectivity by allowing the passive distribution of the eggs and larvae of some species from upstream sites to downstream sites (Lancaster 2008), and high flow events facilitate lateral connectivity by allowing passive and active movement of organisms between the main river channel and the floodplain, which many species require to complete their life history (Bunn and Arthington 2002). Concepts developed in terrestrial ecology about the effects of dispersal at the landscape scale and are often applicable in freshwater ecosystems (Fausch et al. 2002). These include movement from source areas to “sink” habitats that cannot support reproduction (source–sink dynamics) (Lidicker 1975, Van Homne 1983, Roughgarden and Iwasa 1986, Pulliam 1988); movement of organisms among habitats to complement non substitutable resources or supplement substitutable resources (termed habitat complementation and supplementation) (Tilman 1982); and boundaries of habitat patches that facilitate or limit animal movements (neighborhood effects) (Pulliam et al. 1992).

River regulation

Critical to all dispersal behaviours is landscape connectivity, the inverse of which is landscape fragmentation. Habitat fragmentation is one of the most commonly cited threats to species extinction and an ensuing loss of biological diversity, making it perhaps the most important contemporary conservation issue (Wiens 1996). Lord
and Norton (1990) referred to fragmentation as simply the disruption of continuity. Throughout the world, river regulation through the construction of dams and weirs for water abstraction for irrigation, hydroelectricity generation, river transport or other purposes, has resulted in widespread habitat fragmentation (Poff et al. 1997). This fragmentation comes in two main forms; the restriction of dispersal because of physical barriers such as dams and weirs and major changes to natural flow regimes (Poff et al. 1997, Bunn and Arthington 2002).

The natural flow regime is defined by five critical components that regulate ecological processes in river ecosystems: the magnitude, frequency, duration, timing, and rate of change of hydrologic conditions such as high and low flows (Poff and Ward 1989, Richter et al. 1996, Walker et al. 1995). River regulation typically alters one or more of the components of a flow regime which in turn alters the arrangement of habitat patches through space and time (Ward and Stanford 1979, Petts 1984, Calow and Petts 1992). These changes to the natural flow regime are thought to impact on many critical biological functions and processes, such as spawning and recruitment (Humphries and Lake 2000, Bunn and Arthington 2002). Specifically, impacts as a result of river modification can include: the loss of flow-related cues that trigger movements to suitable spawning areas; increased mortality of early life history stages due to an increased risk of drift; and restricted migration and dispersal because of physical barriers such as dams and weirs (Bunn and Arthington 2002). Movement is often a key component of these functions and processes; therefore a species “dispersal capability” and the “inherent mobility” of individuals within each species has a strong bearing on the capacity to adapt to changes in flow and river connectivity. This can strongly influence the occurrence of particular species in modified rivers.
Shrimp

Throughout the world, caridean shrimp (Crustacea, Decapoda) contribute to many trophic interactions and are often a very important component of aquatic food webs (Covich et al. 1991, Pringle et al. 1993, Crowl and Covich 1994, Pringle 1996, Crowl et al. 2001, March et al. 2002). Many shrimp species are opportunistic omnivores (feeding on algae, detritus and small invertebrates) (Pringle et al. 1993, Burns and Walker 2000), and their foraging activities play an important role in ecosystem function, particularly in regards to their role in detrital dynamics and nutrient cycling (Covich et al. 1999, Crowl et al. 2001, March et al. 2001).

Although most caridean shrimps are marine, there are numerous freshwater species, especially in the Families Atyidae and Palaemonidae (subfamily Palaemoninae) (Bauer 2004, De Grave et al. 2008). Many of these species have an amphidromous life history, in which breeding and spawning occurs in fresh water, but larval development takes place in brackish or fully marine waters (McDowall 2007). Often the larvae of these species drift downstream to reach these waters (March et al. 1998, Pringle and Ramírez 1998, Benstead et al. 1999). After larval development, the newly-metamorphosed juveniles find river mouths or freshwater inlets and migrate into the adult riverine habitat (Hunte 1978, Hamano and Hayashi 1992, Hamano and Honke 1997, Holmquist et al. 1998, Benstead et al. 2000). It is thought that this amphidromous lifestyle is a mechanism which has evolved to allow these species to disperse among coastal rivers and streams (Hunte 1978, McDowall 2007), however, can also be related to differences in productivity between freshwater and the ocean, and resultant food availability for different life history stages (Gross et al. 1988).
Although many shrimp species require salt water for larval development, the life history of some species occurs wholly in freshwater (Anger 2013). In such species, the extended planktonic development of their marine ancestors has been replaced with abbreviated or direct development, in which embryos hatch as advanced larval stages or juveniles, which do not require salt water (Mashiko and Shy 2008). Despite this, there is evidence to suggest that some of these wholly freshwater species still undertake significant movements (Lee and Fielder 1979). These species, as with many other stream organisms, may require access to an array of habitat types for feeding and reproduction, and also access to refuges from predators and environmental extremes (Humphries et al. 2006, Price and Humphries 2010). Depending on the spatial arrangement of habitat patches in the landscape, shrimp may have to move some distance to find scarce or critical resources. Consequently, movement can influence a variety of patterns of distribution in stream shrimps, such as source-sink dynamics and colonisation of habitats (Covich et al. 1996), and shrimp assemblage structure (Covich et al. 2006). Thus, sound conceptual and empirical knowledge of movement is necessary to improve our understanding of stream-shrimp ecology and also to inform conservation efforts occurring in systems that are increasingly modified by humans (March et al. 1998, Benstead et al. 1999).

The factors that influence the movement of riverine shrimp remain relatively unexplored. Some studies have related the probability of movement to site-specific characteristics, such as depth or current velocity (Kikkert et al. 2009). Others have examined the influence of factors that occur over larger spatial scales. For example, Hancock (1995) documented a positive relationship between rates of larval shrimp drift and discharge. Kikkert et al. (2009) discovered that the migration of some species is influenced more by discharge, whereas others are influenced more by
season. Factors that vary over very short (e.g., time of day) and longer (e.g.,
daylight) time periods may also influence movement (Lee and Fielder 1979,
Kikkert et al. 2009). Most of the factors studied reflect abiotic conditions, but
attributes of individual shrimp and biotic factors have also been examined. For
example, Hein and Crowl (2010) found that adult shrimp (*Atyalanipes*) will move
upstream to avoid predators.

*Shrimp of the Murray-Darling Basin*

Three species of caridean shrimps occur in the Murray-Darling Basin (Figure 1.1).
There are two atyid species, *Paratya australiensis* and *Caridina mccullochi*, and one
palaeomonid species, *Macrobrachium australiense*. The three species often reach
high densities (Boulton and Lloyd 1991, Sheldon and Walker 1998) and are
important food sources for native fish (Ebner 2006, Baumgartner 2007). These
shrimp are opportunistic omnivores, feeding on algae, detritus and small
invertebrates (Burns and Walker 2000), and their foraging activities provide essential
ecosystem services by accelerating detrital decomposition. As a result, these shrimp
are likely to be a key component in processing of organic material and nutrient
cycling (Wallace and Webster 1996, Covich et al. 1999, Crowl et al. 2001, March et
al. 2001). Thus, knowledge of their distribution and habitat use is essential for an
understanding of the ecology of rivers within the Murray-Darling Basin.

*Paratya australiensis* is the most common and widespread of the three species. Its
distribution extends across south-eastern Australia from coastal streams along the
east coast to the Torrens River in South Australia, and from the northern tip of
Queensland to eastern Tasmania. It most commonly inhabits lowland rivers and
streams, but is also found in non-flowing freshwater environments (Williams 1977),
and some upland streams in Queensland (Hancock and Bunn 1997). *Caridina mccullochi* is found throughout eastern Australia (Richardson et al. 2004, Page and Hughes 2007), however, details of its distribution remain largely unexplored. *Macrobrachium australiense* is found in coastal and inland waters of eastern Australia (Riek 1959, Fielder 1970). Riek (1951) recognized four subspecies within the species *australiense*, although only one species is found in the Murray-Darling Basin (Short 2004). Recent genetic studies have also led to uncertainty regarding the taxonomic status of *P. australiensis* and *C. mccullochi* (Page et al. 2005, Cook et al. 2006). *Paratya australiensis* is currently considered a complex of cryptic species and this may also be the case for *C. mccullochi*, however, differences among lineages are mostly between isolated populations and any differences within the Murray-Darling Basin are likely to be small (Fawcett et al. 2010).

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Figure 1.1. Map of Australia showing the extent of the Murray-Darling Basin.
Physical habitat has a known influence on shrimp in the Murray-Darling Basin (Richardson et al. 2004, Humphries et al. 2006, Richardson and Cook 2006, Price and Humphries 2010). However, it is difficult to establish explicit links between the abundance, distribution of a species and habitat attributes, due to the lack of shrimp occurrence data across large areas of river systems. Linking habitat attributes to distribution, when examined only at one spatial scale, is difficult, because patterns of association change depending upon the scale of observation (Cooper et al. 1998). In general, the current understanding of what drives shrimp distribution and assemblage patterns at the catchment scale and beyond is largely rudimentary and non-quantitative. Major management decisions and environmental policy are often developed for large scales, and the mismatch of scales makes conservation efforts hard to apply (Fausch et al. 2002). One reason for this may be that, even amongst the relatively species-poor shrimp assemblages in rivers of the Murray-Darling, there is deficient understanding of the nature and extent of movement or migratory life histories of these shrimp. This lack of understanding is not restricted to shrimp of the Murray-Darling. In general, conceptual frameworks that describe "rules" governing assemblage structure of many riverine species do not take into account movement behaviour. Consequently, there are conspicuous gaps in our perspectives and understanding of the dynamics of assemblages in rivers.

Recent studies have indicated that the distribution and abundance of shrimp may be negatively affected by changes to the natural flow regime (Richardson et al. 2004, Price 2010). Given ongoing modifications to the hydrology and dynamics of rivers in Australia, and the potential for large-scale changes in stream structure because of climate and landscape change (Thoms and Sheldon 2000), understanding the link between movement and shrimp assemblage dynamics may be crucial to addressing
future impacts on demography, evolution, and community assembly in shrimp living in streams.

Thesis objectives

The overall theme of this thesis focuses on how flow variables interact with movement to influence patterns of distribution of three species of shrimp, *Caridina mccullochi*, *Paratya australiensis* and *Macrobrachium australiense*, in the southern Murray-Darling Basin. It is hypothesised that flow regime and movement behaviour play a significant role in the distribution of shrimp in this region of the Murray-Darling Basin. To test this hypothesis, the dissertation is organized into four research chapters, each focusing on exploring and comparing the distribution, movement behaviour and life history adaptations of the three species for living in flowing waters, to tease apart the key drivers of shrimp assemblage patterns in the Murray-Darling Basin.

Chapter two describes shrimp assemblage patterns throughout the southern Murray-Darling Basin, and focuses on the effect of flow regime on the occurrence of the three species in the southern Murray-Darling, with particular focus on modified flow regimes.

Chapter three compares the temporal and spatial distribution and abundance patterns of the three species of shrimp along the length of the King River, a moderate, unregulated river in the southern Murray-Darling Basin, to determine the main drivers of distribution patterns under relatively natural conditions, and to explore the potential role that movement plays in these patterns.

Chapter four focuses on the mesoscale movement patterns of the three species of shrimp in the King River, to determine whether upstream dispersal/migration events
occur, how these may affect temporal and spatial population dynamics and distribution, and how these relate to breeding and different life history stages.

Chapter five compares the ability of the three species of shrimp to maintain position in, and their behavioural response to, current, to investigate the role that “inherent mobility” plays in distribution and assemblage patterns.

Chapter six presents a synthesis of research from Chapters 2-5, to explain how the interaction between flow and the movement-related life history and behavioural traits of individual species may ultimately affect shrimp assemblage structures and distribution in the Murray-Darling Basin.
CHAPTER 2
EFFECTS OF FLOW REGIME ON THE OCCURRENCE OF THREE SPECIES OF SHRIMP IN THE SOUTHERN MURRAY-DARLING SYSTEM

2.1 Introduction

The flow regime largely drives ecological processes in rivers (Poff et al. 1997, Bunn and Arthington 2002, Lytle and Poff 2004, Poff and Zimmerman 2010). Among other things, it influences the type, availability and persistence of habitat for riverine biota (Hill et al. 1991, Price et al. 2012). It also plays a major role in the movement of these organisms, sometimes facilitating and sometimes impeding their movement among habitats (Poff et al. 1997). Because of the significance of flow, it is believed that many organisms have evolved traits specifically adapted to the natural flow regime in their native habitat (Lytle and Poff 2004).

Because of the temporal dynamics of the flow regime, at any one time a particular habitat patch may be a pool (slow flowing and relatively deep), and then at another time become a run with flowing water when discharge increases. This variation of habitat patches through time can pose a significant challenge to riverine organisms. Highly mobile organisms, such as fish, are able to respond to shifts in habitat arrangement by moving to a new suitable patch, and as result, these shifts may have little impact (Crook et al. 2001, Crook 2004, Humphries et al. 2006). However, for less mobile organisms, such as benthic macroinvertebrates, changes to flow and the resulting effect on habitat availability, may result in substantial mortality and may have a negative impact on recruitment of a species (Lancaster and Hildrew 1993).

River regulation typically changes the natural seasonal magnitude, duration and predictability of high and low flow events (Poff et al. 1997, Bunn and Arthington...
2002), affecting conditions downstream (Poff and Zimmerman 2010). Because of these changes the impacts of river regulation can include physical barriers to movement, loss of flow-related cues for breeding, changes in water quality, loss of habitat and altered food availability (Bunn and Arthington 2002). Given that riverine organisms have evolved under the natural flow regime, it is not surprising that river regulation has been found to have adverse impacts on key life history events, such as spawning, recruitment, dispersal and migrations (Poff et al. 1997, Anderson et al. 2006), which in turn may reduce the abundance and occurrence of sensitive species (Humphries and Lake 2000, Bunn and Arthington 2002, Collier and Quinn 2003). Environmental flow releases are designed to provide flows to mitigate some of these impacts. However, management of environmental flows requires a sound understanding of the relationship between components of a flow regime and key features of organisms, populations and communities.

A few studies have investigated the impact of flow and regulation on freshwater shrimp distribution and assemblage dynamics (Holmquist et al. 1998, Benstead et al. 1999, Bauer and Delahoussaye 2008, Crook et al. 2009), however, the flow requirements of freshwater shrimps remains relatively unexplored, especially compared to other riverine organisms such as fish. Given their size and relatively limited swimming ability compared to fish, shrimp may be less likely to be able to respond to shifts in habitat arrangement than many fish species. A more comprehensive understanding of the role flow regime has in structuring freshwater shrimp assemblages, therefore, would be invaluable, especially considering the extent of river regulation throughout the world.

Many of the rivers in the southern Murray-Darling Basin have experienced dramatic alterations to their flow regimes, particularly lower order rivers with large
impoundments upstream which have been developed for irrigation (Gehrke et al. 1995). Although rainfall patterns are highly variable (Nicholls et al. 1997), the rivers of the southern Murray-Darling Basin in a normal year receive most of their flow from winter rainfall and snow melt in winter and spring (McMahon et al. 1992, McMahon and Finlayson 2003). Because of this, natural flows are usually higher in winter and spring and low in summer and autumn. However, throughout the 20th century, river regulation and diversions for irrigation and hydroelectricity generation have had a major impact on the flow of many rivers, to the point where the long-term mean annual discharge of the whole Murray-Darling system has been reduced by an estimated 56% (Thomson 1994), and the seasonality of the flow regime of some rivers has been reversed (Maheshwari et al. 1995, Thoms and Sheldon 2000).

To date, the impact of flow regulation on the shrimp of the southern Murray-Darling Basin has received little attention. A notable exception is Richardson et al. (2004), who compared the distribution and abundance *P. australiensis, M. australiense* and *C. mccullochi* in the lowland sections of the highly regulated Campaspe River and relatively unregulated Broken River in northern Victoria. Richardson et al. (2004) found that shrimp assemblages varied markedly among sections with different hydrological regimes. *Paratya australiensis* and *M. australiense* occurred along the length of both rivers, whereas *M. australiense* was only present in low abundances in sections of the Campaspe River that received irrigation flows during summer and autumn; a period which would naturally experience low flows. In addition, *C. mccullochi* was completely absent from the heavily regulated sections of the Campaspe River, but was present in the relatively unregulated section, and at all sites on the unregulated Broken River.
Key to these findings may be the hydraulic habitat preferences of these species. In a study of the habitat preferences of the three species, Richardson and Cook (2006) found that *P. australiensis* occurred across a range of hydraulic habitats; *M. australiense* was restricted to still littoral habitats as larvae but showed a preference for faster-flowing habitats as adults, and *C. mccullochi* was restricted to still and slow-velocity habitats at all life stages. In heavily modified rivers, the availability and persistence of still or slow-velocity habitats may be altered (Bunn and Arthington 2002, Bowen et al. 2003, Humphries et al. 2006, Price et al. 2012, Vietz et al. 2013), which in turn may negatively impact upon the abundance and occurrence of species which require these habitats to complete their life cycle.

This chapter examines the distribution of the three caridean shrimp species in the south-eastern Murray-Darling Basin, with the overall aim to identify the impact of flow regime regulation on the distribution of shrimp, based on the work of Richardson et al. (2004), it is hypothesised that flow regulation, particularly the lack of low flow periods during summer in rivers that are used to deliver irrigation water, has a negative impact on the occurrence of *C. mccullochi*.

Specifically, the chapter aims to:

Compare the presence/absence of the three species among hydrologically distinct river sections in the southern Murray-Darling Basin; and

Characterise the flow regime variables of regulated rivers and the effect these regimes may have on the occurrence of the three species throughout southern Murray-Darling.
2.2 Methods

2.2.1 Study Area

The influence of flow regulation on shrimp assemblages was evaluated in the south eastern region of the Murray-Darling Basin in south-eastern Australia (Figure 2.1). Most of the rivers in the southern Murray-Darling Basin experience varying degrees of flow regulation, mostly through the operation of many large in stream storages. There are also some significant diversions for irrigation, including the Murrumbidgee irrigation area in the lower Murrumbidgee, and the Goulburn–Murray and Torrumbarry Irrigation areas, which divert water from the lower Goulburn, Campaspe and Loddon Rivers and the middle section of the Murray River. There is also the Murray Irrigation Area that also diverts water from the middle Murray as well as the Edward River. The Sustainable Rivers Audit (SRA) developed a rigorous method to assess the ecosystem health of rivers in the Murray–Darling Basin based on indexes for hydrology, fish, macroinvertebrates, riparian vegetation and physical form (Davies et al. 2012). The Hydrology theme measures ecologically significant aspects of the flow regime including volume, variability, extreme flow events and seasonality. The SRA uses Flow Stressed Ranking (FSR) hydrology metrics, with some additions and modifications. This characterises the degree of hydrologic ‘regime change’ relative to ‘unimpacted’ reference flow conditions (Davies et al. 2012). Most of the river reaches below major irrigation storages sampled in this study have SRA hydrology condition scores that class them as Poor or Very Poor with only small sections of the Loddon and Campaspe rivers classed as moderate or better (Figure 2.1).
The hydrology of the Campaspe River is characterised by a significant difference from reference condition in flow seasonality, moderate alteration in flow variability and low- and zero-flow events and near to reference condition in high-flow. There is a significant difference from reference condition for the flow regime of within channel flows. The Goulburn Valley river system is characterised by a significant difference from reference condition in flow seasonality and flow variability. A significant difference from reference was also found for low- and zero-flow events and a moderate difference in high-flow events (Davies et al. 2012).

The hydrology of the Lachlan River is characterised by close to reference condition for low over bank floods and flow variability, and a very large difference from reference in low- and zero-flow events. The Loddon Valley river is characterised by a mainstem river reaches with a very large difference from reference condition in flow seasonality, and moderate alteration in flow variability and low- and zero-flow events. The frequency of high-flow events is near to reference condition in the Loddon (Davies et al. 2012).

The section of Murray River sampled in this study was divided into upper (upstream of Lake Hume) and central (Lake Hume to the Murray–Darling junction) by the SRA. The Upper Murray river shows a very large difference from reference condition in flow variability and low- and zero-flow events; and moderate difference from reference in flow seasonality. The Central Murray Valley river system is characterised by a very large difference from reference condition in flow seasonality, a significant difference in high-flow events and moderate alteration in high over bank floods, low over bank floods, flow variability and low- and zero-flow events. The Murrumbidgee Valley river system is characterised by a very large difference from reference condition in flow variability and low and zero-flow events; a
moderate difference in flow seasonality; near reference for high-flow and a moderate difference in high over bank floods. Both the Broken and Ovens river systems are characterised by near reference condition in flow variability, flow seasonality, low- and zero-flow events and high-flow events. The Mitta Mitta River system is also characterised as near to reference condition in low- and zero-flow events however, the Mitta Mitta river system shows a significant difference from reference in flow seasonality (Davies et al. 2012).

2.2.2 Study site selection

Sampling was limited to 13 major tributaries of the Murray River upstream of the junction of the Murray and Darling Rivers. Sampling took place in 47 different river sections, separated by regulatory structures, and characterised by differences in hydrological regimes. Each section selected for the study was required to have a gauging station from which to obtain discharge data. These sections varied in altitude from 286 m on the slopes of the Great Dividing Range, to 57 m in the lowland sections. Sections of river below 200 m were classified as lowland (Table 2.1). Using a map generated with GIS software Arc Map 10.2.2, reaches within each section were established based on access, and reaches were randomly selected where there was more than one access point. To maximize the chance of capturing all species present in each section, 300 m reaches were established.
Figure 2.1. Map of the study area in the south-eastern Murray-Darling Basin showing the location of major rivers and major irrigation storages which regulate flows downstream and the Sustainable Rivers Audit (SRA) condition score for each river reach sampled (Davies et al. 2012).
<table>
<thead>
<tr>
<th>River</th>
<th>Section name</th>
<th>Reach no.</th>
<th>Altitude</th>
<th>Coordinates</th>
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<td>152</td>
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<td>203</td>
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<td>143°53'28&quot;E</td>
<td>35°38'4&quot;S</td>
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</tbody>
</table>

2.2.3 Sampling and processing of shrimp

Each reach was sampled between December 2011 and March 2012, when shrimp populations are normally at their peak (Richardson et al. 2004, Richardson and Humphries 2010). Prior to conducting this study, a pilot study had established that the greatest abundance of shrimp in reaches was found in slackwaters, and particularly in slackwaters that were at least 50 cm deep. This is supported by Kneipp (1979), who found that *M. australiense* prefers depths of at least 30 cm. The
pilot study also established that no additional species were detected when conducting 5 m sweeps of a dip net in more than five slackwaters along a stretch of river (J Dyer unpublished data). In fact, when present in a particular reach, the three shrimp species often occurred in large numbers and were present in most slackwaters with sufficient depth. Therefore, sampling for this study was conducted using a dip net (35 x 25 x 25 cm, 250 µm mesh) to sweep at least 5 m of substrate in each reach. In an effort to maximize the chance of catching all species present in a particular section, five slackwaters, 30-75 cm deep were sampled on each occasion within each reach. Samples were preserved in 70% ethanol for identification (Hawking et al. 2006) at a later date in the laboratory using a dissecting microscope.

2.2.4 Flow regime analysis

Many flow variables were calculated to describe the temporal hydrological patterns throughout the study area. Flow variables were calculated from hydrological data obtained from the NSW Water Information website (www.waterinfo.nsw.gov.au) and the Victorian Water Measurement Information System (www.data.water.vic.gov.au). For each site that was sampled, daily discharge data for 10 years prior to sampling was taken from the gauging station that was in the corresponding river section. Analysis of this data was conducted using the River Analysis Package (RAP) Version 3.0.7 (Marsh et al. 2003). Hydrological variables were chosen to consider high (maximum flow, total and mean duration, and number of 90th percentile flows), low (minimum flow, total and mean duration, and number of 10th percentile flows, number of zero flow days), mean, median and variability (variability and coefficient of variation) of flows (Table 2.2). All variables were calculated separately for two seasonal time-periods of each year of the study - autumn/winter (April to July) representing the non-reproductive season and
spring/summer (August to March), representing the breeding period (Richardson and Humphries 2010). Any missing data points for daily discharge were filled using multiple linear regression, which is a function of the RAP software. Multiple linear regressions were used rather than using neighbouring hydrographs to synthesise flow data for missing dates because in the most cases the use of a neighbouring hydrographs would be misleading due to anthropogenic modification such as weirs and abstraction for irrigation.

2.2.5 Data analysis

Although the chance of non-detection when a species was indeed present was likely to be low based on previous studies (Richardson et al. 2004; J Dyer unpublished data), differences among all the rivers sampled in the current, and the rivers sampled in the previous, studies meant that the detection probability could not be guaranteed to be 100% on any one sampling occasion. Therefore, to obtain estimates of site occupancy (presence or absence of a particular species), single-season occupancy models were generated using the computer program PRESENCE, which uses maximum-likelihood methods to estimate parameters (MacKenzie et al. 2002, MacKenzie and Royle 2005). This method is useful for estimating the site occupancy probability of a target species, in situations where the species is not guaranteed to be detected even when present at a site. This single-season method has been used successfully in many previous studies (MacKenzie and Royle 2005, Joseph et al. 2006). This method also allows for the inclusion of sampling specific covariates, such as local environmental conditions, which may affect the detection probability of a particular species.
The importance of each flow variable was tested separately for each of the three shrimp species using variations in the basic model parameters. These models were ranked according to AIC values (Akaike 1973, Burnham and Anderson 1998) calculated by program PRESENCE. The lowest ranked models for each species were combined to explore if including multiple covariates improved model performance. It should be noted that the models were chosen a priori to compare several variables typical of regulated rivers that based on previous studies were thought to be likely to affect occupancy estimates. The model selected “best” does not necessarily represent all the environmental or biological processes that influenced the probability of occupancy. The top occupancy parameters from the top models (lowest AICc values) were tested for significance using 95% confidence intervals.
Table 2.2. Hydrological variables calculated from Marsh et al. (2003), their abbreviations and definitions, used in exploring relationships between shrimp distribution patterns and hydrology.

<table>
<thead>
<tr>
<th>Hydrological variable</th>
<th>Abbreviation</th>
<th>Definition</th>
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</thead>
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<tr>
<td>No. of low spells</td>
<td>LSN</td>
<td>Number of low flow spells below the 10th percentile</td>
</tr>
<tr>
<td>Mean Duration of Low Spells</td>
<td>LSD</td>
<td>Mean duration of low flow spells below the 10th percentile</td>
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<td>Mean No. of Low Spells in Summer</td>
<td>LSNSum</td>
<td>Mean number of low flow spells below the 10th percentile in summer</td>
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<td>Mean Duration of Low Spells in Summer</td>
<td>LSDSum</td>
<td>Mean duration of low flow spells below the 10th percentile in summer</td>
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<td>No. of High Spells</td>
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<td>Number of high flow spells above the 90th percentile</td>
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<td>Mean Duration of High Spells</td>
<td>HSD</td>
<td>Mean duration of high flow spells above the 90th percentile</td>
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<td>Mean duration of high flow spells above the 90th percentile in summer</td>
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<tr>
<td>Minimum</td>
<td>Min</td>
<td>Minimum flow (ML/day) during the 10 yrs prior to sampling</td>
</tr>
<tr>
<td>Maximum</td>
<td>Max</td>
<td>Maximum flow (ML/day) during the 10 yrs prior to sampling</td>
</tr>
<tr>
<td>Mean</td>
<td>MDF</td>
<td>Mean daily flow (ML/day) in the 10 yrs prior to sampling</td>
</tr>
<tr>
<td>Median</td>
<td>Med</td>
<td>Median daily flow (ML/day) in the 10 yrs prior to sampling</td>
</tr>
<tr>
<td>Coefficient of variation</td>
<td>CV</td>
<td>The ratio of the standard deviation to the mean</td>
</tr>
<tr>
<td>Variability</td>
<td>Var</td>
<td>Variability of flow during the 10 yrs prior to sampling = range (10th–90th percentile) divided by the median</td>
</tr>
<tr>
<td>Zeros</td>
<td>Zer</td>
<td>Number of zero flow days</td>
</tr>
</tbody>
</table>
2.3 Results

2.3.1 Shrimp occupancy and distribution

Overall *P. australiensis* was the most common species and *C. mccullochi* was the least common species collected from the river reaches in the south-eastern region of the Murray-Darling Basin included in the present study. *Caridina mccullochi* only occurred at 16 of the 47 reaches that were sampled. They ranged from the Murray River at Corowa in the east (146°27'13"E  35°59'48"S) to the Murray River at Swan Hill in the West (143°36'13"E  35°19'7"S), and from the Edward River downstream of Moulamein (143°48'6"E  35°2'25"S) in the north and the Goulburn River at Murchison in the south (145°16'52"E  36°36'25"S) (Figure 2.2). This species was restricted to sites below 160 m asl. *Paratya australiensis* occurred at 42 of the 47 reaches that were sampled: from the Murrumbidgee River at Gobarralong in the east (148°17'18"E  34°54'29"S) to the Murray River at Swan Hill in the west (143°36'13"E  35°19'7"S), and from the Lachlan River at Condobolin in the north (147°9'18"E  33°7'31"S) to the Loddon River at Newstead in the south (144°10'35"E  37°7'54"S) (Figure 2.3). The reaches at which *P. australiensis* were absent were all over 200 m asl, and three of the five reaches at which they were absent were in the heavily regulated sections of rivers close to large dams. *Macrobrachium australiense* occurred at 38 of the 47 reaches and also ranged from the Murrumbidgee River at Gobarralong in the east (148°17'18"E  34°54'29"S) to the Murray River at Swan Hill in the west (143°36'13"E  35°19'7"S), and from the Lachlan River at Condobolin in the north (147°9'18"E  33°7'31"S) to the Broken River at Swanpool in the south (146°2'10"E  36°45'44"S) (Figure 2.4). The reaches where *M. australiense* were absent were over 200 m asl, except for the reach at Seymour, which is in a heavily
regulated section of the Goulburn River below Lake Eildon. The proportion of sites at which each species was detected (i.e., naïve occupancy) was 0.34 for *C. mccullochi*, 0.81 for *M. australiense* and 0.91 for *P. australiensis* (Table 2.4).

For *C. mccullochi*, the top occupancy models included the mean number of high flow spells in summer above the 90th percentile (Table 2.3). The parameter estimate for this covariate did not overlap zero in the 95% CI after model averaging (Table 2.4), meaning that there was a significant negative relationship between this flow variable and the occupancy of *C. mccullochi*. The median number of high flow spells in summer across all rivers was 1.5, whereas in rivers where *C. mccullochi* was present, it was 0.8, and in rivers where *C. mccullochi* was absent, it was 2.0 (Figure 2.5).

The flow variable in the top *P. australiensis* occupancy models was Coefficient of variation, and the variable in the top occupancy model for *M. australiense* was Variability (Table 2.3). In both cases, however, the 95% CI for the parameter overlapped with zero after model averaging (Table 2.4), meaning that flow variables did not have a significant effect on the occupancy of these two species (Figures 2.6 and 2.7).
Table 2.3. Results of the flow variable occupancy models for the three species of shrimp in the south-eastern region of the Murray-Darling Basin. Explanations for abbreviations are in Table 2.2.

<table>
<thead>
<tr>
<th>Species</th>
<th>Model</th>
<th>AIC</th>
<th>Δ AIC</th>
<th>AIC wgt</th>
</tr>
</thead>
<tbody>
<tr>
<td>C. mccullochi</td>
<td>psi(HSNSum and HSDSum)</td>
<td>67.18</td>
<td>0</td>
<td>0.98</td>
</tr>
<tr>
<td></td>
<td>psi(HSNSum)</td>
<td>76.12</td>
<td>8.94</td>
<td>0.01</td>
</tr>
<tr>
<td></td>
<td>psi(HSNSum and Var)</td>
<td>77.26</td>
<td>10.08</td>
<td>0.0064</td>
</tr>
<tr>
<td></td>
<td>psi(.,p(.,)</td>
<td>89.61</td>
<td>22.43</td>
<td>0</td>
</tr>
<tr>
<td>P. australiensis</td>
<td>psi(CV)</td>
<td>28.8</td>
<td>0</td>
<td>0.47</td>
</tr>
<tr>
<td></td>
<td>psi(CV and HSNSum)</td>
<td>29.27</td>
<td>0.47</td>
<td>0.37</td>
</tr>
<tr>
<td></td>
<td>psi(HSNSum)</td>
<td>31.7</td>
<td>2.9</td>
<td>0.11</td>
</tr>
<tr>
<td></td>
<td>psi(.,p(.)</td>
<td>33.36</td>
<td>4.56</td>
<td>0.05</td>
</tr>
<tr>
<td>M. australiense</td>
<td>psi(Var),p(.)</td>
<td>47.88</td>
<td>0</td>
<td>0.64</td>
</tr>
<tr>
<td></td>
<td>psi(HSNSum),p(.)</td>
<td>49.58</td>
<td>1.7</td>
<td>0.27</td>
</tr>
<tr>
<td></td>
<td>psi(.,p(.))</td>
<td>51.91</td>
<td>4.03</td>
<td>0.09</td>
</tr>
</tbody>
</table>
Table 2.4. Summary data for the three shrimp species recorded during surveys and flow variable parameter estimates derived from occupancy model sets.

<table>
<thead>
<tr>
<th>Species</th>
<th>Naïve occupancy a</th>
<th>Flow variable in top occupancy model b</th>
<th>Covariate parameter estimate (95% CI) c</th>
</tr>
</thead>
<tbody>
<tr>
<td>C. mccullochi</td>
<td>0.34</td>
<td>Mean number of high-flow spells in summer 2.77 (-0.57 to -2.83) d</td>
<td></td>
</tr>
<tr>
<td>P. australiensis</td>
<td>0.91</td>
<td>Coefficient of variation 1.44 (3.46 to -0.57)</td>
<td></td>
</tr>
<tr>
<td>M. australiense</td>
<td>0.81</td>
<td>Variability 0.06 (0.12 to -0.01)</td>
<td></td>
</tr>
</tbody>
</table>

aProportion of sites at which the species was detected.
bTop models are those with the lowest AICc scores in a model set. Covariates are flow regime variables.
cSize and direction of the relation between the covariate and occupancy. Parameter estimates derived by averaging across all occupancy models that included the covariate.
dSignificant directional trend (i.e., does not overlap with zero in the 95% CI).
Figure 2.2. Occurrence of *Caridina mccullochi* in the south-eastern Murray-Darling Basin.

Present ●  absent ○.
Figure 2.3. Occurrence of *Paratya australiensis* in the south-eastern Murray-Darling Basin.

Present ● absent ○.
Figure 2.4. Occurrence of *Macrobrachium australiense* in the south-eastern Murray-Darling Basin.

Present ● absent ○.
Figure 2.5. Box plots illustrating the relationship between mean number of high flows above the 90th percentile and the occurrence of C. mccullochi, P. australiensis, and M. australiense.
Figure 2.6. Box plots illustrating the relationship between Coefficient of variation (CV) of flow and the occurrence *C. mccullochi, P. australiensis and M. australiense.*
Figure 2.7. Box plots illustrating the relationship between variability of flow and the occurrence *C. mccullochi*, *P. australiensis* and *M. australiense*. 
2.4 Discussion

The results of this study provide new information on the importance of flow regulation to the distribution patterns of shrimp in the Murray-Darling Basin. Paratya australiensis and M. australiense occurred in many river reaches that have heavily modified flow regimes, whereas C. mcalcallochi was absent from many of these same reaches, but frequently occurred in reaches with more natural flows regimes. Although it was previously hypothesised low flow spells in summer are required for the persistence of C. mcalcallochi (Richardson et al. 2004), this study found no evidence to suggest that this is critical to the occurrence of this species. Instead, it was found that C. mcalcallochi was less likely to occur in rivers that are more likely to experience high flow events in summer.

The present study examined the occurrence of shrimp across multiple rivers, whereas Richardson et al. (2004) surveyed a single river. Although that study was important in highlighting, for the first time, possible impacts of flow regulation on occurrence and abundance of shrimp, it did not specifically identify particular flow regime variables responsible for observed patterns, and only hypothesised that it may have been due to a lack of natural low flow events. Taking a different approach, the present study directly compared the occurrence of the three species across multiple rivers with different flow regimes, and was able to identify a particular flow regime variable that influences distribution. That is not to say that low flows spells in summer are not important, as they could well have an impact on abundance of both C. mcalcallochi and M. australiense, as suggested by Richardson et al. (2004). But abundance was not studied in the present study, as this would require sampling to take place across multiple seasons to be sure that abundance differences were not
due to temporal factors, which have been shown to significantly impact on shrimp populations in previous studies (Richardson et al. 2004).

In the present study, *C. mccullochi* was found in rivers that rarely experience low flow events in summer, such as the Murray River. Although low flow events are not common, the amount of flow in the Murray River in summer often varies very little (Maheshwari et al. 1995; see Appendix A), which may result in the extended persistence of the slackwater habitats that are available, which in turn ensures the long-term survival of *C. mccullochi*. Aseasonal high flow events are a feature of heavily regulated rivers used for the delivery of irrigation water in the Murray-Darling Basin (Sheldon et al. 2000). These high flow events can change the availability and persistence of slackwater habitats (Bunn and Arthington 2002, Bowen et al. 2003, Veitz et al. 2013). In addition, high flows may also physically displace shrimp, especially larvae (Covich et al. 1996, Hancock and Bunn 1997), although the ability to cope with current is yet to be investigated. One or both of these effects are likely to have a negative impact on the growth and survival of *C. mccullochi* in these rivers. In addition, Richardson and Humphries (2010) hypothesised that interspecific differences in reproductive traits among the three species may also play a role in the occurrence of the three species. *Paratya australiensis* has typically ‘opportunistic’ traits (small body size, small eggs and high fecundity), whereas *M. australiense* has more ‘equilibrium’ traits (larger body size, larger eggs and moderate fecundity). *Caridina mccullochi* is intermediate, with relatively low fecundity and small size. The opportunistic breeding and spawning traits of *P. australiensis* may mean that it is better able to persist in rivers with altered flow regimes, particularly those with highly variable flows during the spawning season compared to *C. mccullochi*.
The negative effect of river regulation and altered flows on the distribution of a particular species, in this case *C. mccullochi*, is not surprising, given that similar results have been found both in other organisms in the Murray-Darling Basin and other freshwater shrimp species elsewhere in the world. For example, river regulation is thought to have a negative effect on the life history events of some fish species in the Murray-Darling Basin, including: spawning (King et al. 2009b), recruitment (Humphries and Lake 2000, Humphries et al. 2002) and movement (Gehrke et al. 1995, O’Connor et al. 2005). River regulation is also thought to have a negative impact on the distribution of amphidromous shrimp species, by restricting the migration events that are needed for these species to complete their life cycle (Holmquist et al. 1998, Benstead et al. 1999, Bauer and Delahoussaye 2008).

Conclusions

The results of this study suggest that river regulation may have led to the extirpation *C. mccullochi* from some sections of lowland rivers in the southern Murray-Darling Basin. In the next chapter, I will describe the spatial and temporal distribution and abundance patterns of the three-shrimp species at a finer scale in a river that experiences a relatively natural flow regime, in an attempt to further clarify the flow conditions and movement mechanisms that drive the patterns of distribution of these species.
3.1 Introduction

In general, flow, channel gradient and channel morphology change systematically from upstream to downstream in rivers (Vannote et al. 1980, Torgersen et al. 2006). All of these factors directly influence the size, shape, arrangement and quality of riverine habitats, or habitat patches (Poff et al. 1997, Bunn and Arthington 2002, Bowen et al. 2003). In particular, spatial and temporal changes in flow and the resultant current speed can play a dominant role in the distribution of many stream organisms, including shrimp (Covich et al. 2003, Richardson et al. 2004, Humphries et al. 2006, Mejia-Ortiz and Alvarez 2010).

Shrimp tend to show species-specific tolerances to current speeds (Lee and Fielder 1984, Hancock and Bunn 1999), but during the larval stage, most species are vulnerable to flow-induced dislodgment and entering the drift passively (Covich et al. 1996; Hancock and Bunn 1999). Some shrimp can avoid being dislodged during high flow events by hiding in crevices and other suitable microhabitats (Covich et al. 1996). Although these behaviours allow shrimp to temporarily resist dislodgment in elevated currents, it is likely to be energetically costly and will likely lead some species to select habitats with reduced hydraulic stress or move into these habitats for at least part of their life cycle. Therefore, for riverine shrimp species, flow and flow-related habitat variables are likely to play a key role in distribution and abundance patterns.
Most species of freshwater caridean shrimp also need saltwater for larval development (Wehrtmann and Bauer 2013). Females of these species often move great distances towards the sea to release their eggs and later, juveniles migrate back upstream from the estuaries into the rivers and streams (Benstead et al. 2000, Bauer and Delahoussaye 2008). For those species of shrimp that do not require saltwater for part of their life, adults may move upstream at times to compensate for passive or active downstream drift of larvae (Hancock and Bunn 1999, Lee and Fielder 1984). These movement events can have a significant impact on the temporal and spatial structure of shrimp assemblages in rivers and streams (Bauer and Delahoussaye 2008, Benstead et al. 2000). The three species of shrimp found in the Murray-Darling Basin do not require saltwater for larval development (Richardson et al. 2004), although juvenile *M. australiense* have been observed moving en masse over weirs (Lee and Fielder 1979) or downstream (P. Humphries personal communication). The extent to which movements of shrimp affect the distribution and abundance of assemblages in the Murray-Darling Basin remains unknown, however the lateral movements to and from slackwater habitats has been investigated by Price and Humphries (2010).

Few studies have examined the small-scale distribution patterns of the three species of shrimp found in the Murray-Darling Basin. In Chapter 2 *C. mccullochi* was found to be restricted to lowland rivers that experience relatively few high flow events during the spawning season. It was hypothesised that this may be due to the adverse effects of high flows on the persistence and availability of slackwater refuges. This hypothesis is supported by Richardson et al. (2004), who compared the distribution of the three species in the lowland sections of the Campaspe and Broken Rivers in
northeast Victoria, and found that *C. mccullochi* was absent from heavily regulated sections of the Campaspe River.

Although a few studies have examined the distribution and abundance of shrimp species in tropical streams and regulated lowland rivers (Covich et al. 1996, Fievet 1999, Fièvet et al. 2001, Richardson et al. 2004), few have studied the entire shrimp assemblages at numerous locations, headwaters to mouth of an unregulated temperate stream. The King River, northern Victoria, offers an excellent opportunity to study the temporal and spatial distribution and abundance patterns of the three species in largely unmodified river system.

The overall aim of this chapter was to compare the temporal and spatial distribution of three species of shrimp in the King River, a moderate, unregulated river in the southern Murray-Darling Basin, to determine the main drivers of shrimp distribution patterns. Temporal changes in the abundance and age classes of the shrimp populations among the reaches could provide evidence of dispersal among these reaches. For example, if shrimp numbers in the upper reaches are low early in the season but then significantly increase later in the season, then it is hypothesised that this could be a result of dispersal from other reaches.

The specific aims were to:

Describe the longitudinal distribution and abundance patterns of *P. australiensis, C. mccullochi* and *M. australiense* in the King River, Victoria, over 7 months, encompassing the breeding season;

Relate these patterns to changes in physiochemical variables and stream morphology from lower, middle and upper reaches; and
Investigate the extent to which distribution and temporal variation in shrimp abundance may be due to movement.

3.2 Methods

3.2.1 Study area

This study was undertaken in the King River, which is in Victoria within the southern region of the Murray-Darling Basin (Figure 3.1). The King River drains an area of 1400 km² on the northern slopes of the Great Dividing Range. From where the river rises, it runs approximately 120 km north and joins the Ovens River at the town of Wangaratta. Elevation ranges from 152 m to over 1500 m asl.

The King River flows through mountainous, heavily forested National Park and state forest for approximately half its length until it reaches Lake William Hovell. Lake William Hovell is a small Dam with a storage capacity of 12,330 ML. Below Lake William Hovell, the valley widens considerably and the river flows through agricultural land (mostly vineyards and grazing) until its junction with the Ovens River. The King River at the outlet from Lake William Hovell has a mean annual flow of approximately 320,000 ML (Goulburn-Murray Water 2010).

3.2.2 Sampling reach selection and description

Study reaches were selected along the length of the known distribution of shrimp in the King River (J Dyer unpublished data). Based on gradient and substrate, this region of the King River was divided up into upper, middle and lower sections (Figures 3.1 and 3.2, Table 3.1). Gradient was calculated using GIS software.
ArcMap 10.2.2. Two reaches were selected in each of these sections, partly on the basis of access. The most downstream reach was established within the lower three river km from the confluence with the Ovens River. The upper reach was established at what was thought to be the uppermost point of shrimp distribution in the King River. The middle sites were established about midway between the upper and lower reaches and based on substrate and gradient represented the transition between lowland and upland river types (Table 3.1). Between each of the reaches there are no significant barriers to movement such as dams or waterfalls. The midpoint of each reach was randomly established upstream or downstream from the access point at a distance from 1 to 250 m. To maximize the chance of getting a sample representative of the shrimp assemblage patterns, 300 m reaches were established, which included at least three riffle-run-pool sequences.
Figure 3.1. Upper, middle and lower sections (separated by dashed lines) of the King River in the southern Murray-Darling Basin, south-eastern Australia, and the location of the six study reaches as indicated by Xs.
Table 3.1. Description of the six reaches sampled for shrimp on the King River between September 2012 and April 2013.

<table>
<thead>
<tr>
<th>Reach no.</th>
<th>Reach name</th>
<th>Altitude (m asl)</th>
<th>Coordinates</th>
<th>Gradient (m.km⁻¹)</th>
<th>Dominant substrate</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Edi</td>
<td>194</td>
<td>146°25'27″E 36°39'6″S</td>
<td>6.40</td>
<td>Cobbles</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>Moyhu</td>
<td>175</td>
<td>146°23'28″E 36°34'42″S</td>
<td>1.70</td>
<td>Cobbles</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>Docker</td>
<td>163</td>
<td>146°23'11″E 36°31'3″S</td>
<td>0.65</td>
<td>Sand</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>Oxley</td>
<td>160</td>
<td>146°22'40″E 36°26'46″S</td>
<td>1.40</td>
<td>Sand</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>5</td>
<td>Freeway</td>
<td>155</td>
<td>146°20'45″E 36°23'28″S</td>
<td>0.90</td>
<td>Silt</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>6</td>
<td>Wangaratta</td>
<td>152</td>
<td>146°19'50″E 36°21'29″S</td>
<td>0.19</td>
<td>Silt</td>
</tr>
</tbody>
</table>
Figure 3.2. Photos of the six sampling sites; (a) Edi, (b) Moyhu, (c) Docker, (d) Oxley, (e) Freeway and (f) Wangaratta.
3.2.3 Sampling and processing of shrimp

Sampling was conducted monthly between September 2012 and April 2013. This sampling period was selected to encompass the breeding season. Shrimp were captured using a combination of dip netting and baited traps. Dip netting was shown to be an effective method for sampling all life history stages of all three species in a study conducted by Richardson et al. (2004), however Richardson and Cook (2006) showed that *M. australiense* prefer deeper main channel habitats therefore baited traps were also used in the current study. Mejia-Ortiz and Alvarez (2010) used baited traps to capture monitor the seasonal patterns in the distribution of three *Macrobrachium* species along an altitudinal river gradient.

The reaches sampled in this study varied from relatively high gradient, cobble-dominated to low gradient with sandy or silty sediments. Therefore, a method suitable to sampling a variety of habitat types was needed. The method used in this study was based on Mid-Atlantic Coastal Streams Workgroup recommendations and designed by the United States environmental protection agency for use in streams with variable habitat structure. At each site, five slackwater habitats between 50 - 75 cm deep were randomly selected for dip net sampling (see Chapter 2, section 2.2 for rationale). These slackwater habitats were identified by using the methods of (King and Crook 2002). Sampling began at the downstream end of the reach and proceeded upstream. Each sample consisted of a number of jabs with a dip net (35 x 25 x 25 cm, 250 µm mesh) in each slackwater for a total linear distance of 5 m; a single jab consists of forcefully thrusting the net into a productive habitat for a linear distance of 0.5 - 1 m upstream of the net. *Paratya australiensis*, *M. australiense* and *C. mccullochi* larvae all utilise slackwater habitats; therefore dip-netting has been
shown to be an effective method for sampling larvae, in this study and in previous studies, including Richardson et al. (2004). Unlike many amphidromous species drift of larval drift is likely to be relatively limited in these three species, particularly for *P. australiensis* and *C. mccullochi* (Price and Humphries 2010). In addition, five clear bottle traps (Fouilland and Fossati 1996), baited with dry dog food, were also set at each reach at least 15 m apart and in at least 50 cm of water. All samples were preserved in 95% ethanol for processing and identified in the laboratory. At each sampling site on each sampling occasion, the temperature, dissolved oxygen concentration, conductivity and pH were measured (Horiba Multiprobe U-50 Series), some physico-chemical variables have been shown to influence abundance of macro-invertebrates elsewhere in the Murray-Darling Basin (Bunn and Arthington 2002). Discharge data was sourced from a gauge located in the middle of the study reach, as there were no major tributaries along the study reach the hydrology data from this gauge was deemed representative of the whole study reach. In the laboratory, shrimp were identified (Hawking et al. 2006) and their interocular carapace lengths measured to 0.5 mm using a compound microscope with a measurement reticle. The juvenile adult cut-off for *P. australiensis* is 2.9 mm, so individuals below this were classed as juveniles (Hancock and Bunn 1997). *Caridina mccullochi* individuals below 2 mm and *M. australiense* below 4 mm were classed as juveniles (Richardson et al. 2004).

3.2.4 Data analysis

Differences among reaches and months for water quality variables (pH, temperature, dissolved oxygen and salinity) were tested using ANOVAs. Data was log-transformed prior to statistical analyses when necessary to normalise data and
stabilize variances. When significant differences were indicated, Tukey post-hoc tests were undertaken to determine differences between the reaches.

Shrimp abundance data was log-transformed prior to statistical analyses when necessary to normalise data and stabilize variances. To test if abundance was significantly different among sections or sites (nested within section) for the entire season, abundance of shrimp was analysed for each species (where there was enough data) using a repeated measures ANOVA. When significant differences were indicated, Tukey post-hoc pairwise comparisons were undertaken to determine differences among reaches. Where log-transformations failed to normalize abundance data, a generalised linear model with negative binomial distribution and a log-link function was used to determine whether abundances of each species differed among reaches and sampling occasions. Pairwise tests based on estimated marginal means were conducted to determine where significant differences occurred. ANOVAs and generalised linear models were performed using SPSS Version 17 (SPSS Inc., Chicago, IL, U.S.A.).
3.3 Results

3.3.1 Physiochemical variables

Temperature peaked in February and discharge was typical of a normal year (based on findings from Chapter 2), with discharge declining from high spring values to low levels throughout the summer (Figure 3.3). There was no significant difference in mean water temperature (d.f.=5; F=0.034; \( P > 0.05 \)) among reaches, with seasonal changes ranging from lower temperatures of 12 °C in September to higher temps of 26 °C in February. There was also no significant difference in \( \text{pH} \) (d.f.=5; F=0.376; \( P > 0.05 \)) or DO (d.f.=5; F=2.38; \( P > 0.05 \)) among reaches (Figure 3.2). Conductivity varied significantly among reaches (d.f.=5; F=4.995; \( P < 0.05 \)); the post hoc analysis showed that conductivity was higher at Wangaratta than the three most upstream sites Edi, Moyhu and Docker, however, conductivity at Wangaratta was still relatively low (48 – 83 \( \mu \text{S cm}^{-1} \)). Turbidity also varied significantly among sites (d.f.=5; F= 15.995; \( P < 0.05 \)); post hoc analysis showed it was lower at the upstream sites, Edi and Moyhu, than all other sites but turbidity was still relatively low at the downstream sites when compared to other lowland rivers where the shrimp species occur (Richardson et al. 2004).
Table 3.2. Mean ± s.e. (minimum – maximum) values for turbidity, pH, dissolved oxygen and conductivity at each site on the King River between September 2012 and March 2013.

<table>
<thead>
<tr>
<th>Site</th>
<th>Turbidity (NTU)</th>
<th>pH</th>
<th>Dissolved oxygen (mg L(^{-1}))</th>
<th>Conductivity (µS cm(^{-1}))</th>
</tr>
</thead>
<tbody>
<tr>
<td>Edi</td>
<td>6.9 ± 1.4</td>
<td>6.8 ± 0.2</td>
<td>11.2 ± 0.8</td>
<td>37.8 ± 1.4</td>
</tr>
<tr>
<td></td>
<td>(0.8 - 11)</td>
<td>(6.18 - 7.73)</td>
<td>(9.63 - 14.4)</td>
<td>(33 - 41)</td>
</tr>
<tr>
<td>Moyhu</td>
<td>9.6 ± 1.8</td>
<td>6.8 ± 0.2</td>
<td>10.4 ± 0.7</td>
<td>39.7 ± 1.6</td>
</tr>
<tr>
<td></td>
<td>(3.4 - 16.4)</td>
<td>(5.97 - 7.73)</td>
<td>(9 - 11.7)</td>
<td>(34 - 44)</td>
</tr>
<tr>
<td>Docker</td>
<td>25.3 ± 2.0</td>
<td>6.6 ± 0.2</td>
<td>10.3 ± 0.5</td>
<td>42.8 ± 3.1</td>
</tr>
<tr>
<td></td>
<td>(17.7 - 32.4)</td>
<td>(6.3 - 7.1)</td>
<td>(8.64 - 11.7)</td>
<td>(33 - 51)</td>
</tr>
<tr>
<td>Oxley</td>
<td>24.6 ± 1.8</td>
<td>6.6 ± 0.2</td>
<td>10.1 ± 1.0</td>
<td>53.5 ± 6.1</td>
</tr>
<tr>
<td></td>
<td>(17.1 - 30.5)</td>
<td>(5.87 - 6.9)</td>
<td>(6.93 - 10.22)</td>
<td>(35 - 72)</td>
</tr>
<tr>
<td>Freeway</td>
<td>36.8 ± 4.8</td>
<td>6.9 ± 0.1</td>
<td>8.5 ± 0.8</td>
<td>52.3 ± 6.3</td>
</tr>
<tr>
<td></td>
<td>(20 - 50.2)</td>
<td>(6.7 - 7.05)</td>
<td>(6.23 - 13)</td>
<td>(35 - 75)</td>
</tr>
<tr>
<td>Wangaratta</td>
<td>39.6 ± 3.6</td>
<td>6.7 ± 0.2</td>
<td>8.3 ± 0.7</td>
<td>64.0 ± 5.5</td>
</tr>
<tr>
<td></td>
<td>(30.3 - 53.4)</td>
<td>(5.77 - 7.04)</td>
<td>(6.2 - 9.72)</td>
<td>(48 - 83)</td>
</tr>
</tbody>
</table>
Figure 3.3. (a) Day length, (b) mean daily discharge of the King River between September 2012 and April 2013 and (c) mean (± SE) temperature across the six sites on each sampling occasion.
3.3.2 Distribution and abundance

From the sweep net sampling, it was found that *P. australiensis* and *M. australiense* occurred at all sites on the King River, but *C. mccullochi* did not occur in the upper section (Edi and Moyhu sites). *Paratya australiensis* larvae occurred at all sites, *M. australiense* larvae occurred at all sites except Edi and *C. mccullochi* larvae occurred at the Wangaratta, Freeway, Oxley and Docker sites. Larvae were excluded from analysis, as there was insufficient data to make meaningful comparisons, and adult and juveniles were pooled.

The mean abundance of *P. australiensis* varied significantly by section and month, with month contributing the most to the variation (Table 3.3). There was also a significant interaction between section and month. There was no significant site within section differences. Post hoc comparisons showed that the mean abundance of *P. australiensis* was significantly higher in the months of January, February and March than the other four months, with numbers peaking in January at all sites, except Wangaratta, where numbers peaked in February (Figure 3.4). The mean abundance of *P. australiensis* was significantly higher in the upper section than the middle and lower sections, but there was no difference in mean abundance of *P. australiensis* between the middle and lower sections.

The mean abundance of *C. mccullochi* varied significantly by section, month and site within section, with the most variation between sections (Table 3.3). There was no significant interaction between section and month. Post hoc comparisons showed that the mean abundance of *C. mccullochi* was significantly higher in the lower
section (Freeway and Wangaratta sites) than the middle section (Docker and Oxley sites) of the King River.

The mean abundance of *M. australiense* was low relative to the other two species and varied significantly by month and site within section, with month contributing most of the variation (Table 3.3). The mean abundance of *M. australiense* did not vary significantly among sections and there were no significant interactions found between section and month. Pairwise comparisons showed that the mean abundance of *M. australiense* was greater in the months of January, February and March compared to the other four months (Figure 3.3).
Table 3.3. Wald chi-square statistic and associated significance values for generalised linear model of Shrimp captured with dip net with sampling occasion and reach as factors.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>d.f.</th>
<th>Chi-square</th>
<th>P value</th>
</tr>
</thead>
<tbody>
<tr>
<td>P. australiensis</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(Intercept)</td>
<td>1</td>
<td>59.295</td>
<td>.000</td>
</tr>
<tr>
<td>Section</td>
<td>2</td>
<td>21.757</td>
<td>.000</td>
</tr>
<tr>
<td>Month</td>
<td>6</td>
<td>41.756</td>
<td>.000</td>
</tr>
<tr>
<td>Site(Section)</td>
<td>3</td>
<td>5.866</td>
<td>.118</td>
</tr>
<tr>
<td>Section * Month</td>
<td>12</td>
<td>28.400</td>
<td>.005</td>
</tr>
<tr>
<td>C. mccullochi</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(Intercept)</td>
<td>1</td>
<td>25.408</td>
<td>.000</td>
</tr>
<tr>
<td>Section</td>
<td>1</td>
<td>21.292</td>
<td>.000</td>
</tr>
<tr>
<td>Month</td>
<td>6</td>
<td>15.070</td>
<td>.020</td>
</tr>
<tr>
<td>Site(Section)</td>
<td>2</td>
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<td>.000</td>
</tr>
<tr>
<td>Section * Month</td>
<td>6</td>
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<td>.833</td>
</tr>
<tr>
<td>M. australiense</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(Intercept)</td>
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<td>25.886</td>
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<tr>
<td>Section</td>
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<td>1.403</td>
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<tr>
<td>Month</td>
<td>6</td>
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<td>.000</td>
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<tr>
<td>Site(Section)</td>
<td>3</td>
<td>15.920</td>
<td>.001</td>
</tr>
<tr>
<td>Section * Month</td>
<td>11</td>
<td>7.786</td>
<td>.732</td>
</tr>
</tbody>
</table>
Figure 3.4. Mean + s.e. abundance by month of juvenile/adult *Paratya australiensis*, *Caridina mccullochi* and *Macrobrachium australiense* collected from dip net samples from each reach on the King River between September 2012 and April 2013.
Only a few *P. australiensis* and no *C. mccullochi* were captured from baited traps, so individuals of these species captured using this method were excluded from analyses. There were, however, enough *M. australiense* to analyse. Overall the mean abundance of *M. australiense* varied significantly by section and month, with month contributing most of the variation (Table 3.4). There was no significant difference in abundance between site within section or any significant interaction between month and section. Pairwise comparisons showed that the mean abundance of *M. australiense* was significantly higher in March compared to all other months than January (Figure 3.5). The mean abundance was also significantly lower in the upper section than the middle and lower sections, but there was no difference in abundance between the middle and lower sections.

Table 3.4. Wald chi-square statistic and associated significance values for generalized linear model of abundance of trapped *Macrobrachium australiense* juveniles and adults with month, section and site as factors.

<table>
<thead>
<tr>
<th></th>
<th>Chi-square</th>
<th>d.f.</th>
<th>P value</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Intercept)</td>
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<td>.000</td>
</tr>
<tr>
<td>Section</td>
<td>20.492</td>
<td>2</td>
<td>.000</td>
</tr>
<tr>
<td>Month</td>
<td>63.941</td>
<td>5</td>
<td>.000</td>
</tr>
<tr>
<td>site(section)</td>
<td>2.416</td>
<td>2</td>
<td>.299</td>
</tr>
<tr>
<td>Month * section</td>
<td>15.183</td>
<td>9</td>
<td>.086</td>
</tr>
</tbody>
</table>
Figure 3.5. Mean + s.e. abundance of *M. australiense* captured in baited traps from each reach on the King River between October 2012 and April 2013.
3.3.3 Size class frequencies

Both juvenile and adult *P. australiensis* were collected at all sites, however, there were very few juveniles captured from the Docker site (Figure 3.6). Only adult *C. mccullochi* were captured at the Docker site; the most upstream site at which this species occurred. Both juveniles and adults were collected at the other three sites. Juvenile and adult *M. australiense* were captured at all sites in the sweep net samples, with the exception of Edi (the most upstream site), where only a few *M. australiense* juveniles were captured. *Paratya australiensis* larvae were collected at all six sites and *M. australiense* larvae were collected at all sites, except Edi. *Caridina mccullochi* larvae were only captured at the three most downstream sites: Oxley, Freeway and Wangaratta. Only adult *M. australiense* with a carapace length of > 4mm were captured in the baited traps.
Figure 3.6. Proportion of each size class of a) *Paratya australiensis* b) *Caridina mccullochi* and c) *Macrobrachium australiense* from dip net samples at each reach on the King River between October 2012 and April 2013.
3.4 Discussion

The results of this study show the distribution and abundance of *C. mccullochi* and *M. australiense* populations along the King River vary significantly both spatially and temporally between upland and lowland sites. *Caridina mccullochi* was captured at Docker, Oxley, Freeway and Wangaratta sites, but not at the two upstream sites. *Macrobrachium australiense* was captured at all six sites, but occurred in lower abundances at the two upstream sites than the middle or downstream sites. The two upstream sites are typical upland river sites, with clear water (<10 NTU), cobble substrate and pools connected by riffles and runs.

Lowland river reaches differ from other upland reaches in terms of several physical characteristics, including flow. The temporal and spatial arrangement of meso- and micro habitats are likely to differ as a result (Crook et al. 2001). Foremost of the habitat variables influenced by flow are water depth, current velocity, instream cover and riverbed substratum (Bain et al. 1989; Gore et al. 1989). The hydrograph in upland reaches reflects the hierarchical structure of stream drainage networks: upland reaches and tributaries often are subject to high-frequency, low-magnitude flow events, whereas higher-order streams that drain larger areas are subject to low-frequency, high-magnitude flow events (Allan and Castillo 1995). As a result, the temporal arrangement of meso- and micro habitats is often different between upland and Lowland River reaches, which can presumably result in less permanence of habitats that are preferred by some species in upland reaches compared to those in lowland reaches (Allan and Castillo 1995, Hancock and Bunn 1997, Price et al. 2012).
The availability and persistence of slackwater habitats possibly a critical feature in the persistence of shrimp populations in a given river reach. Richardson and Cook (2006) found that *C. mccullochi* is likely to be restricted to slackwaters throughout its entire life history, whereas *M. australiense* is only restricted to slackwaters during the larval stage. *Paratya australiensis* can occur in all flow habitat types at all life history stages, but is mostly associated with slackwater habitats. The variation in the availability and persistence of these slackwater habitats may therefore have accounted for differences in the abundances between the upstream and downstream reaches observed in this study.

Species living in fast flowing upland rivers and streams also need to be able to resist and/or compensate for downstream displacement due to frequent flushing events. In upland reaches of streams, the chances of shrimp being washed out are much higher than in lowland streams (Covich et al. 1996). Even during brief storm events, the narrow and shallower pools typical of higher elevations can quickly change from pools to runs (Allan and Castillo 1995). Some species may be more prone to washout because they are less able to cope with flow compared to others species during these events (Covich et al. 1996). Of the species investigated as part of this study, *P. australiensis* and *M. australiense* have demonstrated an ability to resist downstream displacement by water current in laboratory experiments, although this ability is reduced in gravid females, and larvae are easily displaced at even the slowest current speeds (Hancock and Bunn 1999, Lee and Fielder 1984). The response and ability to cope with flow of *C. mccullochi* is not known, and it is possible that *C. mccullochi* is less able to cope with flow and/or unable to compensate for displacement during high flow events as well as *P. australiensis* and *M. australiense*. 
It is possible that *C. mccullochi*, and to a lesser extent *M. australiense*, are unable to persist in the upper reaches of rivers. This is supported by Richardson et al. (2004), who found that *M. australiense* were in lower abundances, and *C. mccullochi* were completely absent, from heavily regulated middle to upper reaches Campaspe River. These sections received substantial increases in flow during summer because of irrigation releases, which would likely limit the availability and permanence of slackwaters (Humphries et al. 2002). Both species were, by contrast, in high abundance in the lower reaches of the Campaspe River that experiences low flows during summer, typical of the natural flow regime. The results of this chapter were also supported by Chapter 2, where the range of *P. australiensis* extended further upstream in many rivers than that of *M. australiense*, and *C. mccullochi* was restricted to lowland sections.

Physico-chemical conditions, apart from flow and habitat, change longitudinally in rivers. The two upstream reaches where *M. australiense* was in low abundance and *C. mccullochi* was absent, had lower turbidity and conductivity than the lower reaches, however, both *C. mccullochi* and *M. australiense* have been found at other sites where turbidity and conductivity are equally low (Richardson et al. 2004, Richardson and Cook 2006, Price and Humphries 2010).

The patterns in distribution and abundance along an altitudinal gradient observed in this study are also supported by the findings from studies conducted elsewhere in the world. Covich et al. (2006) found that altitudinal variation in abundance and distribution of four amphidromous species of shrimp (*Atyalanipes, Xiphocaris elongate, Macrobrachium carcinus* and *Macrobrachium crenulatum*) was likely to be related to the availability pool habitats with low frequency of washout during high flow events. Fievet et al. (2001) also documented differences in the distribution of
amphidromous shrimp species along an altitudinal gradient, however, to date, the
temporal distribution and abundance of exclusively freshwater species had not
previously been investigated to the extent and scale of the current study.

The temporal abundance patterns observed in the present study provide
circumstantial evidence for the role of movement in influencing the distribution
patterns of shrimp in the King River. The peaks in abundance of *P. australiensis*
collected from dip net samples occurred at similar times at all sites. These peaks in
abundance were largely a result of the high number of juveniles captured at these
times, and because peaks occurred at similar times, it suggests that juvenile
recruitment occurred along the entire length of the King River for these species. The
peaks in abundance of both trapped *M. australiense* and those captured in dip net
samples, also occurred at similar times within section. On the other hand, the peaks
in abundance of *C. mccullochi* varied significantly among sites. It should be noted,
however, that juveniles only made up a small proportion of the *C. mccullochi*
captured. It is likely that the high variation in abundance of this species was
primarily a result of a high level of short-term spatial variation or small-scale spatial
differences.

Another key piece of evidence pointing to the potential role of movement in the
distribution and abundance patterns of the shrimp species is the spatial occurrence of
larvae. *P. australiensis* larvae occurred at all six sites, suggesting that the lifecycle of
this species is likely completed without the need for significant movement to specific
larval nursery habitats. *Caridina mccullochi* larvae also occurred at each of the sites
where adults were present. In contrast, only juvenile *M. australiense* were captured
at Edi, the most upstream site, whereas juveniles, adults and larvae were captured at
all other sites. It is possible that juvenile *M. australiense* move into the upper reaches
during summer, a period typified by long periods of low flow, but are unable persist and complete their life cycle there, due to temporal changes in habitat suitability. Or perhaps they move back downstream as adults to reaches that have more suitable nursery habitats for larvae, as some other *Macrobrachium* species do elsewhere in the world (Bauer and Delahoussaye 2008, Benstead et al. 2000).

**Conclusion**

The present study, conducted in an unregulated, relatively small river, has contributed to our understanding of the ecology of the three shrimp Murray-Darling Basin species however, many questions remain unanswered. In particular, little is known about the temporal and spatial patterns of movement of the species under natural conditions, nor of the ability of the species to maintain position or swim against flow. This is especially true of *C. mccullochi*, which from the results of this chapter, it seems may play a key role in the distribution of this species. The next two chapters of this thesis will attempt to address these knowledge gaps by examining whether each species undertake substantial up or downstream movements/migrations and by comparing the ability of the three species to maintain position in flow.
CHAPTER 4
TEMPORAL MOVEMENT PATTERNS OF SHRIMP IN THE KING RIVER

4.1 Introduction

As with many other stream organisms, shrimp require access to a diversity of habitat types for feeding, reproduction and refuge (Covich et al. 2003, Covich et al. 2006, Martin et al. 2009, Price and Humphries 2010). Depending on the spatial arrangement of habitat patches in the landscape, shrimp may need to move considerable distances to find scarce or critical resources. Consequently, movement may influence a variety of distribution-related patterns and processes in stream shrimps, such as longitudinal size patterns (Richardson et al. 2004), source-sink dynamics (Greathouse et al. 2005), colonisation of habitats (Benstead et al. 2000), and species assemblage structure (Covich et al. 1996).

Many species of freshwater shrimp have an amphidromous life history, in which breeding and spawning occur in fresh water but larval development takes place in brackish or fully-marine waters (Bauer 2004, McDowall 2007, Bauer and Delahoussaye 2008, Bauer 2011). In amphidromous species, larvae drift downstream until they find saltwater, or females move downstream to salt water to release larvae (Figure 4.1). The newly metamorphosed juveniles (postlarvae) then find river mouths or freshwater inlets and migrate to adult riverine habitat (Hamano and Hayashi 1992, Holmquist et al. 1998). It is studies of amphidromous species that have been the first to document the spatial and temporal migration patterns of stream-dwelling shrimp (Kikkert et al. 2009, Rome et al. 2009, March et al. 1998, Pringle and Ramirez 1998, Benstead et al. 1999). These movement events usually
occur at particular times of year, and are often related to in-stream flow conditions (Kikkert et al. 2009) (Figure 4.1). In species that spend their entire lives in freshwater, movement also seems to be important, albeit on a smaller scale. For example, there is evidence to suggest that gravid *Macrobrachium australiense* females move into slackwaters to hatch their eggs in suitable nursery habitats for larval development (Price and Humphries 2010) (Figure 4.1). A comparison of marine, freshwater and terrestrial decapods suggests that the reduction of egg number, abbreviation of larval development, extension of brood care and lecithotrophy of the first post-hatching life stages are key adaptations to fresh water (Vogt 2013).
Figure 4.1. A model of movements by freshwater shrimp: (1) local, home range movements (2); larger scale movements among mesohabitats in response to changes in arrangement of habitat/resources; (3) females hatch larvae in freshwater, and in the case of some species (e.g., *M. australiense*, Price and Humphries 2010), gravid females move to suitable nursery habitats; (4) gravid females migrate down to river mouths to hatch larvae (e.g., *Macrobrachium ohione*, Bauer and Delahoussaye 2008); (5) larvae hatched in freshwater, drift downstream to the sea (e.g., *Xiphocaris elongata*, March et al. 1998); (6) in some freshwater only species, larvae drift downstream among slackwater nursery habitats (e.g., *M. australiense*); (7) in diadromous species, the newly metamorphosed post-larvae move back upstream to the adult freshwater habitat, and migrations often coincide with favourable flow conditions (e.g., *Xiphocaris elongata*, *Macrobrachium* spp. and *Atya* spp, Kikkert et al. 2009); and (8) in some freshwater only species, there is evidence to suggest that juveniles and adults undertake upstream movements presumably to compensate for downstream drift (e.g., *M. australiense*, Lee and Fielder 1979).
There has been some study of the movement patterns of the three Murray-Darling Basin shrimp species, Paratya australiensis, Caridina mccullochi and Macrobrachium australiense. Hancock and Hughes (1999) investigated the movement of P. australiensis, by translocating shrimp between two genetically distinct populations in the upper Brisbane River catchment in southeast Queensland. It was found that these shrimps only moved upstream on a small scale, and downstream movement was very limited and restricted to larvae and juveniles. In contrast, evidence suggests that M. australiense has much stronger dispersal abilities. Lee and Fielder (1979) observed M. australiense climbing over a weir in large numbers in the Dawson River in southeast Queensland. Macrobrachium australiense also appears to easily recolonise intermittent streams after surviving dry periods in refuge pools (Carini et al. 2006). Macrobrachium australiense larvae are known to drift downstream (Price and Humphries 2010), and upstream movements of juveniles and adults likely compensate for downstream larval drift. To date very little is known about the movements of C. mccullochi, with the exception of the work of Price and Humphries (2010), which showed limited dispersal of C. mccullochi larvae, especially compared to M. australiense, which emphasized the importance of retention in slackwaters during critical developmental periods and of the potential impact that flow alteration could have on this species. These authors emphasized the importance of retention in slackwaters during critical developmental periods and of the potential impact that flow alteration could have on C. mccullochi.

Although the research mentioned above has been important in identifying the potentially key role movement plays in the life history of these shrimp, no research has been conducted on the movements of adult shrimp in temperate regions of Australia, where seasonal patterns in flow regime are very different to sub-tropical
regions. Specifically, the movements of shrimp in the Murray-Darling Basin remain unexplored, which is significant, as the occurrence and abundance of shrimp in the Murray-Darling Basin is thought to be negatively affected by flow regime modification (Richardson et al. 2004). The results of Chapter 3 suggest that movement may play a role in the temporal distribution patterns of at least *M. australiense*. In Chapter 3, *M. australiense* were found to be present in the upland reach of the King River, however, no larvae were captured in this reach, so it is hypothesised that the *M. australiense* present in this section were spawned further downstream where there are more suitable nursery habitats and once developed, moved upstream. If these species do indeed undertake significant dispersal events, I would expect to see a disproportionate number of shrimp moving either up or downstream.

The overall aim of this chapter is to determine the spatial and temporal nature of any movements of *P. australiensis*, *M. australiense* and *C. mccullochi*, and relate movement to environmental factors such as discharge, day length and temperature in the King River.

Quantify shrimp movement in the King River over a 6-month period, during the normal breeding season; and

Describe the spatial and temporal nature of any movements and relate movement to changes in discharge and temperature in the King River.

### 4.2 Methods

#### 4.2.1 Study reaches
Sampling was conducted fortnightly between October 2012 and March 2013 at the same six reaches as were sampled in Chapter 3, on the King River, in North East Victoria (Table 3.1 and Figure 3.1). These reaches varied from lowland to upland slopes and covered the extent of the longitudinal distribution of the three species in the King River (see chapter 3). On each sampling occasion, the temperature, dissolved oxygen concentration, conductivity and pH were measured at each site.

4.2.2 Shrimp sampling

Modified versions of the traps developed by Burky et al. (2005) were used to quantitatively monitor the up- and downstream movement of shrimp in the King River (Figure 4.2). Benbow et al. (2004) showed that this trap design was effective in monitoring the movements of the atyid shrimp, *Atyoida bisulcata*. A similar, but larger, trap design was also used effectively by Price and Humphries (2010) to monitor the movements off shrimp into and out of slackwaters, the traps used in that study captured all life history stages of the same three species targeted in this study.

The traps were made from a transparent plastic spring water bottle, 85 mm wide (outer diameter) and 210 mm long (Figure 4.2). One end of the trap was funneled with a 25 mm entrance hole, and 2 mm slits on opposite sides. The other end of the traps consisted of 250 µm netting, which, together with the slits, allows a sufficient amount of water to move through the trap required to enable a rheotactic response. The funnel was removable, making the traps simple and quick to empty.
Figure 4.2. Diagram showing the design of the one-way movement traps used in this study, modified from Burky et al. (2005).

At each site, six paired traps (bi-directional facing) were set at approximately 1 m intervals in a location where the stream channel narrowed (Figure 4.3). This was typically an area of constricted stream flow, where shrimp had to move through riffle/run areas. Traps were tethered to stakes near the edge of the stream in 30-75 cm of water, as this is where shrimp have previously been found to move, presumably to avoid the full force of the current in the main channel (Bauer 2011, Benstead et al. 2000, J Dyer unpublished data). Traps were deployed just before dusk (2000-2100), and retrieved the following morning (0700-0900). This gave a soak time of approximately 12 h per trap. Previous studies and pilot studies (Kikkert et al. 2009, Lee and Fielder 1979, J Dyer unpublished data) have shown that shrimp are more likely to undertake movements at night. The collected shrimp were preserved in 95% ethanol for processing and identification in the laboratory (see Chapter 3 for details on laboratory methods).
Figure 4.3. In stream position and arrangement of traps at each reach for the collection of shrimp in the King River.

4.2.3 Data analysis

Mean abundances of trapped shrimp for each site per 12 hr sampling period were calculated to remove the effect of variation in length of time traps were set and the effect of any missing data, due to lost or broken traps. Thus, all results are based on mean adjusted abundances. There were too few *P. australiensis* and *C. mccullochi* collected for data analysis. There were, however, sufficient numbers of *M. australiense* collected for statistical analysis, except at the most upstream reach, which was excluded from analyses, due to low sample sizes.

After assessing the distribution of the data, a generalized linear model with a negative binomial distribution and a log link function was used to test the effect of direction, reach and month on the numbers of shrimp captured. Pairwise tests based
on estimated marginal means were conducted to determine where significant differences occurred. Generalised linear models were performed using SPSS Version 17 (SPSS Inc., Chicago, IL, U.S.A.). Discharge data was sourced from a gauge located in the middle of the study reach, as there were no major tributaries along the study reach the hydrology data from this gauge was deemed representative of the whole study reach. Day length was also calculated for the study period.

4.3 Results

Water temperatures were warmest in February and were coolest in October. Day length peaked at the end of December (Figure 3.3). The discharge pattern of the River during the sampling period was typical of a normal year, with flow declining from high levels in spring to low flow throughout summer.

A total of 614 shrimp were collected in the directional traps over the entire study period (Table 4.1). Of these, 550 were *M. australiense*, 37 were *P. australiensis* and 27 were *C. mccullochi*. Of the 550 *M. australiense* collected, 10 were classed as juvenile and no larvae were captured. No larvae or juveniles of the other two species were collected.

Table 4.1. Number of *P. australiensis*, *C. mccullochi* and *M. australiense* caught in directional traps in the King River between October 2012 and February 2013.

<table>
<thead>
<tr>
<th>Direction</th>
<th><em>P. australiensis</em></th>
<th><em>C. mccullochi</em></th>
<th><em>M. australiense</em></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Juveniles</td>
<td>Adults</td>
<td>Juveniles</td>
</tr>
<tr>
<td>Upstream</td>
<td>0</td>
<td>20</td>
<td>0</td>
</tr>
<tr>
<td>Downstream</td>
<td>0</td>
<td>17</td>
<td>0</td>
</tr>
<tr>
<td>Total</td>
<td>0</td>
<td>37</td>
<td>0</td>
</tr>
</tbody>
</table>
Paratya australiense was captured in October, November, December and March (Figures 4.4 and 4.6). Caridina mccullochi was captured in November, December and March. Notably, no *C. mccullochi* or *P. australiensis* were captured in January and February. There were too few *P. australiensis* and *C. mccullochi* captured to statistically analyse the difference in the proportion captured moving up and downstream.

By contrast, approximately 4.5 times the number of *M. australiense* were captured moving upstream than downstream (Table 4.1, Figure 4.4). Small numbers of juveniles were captured moving upstream, but none downstream. The mean abundance of *M. australiense* captured varied significantly by month, by reach and direction (Table 4.2). The number of *M. australiense* captured moving upstream was significantly greater than the number moving downstream (452 vs. 98) (Figure 4.5). The significant interaction between direction and month suggests that the difference between the numbers moving up- and downstream varied by month. In particular, the numbers moving upstream in December and January were much greater than the numbers moving downstream (Figure 4.4). There was also a significant interaction between reach and direction, indicating that the proportion moving upstream was greater at some reaches than others. In particular, the difference between the numbers moving upstream compared to the numbers moving downstream seemed to be greater in the three upstream reaches than the two most downstream sites, at least for November-February (Figure 4.5).
Table 4.2. Wald chi-square statistic and associated significance values for generalized linear model of abundance of trapped *M. australiense* in the King River between October 2012 and February 2013, with month, site and direction as factors.

<table>
<thead>
<tr>
<th>Wald Chi-Square</th>
<th>d.f.</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Intercept)</td>
<td>70.096</td>
<td>1</td>
</tr>
<tr>
<td>Month</td>
<td>45.915</td>
<td>5</td>
</tr>
<tr>
<td>Reach</td>
<td>23.634</td>
<td>4</td>
</tr>
<tr>
<td>Direction</td>
<td>31.942</td>
<td>1</td>
</tr>
<tr>
<td>Month * Direction</td>
<td>14.291</td>
<td>5</td>
</tr>
<tr>
<td>Reach * Direction</td>
<td>16.677</td>
<td>4</td>
</tr>
</tbody>
</table>
Figure 4.4. Mean (+ SE) abundance per trap of *P. australiensis*, *C. mccullochi* and *M. australiense* collected from directional traps moving upstream and downstream each month in the King River between October 2012 and February 2013. Note the scale of the y axis differs for *M. australiense*.
Figure 4.5. The proportion of *M. australiense* moving up and downstream at each reach on each month on the King River between October 2012 and March 2013.
Figure 4.6. The proportion of *P. australiensis* moving up and downstream at each reach on each month on the King River between October 2012 and March 2013.
Figure 4.7. The proportion of *C. mccullochi* moving up and downstream at each reach on each month on the King River between October 2012 and March 2013.
Discussion

The results of this chapter provide new information on the potentially important role of dispersal in the life history of *M. australiense*. In contrast, the very limited numbers of *C. mccullochi* and *P. australiensis* captured in the directional traps suggest that *C. mccullochi* and *P. australiensis* are less likely to undertake significant dispersal events across meso-habitats during their life history. *M. australiense* was captured in relatively large numbers in the directional traps, suggesting that this species moves more extensively. This confirms the findings of Richardson and Cook (2006), who reported that *M. australiense* frequently occurred in the flowing water of the main channel. The high comparative numbers of *M. australiense* captured in the present study, moving both up- and downstream, compared to the other two species, may simply reflect the day-to-day foraging of this species among flowing habitats. However, the number moving upstream was significantly greater than the number moving downstream in December and January, whereas in other months there was no significant difference between the numbers moving upstream compared to the numbers moving downstream, suggesting that upstream dispersal is a notable part of the life history of this species. If the greater proportion captured moving upstream was just an artefact of the sampling method you would not expect that to change across the sampling period as it did in this study.

Upstream movements require a significant expenditure of energy, so an individual requires a good reason to undertake such movements. For *M. australiense*, there are two key reasons that this species may undertake such movements. Firstly, upstream movement can allow the species to recolonise rivers and creeks with highly variable
discharges that are prone to disturbance (drying and flooding) (Covich et al. 1991, Covich et al. 2006). Floods and long periods of drought are a common feature of many rivers and creeks in Australia (Puckridge et al. 1998). In fact Carini et al. (2006) found that *M. australiense* quickly recolonised sections of the Warrego River, in the semi-arid northern section of the Murray-Darling Basin, after long periods of drought. There, the rainfall patterns are highly variable, so that rivers are prone to long periods of no flow and at other times large floods (Kotwicki and Allan 1998). Secondly, upstream movement allows the species to inhabit upland river reaches (see Chapter 3), even though the absence of suitable nursery habitats for larvae may limit recruitment in these reaches (Price and Humphries 2010). Indeed, in the current chapter, it was found that at times, the proportion of *M. australiense* moving upstream was greater at the upstream reaches than the downstream reaches.

The number of *M. australiense* captured in directional traps was significantly greater in December and January when water temperature was high, discharge was low and day length was at its greatest (Figure 3.3). However, discharge was equally low and temperature was equally high during February and March yet there was no significant difference in movement direction during this time. For many shrimp species, especially amphidromous species, migrations generally take place when stream flows are seasonally low, but not absent (Bauer and Delahoussaye 2008, Lee and Fielder 1979) this is also supported by the work of Kikkert et al. (2009). Kikkert et al. (2009) found that migration rates of *Macrobrachium sp.* were negatively correlated with high discharge and positively correlated with the length of the period of darkness and moonlight intensity. It should be noted that the observations in the study conducted by Kikkert et al. (2009) were limited to small post-larvae (3-5 mm carapace length) and the effects on adult shrimp might be different, especially given
that M. australiense individuals sampled in the current study were greater than 4 mm carapace length. Moonlight intensity was not measured during this study and is unlikely to have had a significant impact on the movement rates of *M. australiense* because it did not affect the rates of migration of this species over a weir in the study conducted by Lee and Fielder 1979 however, future research and/or experimentation into the influence of the length of the duration of darkness and other temporal variables, would be valuable to help explain the specific trigger for upstream migrations.

If the upstream movements *M. australiense* are correlated with period of darkness and rates of movement are negatively impacted by high discharge as found by Kikkert et al. (2009), anthropogenic modification to the flow regime may significantly affect these movements, since many of the rivers in the southern Murray-Darling Basin that are used to deliver irrigation water experience higher flows during summer than what would otherwise under natural flow conditions. Indeed, Richardson et al. (2004) found that the numbers of *M. australiense* were much fewer in the heavily regulated upper sections of the Campaspe River, which received high flows as a result of irrigation releases in summer, when compared to the nearby relatively unregulated sections at the same altitude in Broken River. It may be that high flows in summer affect the ability of *M. australiense* to disperse and recolonise areas after disturbance events or into upstream reaches where suitable slackwater habitats are rare. The effect of high flows, as a result of river regulation, on the movement success of shrimp species, has not specifically been investigated to date. However, high flows have been found to affect the migration of some species of fish, and the affect has largely been found to be dependent on species-specific features, such as swimming capacities and timing of migration (Northcote 1998,
Winter and Van Densen 2001). Interestingly the proportion of *M. australiense* moving downstream was highest in March at all five sites. Elsewhere in the world, some species of *Macrobrachium* move downstream to find suitable habitats for spawning and larval development (Olivier and Bauer 2011). It is unlikely that this is the case for *M. australiense* as the spawning of this species occurs in the months before March. (see Chapter 3 and Richardson et al. 2004), however other explanations such as changes in available habitat due to low flows may account for this and further investigation is warranted.

In contrast to *M. australiense*, very few *P. australiensis* and *C. mccullochi* were captured in the traps. When these numbers are compared to the abundance of each species in slackwaters (see Chapter 3) at each reach, it can be suggested that very few individuals of either species were moving through runs, and therefore were likely to be restricted to slackwater habitats during the period of this study. These results are supported by Richardson and Cook (2006), who found that *P. australiensis* and *C. mccullochi* appear to prefer slackwaters to flowing-water habitats. These results are also supported by the findings of Hancock (1995), who found significant genetic differences between populations of *P. australiensis* at a relatively small spatial scale, suggesting very limited movement. Of the few individuals of these species that were caught, the proportion moving upstream was similar to the proportion moving downstream for both *P. australiensis* and *C. mccullochi*, so there is no indication from my results that either species undertakes extensive dispersal events.

As noted by Hancock and Hughes (1999), this result is a little surprising for *P. australiensis*, despite the small-scale genetic differences, since this species is found across a large part of Australia, is often abundant in upland streams where the risk of
being washed out is high, and has a planktonic larval stage which drifts. It is possible that this species may be triggered to move upstream during or after significant high flow events to compensate for any downstream displacement, however, no substantial high flow events occurred during the study period in the King River, so this could not be tested. The lack of evidence to suggest that *C. mccullochi* moves among habitats is less surprising, given that it is restricted to the slackwaters of slow-flowing rivers (see Chapters 2 and 3, Richardson and Cook 2006, Richardson et al. 2004). This may be due to either an inability to maintain position in high flows or a lack of a behavioural mechanism to compensate for downstream displacement, or a combination of the two.

Conclusions

Upstream dispersal events seem to play a role in the life history of at least *M. australiense*, and modifications to the natural flow regime may impact upon this. The relative absence of movements at the same scale by *P. australiensis* and *C. mccullochi* may indicate either a lack of a need to move or a lack of “inherent mobility” to undertake such movements. Animals that have restricted movements are often more prone to localised extinction in habitat patches after disturbance events (Fahrig and Merriam 1994), such as floods or droughts. Chapter 5 investigates the ability to maintain position in flow by the three shrimp species, as part of identifying reasons for the distribution and movement patterns observed in the present chapter and the previous two.
CHAPTER 5
MAINTENANCE POSITION AND BEHAVIOUR IN RESPONSE TO WATER CURRENT OF THREE SPECIES OF FRESHWATER SHRIMP

5.1 Introduction

Spatio-temporal variation in current speed and associated hydraulic forces, such as shear stress and turbulence, can directly affect spatial distributions of macroinvertebrates in lotic environments (Statzner et al. 1988, Vinson and Hawkins 1998, Hart and Finelli 1999). Tolerance of current speed is often species-specific in macroinvertebrates, and as a result, variation in current speed is often a potent force in influencing the structure and dynamics of macroinvertebrate assemblages (Hart and Finelli 1999). This influence has been observed both at mesohabitat spatial scales (e.g., riffles and pools) within rivers and between rivers of different sizes (Jowett and Duncan 1990, Growns and Davis 1994, Quinn and Hickey 1994, Rempel et al. 2000, Doisy and Rabeni 2001, Jowett 2003).

Although riverine species have evolved in a flowing environment, the larval stages of many species are vulnerable to current-induced dislodgment and passive entry into the drift (Covich et al. 1996; Hancock and Bunn 1997; Price 2010). It is therefore likely to be important for some freshwater shrimp species to have a compensatory movement mechanism to ensure their long-term presence in areas where downstream drift is common (Waters 1972). This is especially true for shrimp living in streams with high current speeds or those that are prone to sudden flow increases, such as upland and regulated streams (e.g., below hydro peaking dams).
Kikkert et al. (2009) hypothesised that differences in the ability of different shrimp species to resist high flows and resultant current speeds and undertake upstream movements may be due to differences in body morphology. In that study, it was found that the movements of two species (\textit{Xiphocaris elongata} and \textit{Macrobrachium} spp.) were negatively correlated with high flows but there was no correlation evident for a third species (\textit{Atya} sp.). It was found that the \textit{Macrobrachium} spp. had large chelae that caused awkward walking movements and \textit{Xiphocaris elongata} walked on elevated long, thin legs. It is thought that these morphological traits appear to increase the vulnerability of these species to being swept away by pulses of water (Fryer 1977, Fievet 1999). In contrast, \textit{Atya} sp. are small-bodied and appear the best adapted to withstand fast currents (Kikkert et al. 2009).

Adaptations to living in flowing water have evolved under natural flow conditions, however anthropogenic modification, such as the building and operation of in-channel dams, can change temporal patterns of current velocity. Because of these changes, the distributions of the organisms that inhabit the rivers downstream of these structures can be significantly impacted (Poff et al. 1997). Sudden, unpredictable and frequent releases from dams are an obvious change, and often result in elevated current velocities that can wash individuals downstream, and potentially depopulate upstream reaches (Troelstrup Jr and Hergenrader 1990, Smokorowski et al. 2011).

Of the species found in the Murray-Darling Basin, both \textit{M. australiense} and \textit{P. australiensis} adults have been shown to be able to cope with current velocities of at least 10 and 30 cm s\(^{-1}\), respectively, and also exhibit positive rheotaxis (Lee and fielder 1979, Hancock and Bunn 1999). \textit{Paratya australiensis} occurs in high gradient streams with frequent high flow events and high current speeds (Chapter 2, Hancock
and Hughes 1999). Both *P. australiensis* and *M. australiense* are also able to navigate their way through the turbulent water of waterfalls and spillways (Lee and Fielder 1979, Hancock and Hughes 1999). However, the larvae of both species cannot withstand even low velocities (Price and Humphries 2010, Lee and Fielder 1979, Hancock and Hughes 1999). To date, nothing is known about the swimming ability of *C. mccullochi*.

As *C. mccullochi* is restricted to the lowland reaches of rivers (Chapter 2 and 3, Richardson et al. 2004), and is often absent from reaches in the Murray-Darling Basin that have experienced significant flow modification (Chapter 2, Richardson et al. 2004), an assessment of the ability of this species to maintain position in relation to current velocity is needed. In addition, although *P. australiensis* and *C. mccullochi* generally prefer slackwater habitats (Richardson and Cook 2006), from time to time the arrangement and persistence of these habitats may change due to temporal variation in discharge (Bowen et al. 2003, Price et al. 2013). Therefore, individuals may need to deal with increased current speeds until the high flow event subsides or may need to move to find a new suitable habitat. Therefore, it would also be valuable to compare all species under the same conditions, which may help to explain the observed assemblage patterns throughout the Murray-Darling Basin.

The overall aim of this chapter was to compare the ability of the three species of shrimp to maintain position in, and behavioural response to current, to investigate the role that movement ability plays in distribution and assemblage patterns.

Specifically, this chapter aims to:

Compare the ability of adult *P. australiensis*, *M. australiense* and *C. mccullochi* to maintain position and resist displacement under a range of current speeds; and
Compare the upstream movement response relative to current speed of the three species.

If species-specific ability to maintain position in flow plays a significant role in shrimp assemblage patterns in the Murray-Darling Basin, I would expect to see a limited ability to maintain position in current by *C. mccullochi*, whereas I would expect to see a strong ability to maintain position in current by *P. australiensis* and *M. australiense*. In addition for species that are well adapted to living in rivers and streams with relatively frequent high flow events I would expect to see these species have the ability to move upstream against the current, to compensate for downstream displacement.

5.2 Methods

5.2.1 Experimental procedure

All the shrimp used for these experiments were collected from sites at Wangaratta and Moyhu on the King River, to avoid possible intraspecific variation in swimming ability that might result from home stream conditions. All shrimp were collected on the 15\(^{th}\) April 2013 and were transported to the laboratory in aerated buckets. Each species was kept in separate aquaria in a constant temperature room. The temperature was maintained at 24 °C and a natural light/dark regime (12:12) was maintained for the entire study period, to match the in-stream conditions at the time the study was conducted. Each day, shrimp were fed to excess with flaked fish food. The aquaria were part of a flow-through system, so all aquaria had the same water quality. The shrimp were allowed to acclimatize for approximately 24 h before
experimentation, and were kept for no longer than 5 days before being tested. Experiments were conducted between the 16\textsuperscript{th} and 19\textsuperscript{th} of April 2013.

The experiments were carried out in a small Brett-style re-circulating swim flume (Brett, 1964), with a transparent Perspex channel of 50 (L) x 15 (W) x 15 cm (H), with 1-mm mesh at each end (Figure 5.1). The bottom of the channel was covered in sand, as this is a common substrate in King River where the three species were collected. The decision was made to include a non-smooth substrate, since nowhere in the wild do shrimp occur associated with completely smooth substrate, and the primary aim of the study was to determine the ability of shrimp to maintain position. A diffuser made of parallel plastic tubes was placed in the entrance channel to reduce turbulence. The water used in the flume was pumped from a sump tank that was filled with de-chlorinated tap water. Water from the sump tank also flowed through the holding tanks.

Figure 5.1. Plan view of the flume used to compare the response to flow of \textit{C. mccullochi, P. australiensis} and \textit{M. australiense}. 
Before any experiments were conducted, the flume was calibrated and checked for linear flow using dye injection with high-speed photography to achieve stepped velocity levels for use in current speed trials. The flow through the flume was calibrated using a gate valve on the pump outflow and a ball valve on the flume outflow pipe until the desired current speed was reached in the experimental area (Figure 5.1). In this way, the current speed in the flume could be quickly changed without changing the water level in the flume. Current speed was also measured before each trial using a Marsh-McBirney Doppler flow meter to ensure the correct speed had been reached.

The experiments were carried out at current speeds (treatments) of 10, 15, 20 and 25 cm.s\(^{-1}\). Fifteen individuals of each species (*P. australiensis*, *M. australiense* and *C. mccullochi*) were randomly assigned to each treatment and trialled only once: a total of 60 individuals of each species was used in this experiment. For each trial, an individual was placed in the middle of the experimental section and allowed 1 min to acclimatise, and then the flow was gradually increased until the desired current speed was reached. The current speed was then maintained for a 2-min observation period and each period was filmed with a video camera. At the end of each trial, the shrimp was removed and its carapace length was measured. The carapace length of *C. mccullochi* ranged between 3 and 5 mm, with a mean of 3.6 mm. The carapace length of *P. australiensis* ranged between 3.5 and 6.3 mm with a mean of 4.3 mm and the carapace length of *M. australiense* ranged between 4.2 and 19.4 mm with an mean of 11.2 mm.

From the video of each individual trial, the total time spent moving against the current was recorded. It was also noted if the individual was dragged by the current
and recovered to swim again (partial drag), and if the individual was displaced downstream to the screen at the end of the channel and remained there (total drag).

5.2.2 Data analysis

To test if the number of dragged individuals was independent of species, a Pearson Chi-Square test on the frequency of partially and totally dragged individuals was performed. To determine the relationship between shrimp orientation and current velocity, an orientation factor \( (F_o) \), as the ratio of counter-current swimming and total swimming time, was calculated (Yannicelli et al. 2002). The distribution of the data was examined and a generalised linear model with a gamma distribution and log-link function was used, with Species and Speed as factors. Pairwise tests based on estimated marginal means were conducted to determine where significant differences occurred between species. Size of the individuals (Carapace length) was first used in the analysis as a covariate, but it was found to be not significant (Wald Chi-Square = 0.459, df=1, \( P > 0.05 \)), and therefore, it was discarded. All statistical analyses were performed using SPSS Version 17 (SPSS Inc., Chicago, IL, U.S.A.).
5.3 Results

The frequency of partially dragged individuals was significantly different among species (Pearson Chi-Square = 18.22, df=2, P< 0.001) (Table 5.1). *Caridina mccullochi* was partially dragged at all current speeds, with 13, 47, 53 and 73% of individuals partially dragged at 10, 15, 20 and 25 cm.s\(^{-1}\), respectively. *Paratya australiensis* did not suffer partial dragging at 10 cm s\(^{-1}\), whereas at 15, 20 and 25 cm.s\(^{-1}\), 27, 60 and 67% of individuals, respectively, were, at some time during the observation period, swept by the current. *Macrobrachium australiense* did not suffer partial dragging at 10, 15 or 20 cm.s\(^{-1}\), however, 40% individuals were partially dragged at 25 cm.s\(^{-1}\).

The frequency of individuals totally dragged by the current also differed significantly among species (Pearson Chi-Square = 9.9, df=2, P< 0.01) (Table 5.1). No *M. australiense* were permanently displaced downstream at any current velocity and three (20%) *P. australiensis* were permanently displaced at 25 cm.s\(^{-1}\) (Table 5.1). By contrast, 4 (27%) *C. mccullochi* were totally dragged at 20 cm.s\(^{-1}\) and all 15 were totally dragged at 25 cm.s\(^{-1}\) (Table 5.1).
Table 5.1. Number of *C. mccullochi*, *P. australiensis* and *M. australiense* that were partially dragged (P) and totally dragged (T) during swimming response experiments. Number of individuals per treatment was 15.

<table>
<thead>
<tr>
<th>Current speed (cm s(^{-1}))</th>
<th>C. mccullochi</th>
<th>P. australiensis</th>
<th>M. australiense</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>P</td>
<td>T</td>
<td>P</td>
</tr>
<tr>
<td>10</td>
<td>2</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>15</td>
<td>7</td>
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</tr>
<tr>
<td>20</td>
<td>8</td>
<td>4</td>
<td>9</td>
</tr>
<tr>
<td>25</td>
<td>0</td>
<td>15</td>
<td>10</td>
</tr>
</tbody>
</table>

All three species exhibited a positive rheotactic response to current (Figure 5.2). The mean orientation factor of *C. mccullochi* varied between 0.52 at 10 cm.s\(^{-1}\) and 0.88 at 15 cm.s\(^{-1}\) (Figure 5.2a). The mean orientation factor for *P. australiensis* varied between 0.83 at 25 cm.s\(^{-1}\) and 0.98 at 15 cm.s\(^{-1}\) (Figure 5.2b). The mean orientation factor of *M. australiense* varied between 0.66 at 15 cm.s\(^{-1}\) and 0.89 at 20 cm.s\(^{-1}\) (Figure 5.2c).

Orientation factor (Fo) differed significantly among species (Wald Chi-Square = 6.46, df=2, *P* < 0.05). Pairwise comparisons showed that the mean Fo of *P. australiensis* was significantly greater than both *C. mccullochi* and *M. australiense* (*P* < 0.05). There was no significant difference in mean Fo between *M. australiense* and *C. mccullochi* (*P* > 0.05).
Figure 5.2. Mean (±1 SE) orientation factor (Fo) of (a) *C. mccullochi*, (b) *P. australiensis* and (c) *M. australiense* under different current velocities. The orientation factor (Fo) is the proportion of total time shrimp spent swimming countercurrent.
5.4 Discussion

The results of the flume experiments in the present study showed that, compared to
*P. australiensis* and *M. australiense*, *C. mccullochi* has a limited ability to maintain
position in flow. *Caridina mccullochi* could maintain position only at current speeds
of 20 cm.s\(^{-1}\) or less, whereas *P. australiensis* and *M. australiense* were able to
maintain position at current speeds of at least 25 cm.s\(^{-1}\). These results are supported
by Hancock and Bunn (1999), who found that *P. australiensis* can maintain position
at current speeds of at least 30 cm.s\(^{-1}\). Previously, the ability to maintain position of
*M. australiense* had not been tested beyond 10 cm.s\(^{-1}\) (Lee and Fielder 1984), and the
ability to cope with flow of *C. mccullochi* had not been tested at all.

The results of the present study have provided important context to the results of
Richardson and Cook (2006), who found that *C. mccullochi* is restricted to
slackwater habitats for its entire life history, whereas *P. australiensis* and *M.
australiense* were often found in mesohabitats with moderate current speeds (17 – 47
cm.s\(^{-1}\)). It was also found in Chapters 2 and 3 that *C. mccullochi* were restricted to
relatively slow flowing lowland sections of River. Richardson et al. (2004) also
found that *C. mccullochi* was absent from sections of the Campaspe River which
received high flows in summer. It was hypothesised in that study that this was due
to high flow events limiting the availability of slackwater habitats, which were
thought to be important for the larval development and recruitment.

The results of the present study suggest that the availability of slackwater habitat is
likely important for all life history stages of *C. mccullochi*, because this species has a
demonstrated a poor ability to maintain position in current as adults. Indeed,
elsewhere in the world research has shown that the hydraulic preferences of certain
shrimp species are significant and often a predictor of their distribution. Girard et al. (2014) found that the preferences of shrimps for high (A. scabra, M. heterochirus) or low (X. elongata) velocities are probably linked to their capacity to resist currents or not. Indeed, A. scabra and M. heterochirus are larger in comparison to the other species of the same family (M. poeyi, M. faustinum) and have larger morphological attributes (pincers, legs, spines on pincers) (Lim et al., 2002) that allow them to move in rapids where densities of drifting benthos, particles and/or individuals are higher (Orth and Maughan 1983, Brooks et al. 2005). Of the three species in species in this study M. australiense is much larger than both C. mccullochi and P. australiensis. However, P. australiensis and C. mccullochi are very similar in size, as were the individuals used in the experiments in this study (see methods section) therefore it is highly unlikely that variation in size was driving the highly significant difference in observed ability to resist current between these two species.

Caridina mccullochi also exhibited a significantly lower orientation factor than that of P. australiensis. At all current speeds, P. australiensis individuals spent the majority of the time moving against the current and trying to move upstream beyond the mesh barrier. These results are supported by Hancock and Bunn (1999), who found that P. australiensis exhibited a strong rheotactic response at similar speeds to the current study, and also found that this response was not influenced by the time of year of collection or time of day tested (day/night). The C. mccullochi individuals observed in the current study spent much of the time holding on to the substrate and moved very little.

The tendency of shrimp and other riverine animals to move upstream is generally understood to be a compensatory mechanism to maintain populations which experience downstream losses as a result of larval drift and adult displacement
during high flow events (Elliott 1971, Williams and Williams 1993, Pachepsky et al. 2005). Hancock and Bunn (1999) found that the larvae of *P. australiensis* are unable to maintain position in flow, even at slow current speeds. This helps to explain the often high numbers of these larvae collected in drift samples (Hancock 1995, Price 2010), and the low abundance of larvae following high flow events (Hancock and Bunn 1997, Price 2010). As with *P. australiensis*, *C. mccullochi* and *M. australiense* are also commonly captured in drift samples (Price 2010), although to date there is little evidence to suggest that *C. mccullochi* larvae drift in large numbers.

Price and Humphries (2010) suggested that *C. mccullochi* larvae take measures to avoid drifting and remain in slackwater habitats throughout their larval development stage. Even so, the limited ability of this species to maintain position in flow suggests that this species may be vulnerable to catastrophic drift during high flow events, and because this species displays little behavioural response to flow, it may mean that this species is unable to persist in rivers where high flows that have the potential to cause catastrophic drift are common. *Caridina mccullochi* and *P. australiensis* are very similar in size and morphology, but their response to flow and ability to maintain position in current are very different. Both species prefer to spend most of their time in slackwaters (Richardson and Cook 2006), however, the relatively subdued response by, together with limited ability to maintain position in flow of, *C. mccullochi* compared to *P. australiensis* is likely to account for differences in distribution patterns observed in Chapter 2 and 3 and by Richardson et al. (2004). In their study, Richardson et al. (2004) found that in the Campaspe and Broken rivers, *P. australiensis* had a broad distribution across a range of different flow regimes, whereas *C. mccullochi* was restricted to slow-flowing lowland river reaches, which had relatively few high flow events in summer.
To my knowledge, a comparison of the ability to maintain position in flow of different riverine shrimp species under the same experimental conditions has not been conducted previously in the Murray-Darling Basin or indeed elsewhere in the world, however, similar studies have been conducted of riverine fish. For example Scott and Magoulick (2008) observed the swimming ability and behaviour during high flows of five species of fish from the Illinois River in Arkansas and linked this to observed assemblage patterns. Scott and Magoulick (2008) hypothesised that some species are better able to persist in rivers during and after high flow events because of both a better ability to maintain position and their behavioural response to high flows.

Conclusions

Aseasonal high flow events are a feature of heavily regulated rivers in the Murray-Darling Basin (Sheldon et al. 2000). These high flow events can change the availability and persistence of slackwater habitats (Bunn and Arthington 2002; Bowen et al. 2003; Vietz et al. 2013). In addition, high flows can significantly increase current speeds overall, which in turn can physically displace shrimp, in particular C. mccullochi. This is likely to have a negative impact on the growth and survival of C. mccullochi in regulated rivers.

In the next Chapter, I will bring together the findings of Chapters 2-5 in a discussion of how the interaction between flow, flow regulation and the movement-related life history and behavioural traits of individual species may affect shrimp assemblage structure and distribution in the Murray-Darling Basin.
6.1 Summary of Results

The overall aim of this thesis was to examine the distribution patterns of three species of shrimp, *Caridina mccullochi, Paratya australiensis* and *Macrobrachium australiense*, in the south-eastern region of the Murray-Darling Basin and explore the roles of movement and movement ability, in the context of flow regime, in explaining these patterns. Specifically, four questions were asked: Q1, where do the three species occur in the southern What impact does flow regime have on the distribution of *C. mccullochi, M. australiense* and *P. australiense* in south-eastern region of the Murray-Darling Basin, specifically in relation to modified flow regimes (Chapter 2); Q2, Are the distributions and abundances of these species along an longitudinal gradient in a moderately sized river temporally and spatially dynamic? (Chapter 3); Q3, what role does movement play in these changes in shrimp assemblage dynamics? (Chapter 4); and finally, Q4, what is the role of ability to maintain position and behavioural response to current in the observed distribution patterns (Chapter 5).

The results of Chapter 2 demonstrated that flow regime seems to play a role in the distribution and composition of shrimp communities throughout the south-eastern Murray-Darling Basin, and movement and movement ability are likely to influence this relationship. *Caridina mccullochi* was restricted to lowland rivers that experience relatively few high flow events in summer, which is typical of the natural flow regime in the southern Murray-Darling Basin. *Macrobrachium australiense*
and *P. australiensis*, on the other hand, seem to be more tolerant of frequent high flow events in summer than *C. mccullochi*. Many of the sections of river where *C. mccullochi* was absent experience high flows in summer because of the delivery of irrigation water from major storages. These results were consistent with previous studies conducted on smaller scales (Richardson et al. 2004, Price 2010), but provided clarification on the specific aspects of regulated flow regimes that have a negative effect on the distribution of *C. mccullochi*.

Chapter 3 assessed the assemblage dynamics of shrimp in the relatively unmodified King River and provided important baseline information on the temporal and spatial distribution patterns of *C. mccullochi*, *P. australiensis* and *M. australiense* on a longitudinal and altitudinal gradient, in a relatively natural setting. The results of this chapter showed that *C. mccullochi* is restricted to lowland river habitats and that *P. australiensis* can complete its life history in upland river reaches. *Macrobrachium australiense* occurs further upstream than *C. mccullochi*, but it appears that the former species may not be able to complete its life cycle in the upper reaches, and the individuals present in these reaches are likely to have moved from downstream.

Chapter 4 explored the extent of reach-scale movement among the three species of shrimp, which helped to explain the assemblage patterns found in Chapter 3. The results of Chapter 4 provided evidence of significant upstream movement by *M. australiense* during mid-to-late summer when day length was at its greatest and discharge was low. In contrast, there was no evidence to suggest that *P. australiensis* and *C. mccullochi* undertake significant movement, and are likely to be restricted to the relatively small area of a slackwater refuge for their entire life history. This is significant, as refuge-dependant animals with small home ranges are more at risk from stochastic disturbances than those that travel over large areas (Rodríguez 2002).
In particular, in the event of significant floods or droughts, which result in reductions to the local population, *P. australiensis* and *C. mccullochi* may be slow to move back into these areas and as a result, the local population may take some time to recover (Townsend et al. 1997, Parkyn and Collier 2004). Compared to *P. australiensis* and *C. mccullochi*, *M. australiense* is more mobile and not restricted to slackwater refugia. Therefore, it should be no surprise that this species has been found to quickly recolonise areas after disturbance events, particular drying periods due to drought (Carini et al. 2006). Given that the many rivers in the Murray-Darling Basin are prone to flow-related disturbance events, such as floods and drying (Puckridge et al. 1998), movement behaviour is likely to be a particularly important component of shrimp assemblage dynamics in these rivers over the long term.

Chapter 5 compared the ability of adult *P. australiensis*, *M. australiense* and *C. mccullochi* to maintain position and resist displacement under a range of current speeds; and compared the upstream movement response relative to current speed of the three species. It was found that *C. mccullochi* has a more limited ability to maintain position in flow than *P. australiensis* and *M. australiense*, and lacks a strong rheotactic response to flow. The contrast with *P. australiensis* is notable, considering both species have a similar preference for slackwater habitats and are of a comparable size and morphology. This is noteworthy, since even though there was little evidence to suggest that *P. australiensis* undertakes significant movements throughout its life history (Chapter 4; Hancock and Hughes 1999), the strong rheotactic response observed in Chapter 5, and also by Hancock and Bunn (1999), may mean that this species is able to persist in upland streams where pools and slackwaters are more prone to scouring (Allan and Castillo 1995). With no such mechanism to compensate for downstream displacement, *C. mccullochi* is likely to
struggle to survive in upland and heavily regulated rivers, where flow disturbances are more frequent. In addition, *C. mccullochi* has intermediate reproductive traits (relatively small egg size and moderate fecundity), whereas *P. australiensis* has ‘opportunistic’ reproductive traits (small eggs and high fecundity), which means that *P. australiensis* is better able to take advantage of favourable spawning and recruitment conditions when they occur, especially in regulated rivers with variable flows (Richardson and Humphries 2010).

6.2 Significance of the Results

Theoretical implications

The distribution and assemblage composition of stream organisms, across *riverscapes*, has received considerable attention by ecologists e.g. (Fausch et al. 2002, Moyle et al. 2003, Arthington et al. 2005, Balcombe et al. 2006, Taylor et al. 2006, Torgersen et al. 2006). A subset of this work has included relating these patterns to flow and flow-related habitat variables, including in the Murray-Darling Basin (Humphries et al. 2008, Rayner et al. 2009, Price 2010). However, this research generally has not considered the mechanisms driving those patterns (White et al. 2014). By contrast, behavioural ecology studies have significantly contributed to the understanding of the mechanisms involved in activities, such as migration and habitat selection and processes, such as reproduction and feeding (Fievet 1999, Lucas et al. 2001, Humphries et al. 2006, Hein and Crowl 2010). But the *riverscape* context within which these behaviours operate is often lacking (White et al. 2014). Frameworks used to make predictions of the distribution, composition and dynamics of stream organisms should, in fact, incorporate aspects of both *riverscape ecology*
and behavioural ecology, and include the life histories, movements, and large-scale habitat relationships and distribution patterns within the riverscape (Schlosser 1995, Schlosser and Angermeier 1995, Fausch et al. 2002).

My efforts to understand the role of inherent mobility and dispersal behaviours in shrimp assemblage dynamics, in the context of the flow regime, represent a step in this direction by demonstrating the value of incorporating shrimp behavioural ecology and riverscape ecology. Movement is an important ecological process that occurs at the individual level, but has ramifications for broader populations and assemblage dynamics (Baker 1978, Dodson 1997, Nathan et al. 2008, Morales et al. 2010). Until recently, the role of movement has not been fully incorporated into theories regarding community and assemblage dynamics (Nathan et al. 2008). In the past, this has largely been due to the difficulties in observing the movement of animals, but also likely because it adds significant complexity when attempting to interpret and model assemblage dynamics. As suggested by Nathan et al. (2008), ecologists should be encouraged to embrace the complexity of the role of movement, as this will yield more realistic and more useful frameworks for understanding, conserving and managing natural systems, I believe the work presented in this thesis is a good example of this.

**Consequences for research and conservation in the Murray-Darling Basin**

Modification to the natural flow regime because of watershed degradation, the building of dams and weirs and extraction of water for irrigation has seen a reduction in both the distribution and abundance of native riverine species throughout the Murray-Darling Basin (Gehrke et al. 1995, Sheldon and Walker 1997, Humphries and Lake 2000, Kingsford et al. 2011). While the importance of managing this
problem has received much attention, many restoration and management efforts are often hampered by the lack of background data associated with the ecology, life history, and behaviour of the species that occur in the basin (Humphries and Lake 2000, King et al. 2009a, Richardson and Humphries 2010). Behavioural studies are particularly important in conservation biology, as they can contribute greatly to a stronger, more complete understanding of species-specific resource utilization patterns and habitat requirements (Festa-Bianchet and Apollonio 2003). The current study has identified specific movement traits of Murray-Darling Basin shrimp that are potentially influenced by flow and flow regime, and together with the work of Richardson et al. (2004), this study has shown that it is likely that the construction of dams and weirs and the resultant flow regulation has a significant impact on the distribution and assemblage dynamics of shrimp in the Murray-Darling Basin. In addition, because these species are landlocked (Williams 1977) the ability of these shrimp species to recolonize from other populations via oceanic currents as many other shrimp species do, then the importance of managing these species to sustain their populations is extremely important to avoid irreversible loss. This should be the focus of future conservation efforts of these species.

Understanding the distribution and assemblage dynamics of stream organisms is not just important for the conservation of individual species, but can also be important for understanding broader ecosystem functions and community dynamics (Palmer et al. 1997, Fausch et al. 2002, Covich et al. 2006). Shrimp have been found to be an important component of the biota of rivers, because of their direct influence on ecosystem-level processes, such as organic matter processing, sedimentation, and the composition of benthic algal and invertebrate communities (Pringle et al. 1993, Pringle 1996, Covich et al. 1999, Covich et al. 2006). The role of Murray-Darling
Basin shrimp in processing of organic matter and nutrient cycling has not yet received much attention, however, shrimp are often in great abundances and dominate macroinvertebrate assemblages (Sheldon and Walker 1998; Boulton and Lloyd 1991). In many rivers throughout the world, detritivorous fish species often make up the greatest biomass and play the greatest role in processing of organic material (Jepsen and Winemiller 2002). Given that the southern Murray-Darling Basin is poor in detritivorous fish species (Humphries and Walker 2013), shrimp may fill this role in these rivers. Therefore, because it has been found that flow regulation apparently has a negative effect on shrimp assemblage dynamics, it may also have broader consequences for food web dynamics in the Murray-Darling Basin.

Much of the management and conservation of organisms in the Murray-Darling Basin have in the past focused directly on fish species with high social and economic value (Koehn and Lintermans 2012). Management actions, such as environmental watering, are often taken with little regard for the species' place in the broader ecological community. Given that shrimp are often the primary food source for many fish species (Ebner 2006, Baumgartner 2007), there may well be a link between the abundance, distribution and assemblage dynamics of shrimp and the growth and condition of the species of fish that are of significant social and economic value. If these links do exist, then no matter how much effort is put into developing conservation plans for species of concern, the single-species approach is not viable in the long-term. It is important that a broader, more holistic, approach is taken; one which considers the consequences of river regulation, on the whole river ecosystem, rather than just focussing on a few species.
6.3 Limitations and directions for future research

Data on the movement and distribution patterns of shrimp in this study were obtained from studies conducted in a single season, and the observations of shrimp movements were indirect, so these results should be treated as preliminary. Nonetheless, considering that there is very little data on the movement patterns or broad-scale distribution of shrimp in the Murray-Darling Basin, these results can serve as a basis for more refined analysis investigating the role of movement during life history stages other than adults and at other times of the year. In the future, I suggest that studies of shrimp movement patterns and assemblage dynamics should be conducted across a number of seasons to incorporate a greater range of both high and low flow events. Research that quantifies shrimp movement during specific managed flow events may also provide useful data on impacts of river regulation more generally. In addition, observations of shrimp movements in the natural environment would ideally be conducted in a more direct way than what was conducted in this study.

Directly observing the movements of animals is one of the most difficult disciplines in behavioural ecology, as these movements often occur in short time periods over large distances (Harris et al. 1990, Cunjak et al. 2005, Börger et al. 2006). In addition, many riverine animals are too small to carry tags. The practical limitations of observing individuals using methods such as mark-recapture have long hindered movement studies. But the rise of alternative means of tracking movement (e.g., radiotelemetry, trapping, PIT tags, stable isotopes, genetic identifiers) promises to greatly expand the range of spatial and temporal scales of movement that can be directly observed (Nathan et al. 2008). Collecting data on the timing and distance of
short-, medium- and long-term movements of shrimp would be invaluable for explaining the underlying behavioural mechanisms.

This thesis focussed on the dispersal behaviour and “inherent mobility” of the three species found in the Murray-Darling Basin and related these characteristics to their occurrence across multiple rivers with different flow regimes types and explored the potential impact of altered flow regimes. The results of Chapter 2 and Chapter 3 suggest that other aspects of flow regulation such as temperature and barriers to movement may also play a role observed shrimp assemblages in the southern Murray-Darling Basin. Barriers to movement may potentially have significant impact on the dispersal of *M. australiense*. Although Lee and Fielder (1979) observed that this species was able to crawl upstream over a low-level weir it was only observed doing so whilst water was spilling over the top of the weir, however large aggregations of shrimp where still observed congregating below the weir particularly when water was not spilling over the weir. The observations of Lee and Fielder (1979) and in Chapter 3 of this study suggest that upstream dispersal is a significant part of the life history of *M. australiense* therefore barriers to these dispersal events could have a significant effect on populations particularly if these dispersal events are a part of movement from source areas to “sink” habitats that cannot support reproduction (source–sink dynamics) (Lidicker 1975, Van Homme 1983, Roughgarden and Iwasa 1986, Pulliam 1988). Further exploration of the importance of longitudinal connectivity for *M. australiense* is warranted given the potentially significant impacts.

This study observed only the longitudinal in-channel distribution and movement patterns of shrimp. There is no doubt that lateral connectivity of rivers to their flood plains can also affect the habitat availability for shrimp (Roach and Winemiller
The expansion of suitable habitat onto the flood plain during flooding creates spawning, nursery and foraging areas for many riverine organisms (Ward et al. 1999, Bunn and Arthington 2002), including freshwater shrimp (Górski et al. 2014). In addition, floodplain waterbodies may act as a refuge for shrimp during high flow events, from which they can repopulate river reaches when flows subside (Jeffres et al. 2008). Therefore, the interaction between flows and lateral floodplain connectivity may have a significant impact on the distribution and assemblage dynamics of shrimp. Future studies which investigate the movement of shrimp between the flood plain and main river channel during high flow events would be valuable to explain the role that flood plain connectivity plays in the persistence of shrimp populations in any given river reach.

There is increasing recognition of the ecological significance of dispersal in maintaining species diversity, this has highlighted the need to consider connectivity in conservation planning. Understanding connectivity is of fundamental importance because it underlies landscape-scale ecological processes such as species invasion, immigration and metacommunity dynamics (Nathan and Muller-Landau 2000, Hubbell 2001, Wright et al. 2003, Leibold et al. 2004). Understanding connectivity requires an understanding of the processes that connect habitats. These processes include; patterns of habitat utilisation, the modes, scale, and pattern of dispersal in the landscape, landscape barriers to dispersal, evidence that supports the ecological significance of dispersal.

Patterns of habitat utilisation of the three shrimp in the Murray-Darling basin were assessed by Richardson and Cook (2006). The modes, scale, and patterns of dispersal of the three species were explored in Chapters 4 and 5 of this study and the study conducted by Price and Humphries (2010). The potential significance of barriers to
dispersal of the three species were explored in Chapter 5 and by Lee and Fielder (1979), evidence that supports the ecological significance of dispersal for each of the three species was explored in Chapters 3 and 4. As freshwater shrimp are likely important component of food webs in the Murray-Darling it may be worthwhile using all this information to develop habitat models for each species. These models could then be used to guide the development of management plans that relate to connectivity and flow regimes that benefit not just shrimp in the Murray-Darling but also other biota as well.


Riek, E. 1951. The Australian freshwater prawns of the family Palaemonidae.


Appendix A. Summary of flow variables used in Chapter 2.

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