Patterns and processes in zooplankton and water quality across the Chowilla Floodplain during a large flood.

by

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Deborah Jane Furst

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SUMMARY

Within riverine ecology a generalised concept such as the Flood Pulse Concept or the River Continuum Concept is yet to be developed that accurately describes patterns and processes within lowland rivers of arid or semi-arid climates (hereafter termed dryland rivers). A lot of the difficulty associated with developing a concept for these systems is in part due to the extreme hydrological variability. Australian dryland systems are rated amongst the most variable systems in the world where the variability in flow plays a crucial role in driving ecological processes.

The objective of this thesis was to investigate how a large dryland river floodplain responds to flood and the quantity of nutrient, phytoplankton and zooplankton resources contributed to the riverine food-web. Five permanent channel and four ephemeral floodplain sites were sampled within the Chowilla Floodplain and adjacent River Murray in South Australia from the 17 December 2010 until 18 November 2011. Five hydrological phases were defined based upon the degree of hydrological connectivity.

During the first hydrological phase water flowed through the anabranch system yet remained confined within the banks of the creeks and lakes. Zooplankton communities were diverse with up to 63 species per site and these communities were dominated by rotifers. Supplemented by the pre-existing egg bank, communities within the floodplain lakes (up to 10,409 individual's litre^{-1}) were considerably more abundant in comparison to the permanent sites (up to 613 individual's litre^{-1}).

During the expansion phase, water began to spill over the banks of creeks, lake and wetland depressions onto the flatter areas of the floodplain. This significantly increased the inundated area, the area of lotic habitat and floodplain discharge. During this phase the dissolved oxygen concentration and turbidity differed between sites but the bulk river flow drove similarities in conductivity, chlorophyll-a and particulate organic material[1] and increased mixing of zooplankton communities across the floodplain. Substantial export of nutrients from the floodplain occurred in dissolved and particulate forms and continued into the contraction phase as river flows decreased causing floodplain drawdown. The recession of water into the main river channel brought with it high concentrations of filterable reactive phosphorus (FRP), phytoplankton, zooplankton and other fine particulate

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[1] Particulate organic material = volatile solid concentration which is the concentration of solids in water that are lost on ignition of the dry solids at 550 degrees C.

organic material. The calculated load of each of these resources were approximately 182 tonnes of FRP, 466 tonnes dry weight phytoplankton, 368 tonnes dry weight zooplankton and 7515 tonnes of fine particulate organic material in the two phases from 11 February until 5 May 2011. Both alpha (habitat) and gamma diversity (landscape) were highest during floodplain connectivity (phases 1-3).

The major waterbodies were isolated during the disconnection phase and during the fifth water evaporated and habitats became dry. Isolated habitats became increasingly dominated by copepods and were associated with increasing conductivity. Due to the production of diapause eggs primarily by species that were imported within the floodwaters the egg bank was more diverse after than before flooding.

The findings discussed above enhance our broader and integrative understanding of the natural processes that occur within the system during large scale and magnitude floods within the lowland reaches. This understanding is an essential perquisite to viable ecosystem management. This study has highlighted a number of key factors that need to be considered when managing regulators. This includes:

(1) The inundation of a range of habitat types to promote physico-chemical diversity with the aim of satisfying a wider range of organisms and life history stages and therefore promoting high biodiversity.

(2) The generation of high lateral connectivity between the river and the floodplain promoting the exchange and mixing of resources between habitats fuelling both the riverine and floodplain food-webs.

(3) The use of regulators and environmental flows in tandem. This could include the use of multiple floodplains using the same environmental water to ensure that resources and propagules exiting upstream floodplains are delivered to downstream floodplains using the main river channel as a conduit. This is especially important following periods such as drought as egg banks degrade during these periods, decreasing the resistance and resilience of these environments.

Flows within these systems vary in scale both spatially and temporally. There are large flood such as that in this study which are low in frequency and cover large areas of floodplain and play an important role in resetting the environment to earlier successional stages(Pettit, Froend *et al.* 2001; Stanley, Fisher *et al.* 1997), stimulating ecological processes, connecting habitats, transferring resources between floodplain and main channel environments and dispersing microfauna. However smaller and more frequent floods are important for other biological and biogeochemical functions. Other aspects such as the duration, timing and frequency of inundation also play a crucial. The next step in dryland river management and possibly one of the biggest challenges is in understanding how these different flooding characteristics interact and then to use this knowledge to restore the ecological health of what are now and are likely to remain highly regulated systems.

FOREWARD

This thesis has been prepared as a series of chapters in a format that will be suitable for future publication in scientific journals. To maintain sense of individual chapters, this has inevitably led to some repetition between chapters.

Chapter 1. General Introduction

1.1. Riverine ecosystem concepts

Various concepts exist that describe how flow drives patterns and processes within riverine ecosystems. Perhaps the most influential to date is the river continuum concept (RCC) which suggests that allochthonous inputs occur in the headwaters and are processed into smaller particles by heterotrophic organisms along the downstream gradient. Within the lower reaches, the river channel broadens and water velocity slows providing greater opportunity for autochthonous production. Disruptions to these resource gradients due to impoundments are integrated by the serial discontinuity concept (SDC) (Ward and Stanford 1983). Yet these concepts focus on processes that occur longitudinally and overlook the role of floodplain dynamics. The flood pulse concept (FPC) (Junk, Bayley *et al.* 1989) and its extension to semiarid and arid-zone rivers (Tockner, Malard *et al.* 2000) emphasise the importance of lateral exchanges and suggest that the majority of riverine animal biomass is derived directly or indirectly from the floodplain. The most recent concept, the Riverine Productivity Model (RPM) was originally proposed for highly regulated systems (Thorp and Delong 1994) yet has since been broadened to unregulated floodplain rivers (Thorp and Delong 2002). The RPM proposes that most energy assimilated by organisms is sourced from autochthonous production and the riparian zone during all flow periods. However each of these concepts were originally developed on specific types of systems and are not necessarily applicable universally.

1.2. Dryland river systems

Rivers within arid or semiarid climates (hereafter termed ‘dryland rivers’) are characterised by extreme variability both spatially and temporally. This variability is a product of the hydrological, geological and climatic conditions in which they are exposed. Dryland river systems are amongst some of the most hydrologically variable throughout the world (Puckridge, Sheldon *et al.* 1998) which is driven by seasonal, annual and inter-annual cycles. These cycles result in periods of both extreme high and extreme low flow, these contrasting conditions are frequently discussed in relation to ‘boom’ and ‘bust’ ecology (e.g. Arthington, Balcombe *et al.* 2005; Balcombe and Humphries 2006). During high flow, flood pulses stream across vast areas of floodplain, connecting a diverse range of habitats and drive a surge in productivity – the ‘boom’. As the floodwaters recede, lateral connectivity is disrupted while the remaining floodplain waterholes provide important refugia for aquatic biota – the ‘bust’ (e.g. Balcombe, Bunn *et al.* 2005; Bunn, Thoms *et al.* 2006). Despite exhibiting distinct ‘boom and bust’ periods, currently dryland rivers cannot accurately be described by any single concept. The development of a generalised concept is sought for these systems as it is likely to significantly increase our ability to manage them effectively.

1.2.1. ***Towards a general model for dryland systems***

The variable and unpredictable flow regime characteristic of dryland systems creates variability in the origin, degree or pathway in which energy is assimilated into the system. This has led to a number of authors suggesting that large rivers, including dryland systems, are perhaps best described by a combination of the RCC in upland reaches and the FPC in unconstrained lowland floodplain reaches (Robertson, Bunn *et al.* 1999; Walker, Sheldon *et al.* 1995). Studies have provided some support for this theory. An increase in autochthonous production with increasing distance from the headwaters has been demonstrated in three Australian Rivers and supports one aspect of the RCC concept (increasing chlorophyll-a concentrations in the Gwydir, Ovens and Logan Rivers in Hadwen, Fellows *et al.* 2010). The presence of large pools of allochthonous material (Robertson, Bunn *et al.* 1999), the associated increase in available nutrients (Baldwin 1999) and population surges in aquatic invertebrates (Ning, Gawne *et al.* 2012), birds (Kingsford, Curtin *et al.* 1999) and fish (Balcombe and Arthington 2009; Balcombe, Arthington *et al.* 2006; Burford, Cook *et al.* 2008) during floodplain connection also supports aspects of the FPC. These studies however are isolated and our holistic understanding of when and how these concepts are applicable is still lacking.

For the majority of the time, lowland reaches experience low flow conditions where flows are largely confined to the main river channel with little to no floodplain connection. A number of recent studies conducted during low flow conditions on Australian dryland systems support key elements that underpin the RPM. One of these is that the primary source of energy available and assimilated into the aquatic food-web is of autochthonous origin with additional smaller subsidies from riparian and macrophytic plants (Balcombe, Bunn *et al.* 2005; Bunn, Davies *et al.* 2003; Fellows, Wos *et al.* 2007; Gawne, Merrick *et* *al.* 2007; Hadwen, Fellows *et al.* 2010; Medeiros and Arthington 2011; Oliver and Lorenz 2013; Oliver and Merrick 2006; Pease, Justine Davis *et al.* 2006). On a number of occasions benthic algae has been found to be a key energy source (Bunn, Davies *et al.* 2003; Hadwen, Fellows *et al.* 2010; Medeiros and Arthington 2011). Also consistent within the RPM is the weak coupling found between decomposer and metazoan carbon metabolism pathways (Hadwen, Fellows *et al.* 2010; Thorp and Delong 2002). For example, reliance on benthic algae was also demonstrated in the presence of considerable quantities of terrestrial organic material (Bunn, Davies *et al.* 2003). Some studies also support aspects of the SDC where phytoplankton abundance decreases following releases from impoundments (Gawne, Merrick *et al.* 2007; Vink, Bormans *et al.* 2005). Thus perhaps, large dryland systems are best described by the RCC in upland reaches while in the unconstrained lowland floodplain reaches the RPM combined with aspects of the FPC during high flow periods.

1.2.2. *Dryland river floodplains and their role in the broader landscape*

1.2.2.1. *Floodplains*

Dryland river floodplains are recognized for their high heterogeneity created by the complex geomorphology and hydrological variability. They are often comprised of a range of lotic, semi-lotic and lentic environments including side channels, abandoned meander loops, backswamps and marshes and tributary streams (Ward 1998). These habitats range in their physical, chemical and biological attributes that vary across spatial and temporal patches and gradients in which biota adapt (Walker, Sheldon *et al.* 1995). Adaption to spatio-temporal heterogeneity promotes high biodiversity in which natural disturbance such as floods plays a key role in maintaining.

The fluvial dynamics of floodplain connectivity and local habitat influences are a key driver of physico-chemical diversity across habitats. Diversity in physico-chemical components can be influenced by regional processes acting at the catchment scale and/or local processes occurring at the floodplain scale (Thomaz, Bini *et al.* 2007). During flood-pulses regional forces are thought to become more influential. This inference has been based on findings that hydrological connectivity between floodplain habitats resets the ecosystem. They do this by increasing the exchange of water, dissolved nutrients, suspended sediments, and organic materials (e.g. Tockner, Pennetzdorfer *et al.* 1999) and disrupting the structure and function of the resident biotic communities. Uniformity is then created between habitats that respond to regional influences such as seasonality.

As hydrological connectivity decreases, habitats become isolated, water residence time's increase and local forces such as water source (e.g. groundwater, ice, etc), flow paths, soil type and morphology become more dominate. These then drive autogenic processes (produced from within individual waterholes) affecting the physico-chemical environment of individual water bodies (Tockner, Malard *et al.* 2000). This physico-chemical diversity determines habitat availability for biotic communities such as aquatic plants, microinvertebrates, macroinvertebrates and amphibians and the ecological succession that follows (e.g. Collier 1995; Gillooly 2000; Kutka and Bachmann 1990; Roman, Gauzens *et al.* 1993). This general pattern from low to high physico-chemical diversity has been investigated in a number of tropical and temperate rivers (see Thomaz, Bini *et al.* 2007) yet only one within arid or semi-arid climates (Sheldon and Fellows 2010). However, it has been demonstrated in a range of biotic components within the Cooper Creek catchment in Central Australia including phytoplankton (McGregor, Marshall *et al.* 2006), vegetation (Capon 2003), macroinvertebrates (Marshall, Sheldon *et al.* 2006) and fish (Balcombe, Bunn *et al.* 2007).

1.2.2.2. *Functional processes*

The importance of floodplains within large dryland river systems has certainly been acknowledged however relatively little is known regarding their role in the functioning of the broader river landscape. Flood-pulses provide important vectors for ecological exchange between patches where the transition zones between these patches are ecotones and connectivity is the ease in which organisms and matter move between them (Ward, Tockner *et al.* 1999). Depending on the degree and direction of these exchanges, floodplains can act as sources, sinks or transformers of resources, with their functional role dependent upon the frequency, extent, duration and timing of inundation. As water moves across the floodplain and water velocity decreases, sediment particles are often deposited while dissolved nutrients are incorporated into abiotic and biotic complexes (Gurnell 1997). Through these processes floodplains act as a sink for suspended sediments and dissolved nutrients (e.g. Tockner, Pennetzdorfer *et al.* 1999). Areas of the floodplain that experience wetting-drying cycles develop into biogeochemical “hotspots” (McClain, Boyer *et al.* 2003) as nutrients are mobilised from the sediment and leached from organic material upon wetting. The warmer water temperatures, longer water residence times (WRT) and elevated nutrients can result in relatively high primary production (e.g. Glazebrook and Robertson 1999). This productivity can then be assimilated back into the food-web by both the emerging and colonising aquatic biota (Balcombe, Bunn *et al.* 2005; Bunn, Davies *et al.* 2003). These resources may then be transported into the main river channel, fuelling primary production and providing food for higher order consumers downstream (e.g. Bouvet, Pattee *et al.* 1985; Cellot 1996; Eckblad, Volden *et al.* 1984; Fisher 2011; Hein, Baranyi *et al.* 2003). This is however, a simplistic overview of floodplain function. In reality it is highly complex due to factors such as geomorphology and hydrological variability.

1.2.2.3. *Zooplankton*

One of the key opportunistic groups that rapidly colonise, exploit and thrive within the variable and complex nature of dryland river floodplains is zooplankton. Upon floodplain inundation many species are imported with the floodwaters (Jenkins and Boulton 2003) while others emerge from resting stages with the sediment (e.g. Boulton and Lloyd 1992; Ning and Nielsen 2011). After floodplain colonisation, zooplankton reproduce rapidly and feed on the bounty of bacteria, phytoplankton and organic material (e.g Desvilettes, Bourdier *et al.* 1997; Jumars, Penry *et al.* 1989; Kobayashi and Church 2003). They themselves are preyed upon by organisms such as other zooplankton, fish, birds, amphibians and macroinvertebrates (Arumugam and Geddes 1988; Crome 1985; Lynch 1979; Meredith, Matveev *et al.* 2003; Ranta and Nuutinen 1985) and thus play a vital role within the function of the ecosystem.

Floodplains have been recognised for their extremely diverse zooplankton communities, in part due to their emergence from resting stages within the sediment. Many zooplankton species have the ability to produce diapause eggs to bridge periods of unfavourable conditions, including physical (e.g., salinity, desiccation) and biological factors (e.g. limited food availability, predation, competition) (Brendonck and De Meester

2003; Green, Jenkins *et al.* 2008). Once produced most sink to the benthos (Hairston 1996) where they collectively form an ‘egg-bank’. Within ephemeral floodplains only a fraction of the organisms within the egg-bank emerge and combine with those imported with the floodwaters (hereafter termed the ‘imported community’). This fraction is the ‘active egg-bank’ (as defined by Caceres and Hairston Jr 1998), while the remaining eggs supplement the ‘persistent egg-bank’ (see Brendonck and De Meester 2003). The majority of hatching within the active egg-bank occurs within hours to days following inundation due to cues that identify suitable growth and reproduction such as temperature, osmotic potential and oxygen concentrations (Brendonck 1996). The remaining eggs within the persistent egg-bank provides an important buffer against periods when the active egg-bank becomes depleted due to factors such as mortality and displacement. Due to this tendency for eggs to accumulate, especially within ephemeral environments, the egg-bank can store a diverse array of organisms from past floods. Egg banks however are susceptible to degradation due to factors such as senescence, predation, disease and dispersal (Brendonck and De Meester 2003; Caceres and Hairston Jr 1998; De Stasio 1989). For this reason factors such as the frequent inundation play an important role in maintaining a healthy functioning egg bank (e.g. Boulton and Lloyd 1992).These egg-banks play an important role in future populations and communities of zooplankton and thus are important for the functioning of aquatic ecosystems.

Behavioural characteristics, life history traits and drivers of population dynamics support the premise that the distribution and development of zooplankton is likely to be coupled with the shifts found between homogeneity and heterogeneity in other factors. Homogenisation is likely to occur as the passive dispersal of zooplankton leads to the importation of early colonists (Jenkins and Boulton 2003) and therefore all habitats are likely to initially reflect a typical riverine assemblage. Rivers are typically dominated by rotifers due to the inability of cladocerans and copepods to reproduce in fast flowing water (Rzoska 1978). In addition, zooplankton are highly sensitive to their direct environment and the abiotic factors and biotic communities that are often homogenised during flood affect emergence and subsequent population dynamics (e.g. turbidity Dejen, Vijverberg *et al.* 2004; e.g. temperature Gillooly 2000; e.g. predation Gliwicz and Pijanowska 1989; e.g. salinity Nielsen, Brock *et al.* 2003; e.g. water residence time (WRT) Obertegger, Flaim *et al.* 2007; e.g. pH Roman, Gauzens *et al.* 1993). It follows that with a loss of connectivity the influence of flow decreases and local habitat influences (e.g. competition, predation, riparian vegetation cover) play a bigger role in structuring zooplankton communities.

One of the key factors known to affect zooplankton populations is WRT, which often has a strong positive relationship with zooplankton abundance and biomass and results in a shift from rotifer to crustacean dominated communities (e.g. Baranyi, Hein *et al.* 2002; Basu and Pick 1996; Obertegger, Flaim *et al.* 2007). High zooplankton abundance is favoured by increased WRT as it allows for reproduction and also favours the development of abundant phytoplankton communities (e.g. Bahnwart, Hübener *et al.* 1998; e.g. Boyer, Kelble *et al.* 2009; Schindler 2006; Søballe and Kimmel 1987). The zooplankton community composition on the other hand shifts in dominance with WRT due to the susceptibility of slower reproducing zooplankton to advective loss in short residence systems (e.g. Pace, Findlay *et al.* 1992) and their competitive advantage in exploiting resources in higher residence systems (Obertegger, Flaim *et al.* 2007). Consequently, longer WRT's favour zooplankton development within off-channel sites including floodplain lakes, billabongs and impoundments. Within in-channel sites, zooplankton development occurs predominantly in littoral areas and storage zones (Lancaster and Hildrew 1993; Reckendorfer, Keckeis *et al.* 1999; Reynolds, Carling *et al.* 1991).

Due to the combined effects of higher WRT's and egg bank emergence, floodplains host both abundant and diverse zooplankton communities that are thought to act as zooplankton sources for faster flowing environments. However, very little direct evidence of this process has been produced, with contrasting results from the few studies that have investigated this (Eckblad, Volden *et al.* 1984; Gigney, Petrie *et al.* 2006; Ning, Gawne *et al.* 2012; Saunders and Lewis 1988b; Saunders and Lewis 1989). Presumably, the key factors influencing these differing results is hydrology, as it controls the availability of and transportation from habitat suitable for zooplankton growth (e.g. Saunders and Lewis 1988b). A number of studies have shown that increases in abundance within the river channel correspond to periods of higher flows and floodplain connection (Ning, Gawne *et al.* 2012; Saunders and Lewis 1988a). Studies have also found higher abundances at low discharge and no floodplain connectivity (e.g. Saunders and Lewis 1988b). Because of the lower water velocities and higher water residence times during these periods, increases in zooplankton abundance can occur at rates that allow substantial growth (Pourriot, Rougier *et al.* 1997; Talling and Rzoska 1967). Therefore, within river floodplain systems, it is likely that the highest zooplankton abundances occur during low and high discharge and the lowest during medium discharge.

1.2.2.4. *Landscape ecology: integrating patterns and processes*

The importance of viewing systems from a landscape perspective has been highlighted as an important step towards the more effective management and restoration of river systems (Ward, Tockner *et al.* 2002; Ward 1998; Ward, Malard *et al.* 2002). Landscape ecology is a hierarchical approach which by segregating the landscape into functional units integrates patterns and processes, revealing interactive pathways between ecological biotopes. Methods that relate landscape spatio-temporal heterogeneity to ecological functions and processes are yet to be fully developed. However the use of indices such as the coefficient of variation (CV) (e.g. Thomaz, Bini *et al.* 2007; Ward and Tockner 2001) and species diversity indices including alpha (α), beta (β) and gamma (γ) diversity have been proposed as a valuable approach (Ward 1998; Ward, Malard *et al.* 2002; Ward and Tockner 2001). The CV is a common standardized measure of variability that adjusts the sample variance by the mean making it a better comparative measure than variance alone when measuring heterogeneity (Crowl, Townsend *et al.* 1997; Palmer, Hakenkamp *et al.* 1997; Ward and Tockner 2001). Alpha diversity is a measure of species diversity within a defined unit (e.g. a lake), gamma diversity is a measure of species diversity within a defined region (e.g. a whole floodplain) and beta diversity is the measure of turnover between units (Ward, Malard *et al.* 2002). What constitutes a unit or region varies, depending of the scale of the study being undertaken. The use of biodiversity indices to investigate landscape ecology has the potential to provide significant insight into processes such as disturbance, ecological succession, resource partitioning, ecotones and connectivity (Ward, Malard *et al.* 2002; Ward and Tockner 2001).

1.3. **The Murray Darling Basin**

The Murray-Darling Basin is Australia’s largest and most iconic river system (Figure 1-1), where the two main sub catchments are the Murray and Darling River systems. The Darling River is 2740 km in length, beginning in south-east Queensland and flowing to the confluence with the River Murray at Wentworth. The major contributor, the River Murray is 2530 km in length and begins in the Snowy Mountains and flows to the Southern Ocean in South Australia (MDBA 2013).

Figure 1-1: The Murray-Darling Basin. Blue lines represent tributaries where the thicker lines indicate the larger tributaries (modified from Ben Spraggon at ABC 2013).

The majority of the basin has an arid or semi-arid climate with highly variable rainfall and flow (Maheshwari, Walker *et al.* 1995). Despite this natural variability, the basin produces around one-third of the nation’s food supply (MDBA 2013). To provide a secure water supply for this agricultural production (as well as for industrial and domestic purposes), there have been significant hydrological alterations made to the system. This came in the form of significant developments between 1920 and 1940, including: 13 low level weirs between Blanchetown and Torrumbarry; a high level weir at Yarrawonga; the Hume Dam; barrages across the Murray Mouth; and a regulator at Lake Victoria (Maheshwari, Walker *et al.* 1995). Regulation also continued after 1950 as the irrigation industry expanded rapidly (Close 1990, in Maheshwari, Walker *et al.* 1995). The high level of water extraction and regulation has resulted in a large reduction in the average annual discharge, as well as a large reduction in the flow variability (Maheshwari, Walker *et al.* 1995) (Figure 1-2).

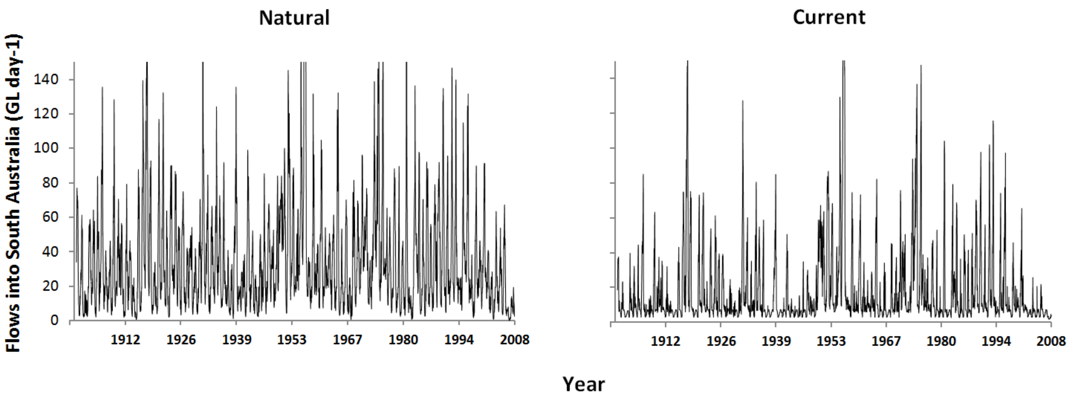

Figure 1-2: The calculated flows at the South Australian border based on the modelled flow regime that would have occurred if there was no river regulation and extractions (Natural) and the actual flow regime with regulation and extractions (Current) (ML day^{-1}). Note that the vertical axis maximum is 150000 ML day^{-1} and at times flows go beyond this.

Many of the environmental effects of river regulation on the Murray-Darling Basin are complex and have occurred over long periods of time. These include soil erosion and deposition, salinisation, reduced groundwater recharge and subsequent lowering of the water table (MDBA 2013). The ecosystems rapid decline over the last few decades has prompted the development of various management strategies. The provision of environmental water[2] is considered to be particularly important and aims to recover some of the natural water regime to which the ecosystems are intrinsically linked (MDBA 2013). The Macquarie Marshes (New South Wales) was the first ecosystem within the Murray Darling Basin to receive an environmental water allocation in 1980 (MDBA 2013). Some additional *ad hoc* approaches throughout the 1980's were employed however it was not until 1993 that the second official allocation of 100,000 ML to the Barmah-Millewa Forest

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[2] The water regime provided to achieve environmental objectives (Australian environmental water management).

was made (MDBA 2013). Throughout the 1990s it was recognised that the incorporation of environmental water provisions in water management was needed and led to the Council of Australian Governments Water Reform Agreement in 1994 (MDBA 2013). Reiterating this agreement, the Intergovernmental Agreement on a National Water Initiative was signed in 2004 by the Australian Government and the state and territory governments (MDBA 2013). The official consideration and delivery of environmental water then progressed under programs such as The Living Murray, Australia's largest river restoration program at the time (MDBA 2013). Initially The Living Murray program focussed on securing water entitlements to achieve environmental objectives at six icon sites selected for their ecological, economic and cultural significance. These included: (1) The Barmah-Millewa Forest; (2) The Gunbower-Koondrook-Perricoota Forest; (3) Hattah Lakes; (4) The Chowilla Floodplain and Lindsay-Wallpolla Islands; (5) Lower Lakes, Coorong and Murray Mouth and; (6) The River Murray Channel (MDBA 2013).

Throughout the 2000's severe drought throughout the basin exacerbated the impacts of regulation on the river ecosystem, leading to the Murray-Darling Basin Plan. The Basin Plan includes the recovery of up to 2800 GL year^{-1} of water for environmental water provisions (MDBA 2013). During the drought, environmental water was delivered to floodplain habitats by pumping water from main channel habitats. This water was held in place using embankments and left to evaporate (MDBA 2013). However, to improve the delivery of environmental water, the planning of major environmental structures, including regulators, levees, channels and fishways begun (MDBA 2013). A number are now currently under construction and with their completion a much broader range of management options will be possible for these areas. There are likely to be significant ecological outcomes for those species that respond to inundation however there is a risk that the processes that rely on flow will be interrupted and therefore there is a need to understand connectivity.

1.3.1. *From drought to flood*

Aseasonal factors have a strong influence on the hydrology of dryland rivers throughout the world. The atmospheric phenomenon El Niño Southern Oscillation (ENSO) has a major influence on the hydrological variability of Australian dryland systems (Leigh, Sheldon *et al.* 2010; Puckridge, Walker *et al.* 2000). The ENSO is "a major see-saw in air pressure and rainfall patterns between the Australian/Indonesian region and the eastern Pacific" (BOM 2014a). It is measured using the Southern Oscillation Index (SOI) and can be related to the temperature of the underlying ocean, otherwise known as El Niño and La Niña events (BOM 2014a). El Niño events are associated with a strong negative SOI and higher air pressure over Australia, this sometimes causes dryer than average conditions throughout areas of the country. La Niña events are associated with a strong positive SOI and lower air pressure over Australia which sometimes causes wetter than average conditions (BOM 2014a). Beginning in autumn 2010 *El Nino* weather conditions transitioned into *La Nina*. The second half of 2010 was the wettest on record with most of Australia experiencing unusually heavy rainfall and a record high December SOI value of 27.1 (BOM 2014a). This pattern continued in 2011, with Australia experiencing the third wettest year since comparable records began in 1900 (BOM 2014a). The 2010-11 *La Nina* events combined were one of the strongest on record and dominated weather patterns (BOM 2014a). Floods, hereafter termed the 2010-11 floods, occurred throughout the country, especially within Queensland, New South Wales and Victoria (Kearns, Hairston *et al.* 1996). The combination of significant flows within both the Darling and the Murray River's at Wentworth reached its maximum of approximately 93 000 megalitres per day at the South Australian border (DEWNR 2012). Approximately 144 wetlands (98%) and 7444 hectares of wetland (96%) were inundated between the Hume Dam (near Albury in Victoria) and Wellington (approximately 35 kilometres downstream of Murray Bridge in South Australian) (Overton, McEwan *et al.* 2006).

1.4. **Study Site**

1.4.1. ***The Chowilla Floodplain***

The Chowilla Floodplain (33°57'0.41"S, 140°56'29.64"E) is one of the major floodplains adjoining the River Murray covering 17,700 hectares and has a semi-arid climate with an annual rainfall of approximately 260 mm (Figure 1-4) (Kearns, Hairston *et al.* 1996). Chowilla is one of six 'Icon Sites' of The Living Murray program (MDBC 2007). The natural character of the floodplain is now under threat and of all the Icon Sites Chowilla is the most affected by flow regulation (MDBA 2013). However, Chowilla still remains the largest floodplain forest on the lower River Murray (Roberts and Ludwig

1991) and is a major component of the Riverland Ramsar wetland of international significance and a National Parks and Wildlife Service Game Reserve (MDBA 2010).

Chowilla is a complex floodplain due to its geomorphology and hydrological variability. Once flows breach the banks at approximately 33000 ML day^{-1}(measured within the River Murray upstream of the main inlet to Chowilla Floodplain) (see Figure 1-3 for connection and disconnection dates in relation to the hydrograph of the 2010-11 floods) a range of habitats including, fast and slow meandering creeks, ephemeral depressions, abandoned channels and swales and cut-off meanders are inundated (Mackay and Eastburn 1990; Shiel, Green *et al.* 1998). Upstream of Lock 6, water is diverted from the River Murray into a network of streams on the Chowilla Floodplain. These converge to form the main anabranch of the floodplain, Chowilla Creek (Figure 1-4), which flows back into the river below Lock 6 (Jolly, Walker *et al.* 1994).

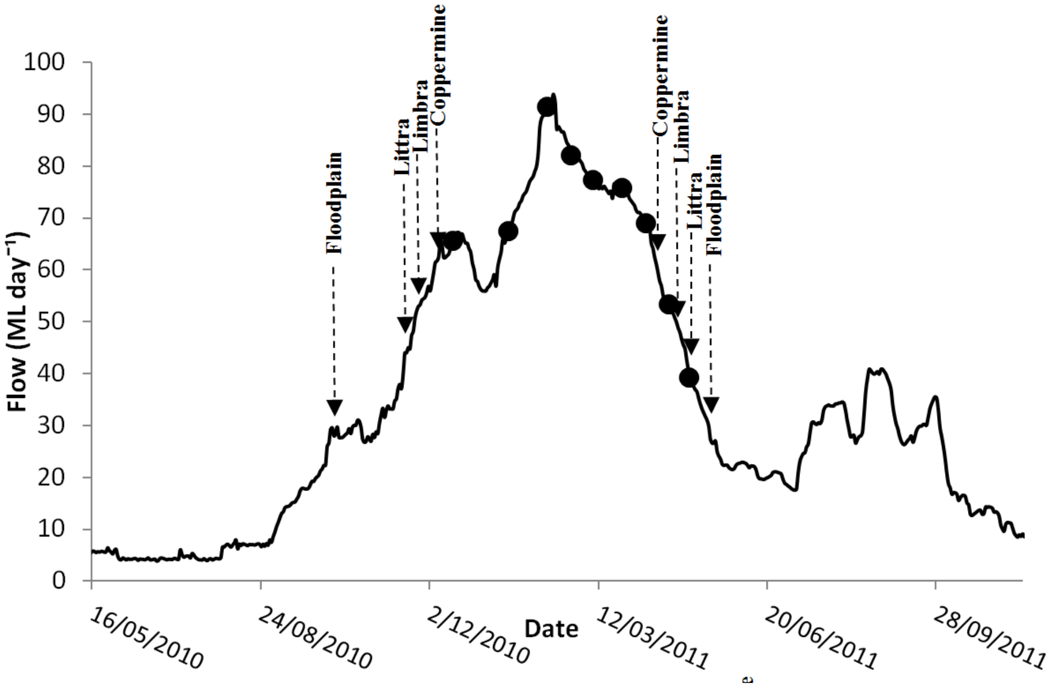

Figure 1-3: Hydrograph of flows to South Australia (data sourced from DEWNR 2012). Connection and disconnection dates of Lake Littra, Lake Limbra, Coppermine Waterhole and the remainder of temporary floodplain habitats (Floodplain) are indicated with broken arrows. Sampling dates are indicted as ●. Broken lines identify the five phases of hydrological connectivity as defined in the text.

The area has been recognised for its high species diversity in mammals, reptiles, amphibians, macrophytes, macroinvertebrates, macrocrustaceans, microinvertebrates and fish (Boulton and Lloyd 1991; Boulton and Lloyd 1992; O'Malley and Sheldon 1990;

Roberts and Ludwig 1991; Thompson 1986). The most dominate types are River Red gum (*Eucalyptus camaldulensis*), Black box (*Eucalyptus largiflorens*), River cooba (*Acacia stenophylla*) and Lignum (*Muehlenbeckia florulenta*) and these are distributed according to hydrological, soil and salinity gradients (MDBC 2013; Sharley and Huggan 1995). The Chowilla Floodplain displays variability in salinity over its entire area. The floodplain overlays an extensive unconfined/semi-confined aquifer and the varying soil types influence the rate of salinisation and leaching of salt in the soil during floods (Overton and Doody 2008). Vegetation clearance has increased the inflow of saline groundwater in some areas however in other areas the groundwater is fresh. In areas closer to the river the groundwater is often fresher due to the river recharging the adjoining aquifer (Overton and Doody 2008). The diversity of habitats available support significant populations of aquatic and terrestrial biota including rare, endangered and nationally listed threatened species (MDBC 2013).

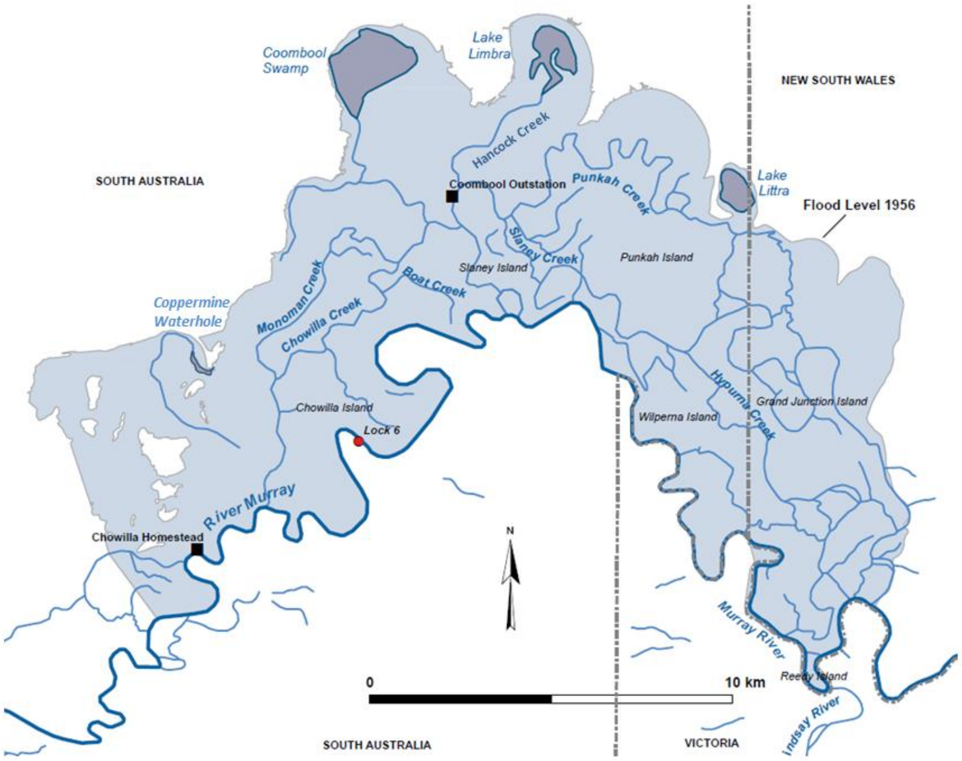

Figure 1-4: The Chowilla Floodplain and adjacent River Murray which flows from the east to the west (MDBA 2013).

Figure 1-5: Punkah Creek in the Chowilla Floodplain where salinity has been brought to the surface by the water table, severely stressing and killing river red gums and black box trees (photo courtsey of Arthur Mostead).

Due to its low rainfall the floodplain relies on upstream flows from the upper Murray and Darling Rivers which have been significantly reduced and have severely affected the flooding frequency, extent and duration of floods (Figure 1-6). As part of The Living Murray program, individual lakes and wetlands within the Chowilla Floodplain received environmental water allocations between 2006 and 2009, improving the health of small areas of the floodplain {e.g. \Holland, 2009 #581;Marsland, 2009 #580. However, on the broader floodplain conditions continued to deteriorate throughout the drought, which had severe implications for both the fauna and flora communities. For example, a large proportion of the floodplain vegetation was severely stressed with over half in poor health or dead (Overton and Doody 2008) (Figure 1-5). With the perilous state of the floodplain ecosystems and severe water shortages, a major environmental regulator for Chowilla Floodplain was proposed; with construction beginning in 2010. The regulator is located at downstream end of Chowilla Creek. It will be used to hold water to the level of Lock 6, resulting in the inundation of large areas of the floodplain (30 – 50%) under relatively low flows (MDBA 2010). The regulator will be operated one year in three for three to four months at a time (MDBA 2010).

Figure 1-6: Flooding extent, frequency, and duration under natural and current conditions at Chowilla (table from DEWNR 2006). Column one shows actual flows where floodplain inundation was measured, except those marked with asterisk, where inundation data are interpolated (Sharley and Huggan 1995).

River Murray flow (ML/day)	Area inundated (ha)	Return period ** (Number of times peak flows occur in 100 years)		Duration (Number of months flow is exceeded)	
		Natural	Current	Natural	Current
3000	-	100	100	11.8	11.9
10 000	-	100	94	10.1	4.6
20 000	-	99	63	7.8	4.6
40 000	1400	91	40	4.9	3.3
45 000	1700	83	34	4.6	3.2
55 000	3100	-	-	-	-
65 000	4800	-	-	-	-
75 000	6700	45	-	-	-
80 000	8200	45	12	3.2	2.6
90 000	11 100	37	11	3.1	2.1
110 000	14 200	27	5	2.4	3.2
140 000	16 800	14	4	2.1	2.5
200 000	17 700	3	1	2	2
300 000	17 700	1	0	2	-

**Figures refer to highest daily flow in the month, not average daily flows for the month.

1.4.2. *Floodplain sites*

Two channel sites within the floodplain were included in this study: one temporary (Figure 1-7: Hancock Creek) and one permanent (Figure 1-8: Chowilla Creek). Three lakes where chosen to span the range of salinities normally observed on the floodplain. Despite all still typically categorised as fresh, Lake Limbra is commonly the least fresh and Coppermine Waterhole is the freshest. All three lakes are characterised by a fringing band of river red gums (*Eucalyptus camaldulensis*) with extensive stands of tangled lignum (*Maehlenbeckia florenta*). See Table 1-1 for a summary of key lake features.

Figure 1-7: Hancock Creek, the inlet and outlet to Lake Limbra from Chowilla Creek.

Figure 1-8: Chowilla Creek, the main anabranch of the Chowilla Floodplain.

1.4.2.1. *Lake Littra*

Lake Littra is a shallow (c. 1m), ephemeral deflation basin that fills from Salt Creek (Figure 1-4 and Figure 1-9) and has a nominal capacity of approximately 1,000 ML. The lake begins to fill at about 47,000 megalitres per day (ML day^{-1}) flowing into South Australia[3] (see Figure 1-3 for connection and disconnection dates in relation to the hydrograph of the 2010-11 floods). Lake Littra received environmental water in September 2005 (topped up in December), March 2008 (topped up in May) and again in October 2009. The area inundated is estimated to be 86 ha.

Figure 1-9: Lake Littra (photo courtesy of Dr. Todd Wallace).

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[3] The Murray Darling Basin Authority calculates the flow into South Australia by summing the daily flow at sites 426200A River Murray D/S Rufus River and 414211A Mullaroo Creek D/S of Offtake and subtracting 250 MLday^{-1} for the Lindsay River allowance (for site locations see DEWNR (2012) WaterConnect Surface Water Archive. Department of Environment, Water and Natural Resources. Government of South Australia. Accessed: 19th September. 2012 at https://apps.waterconnect.sa.gov.au.

1.4.2.2. *Coppermine Waterhole*

The Coppermine waterhole complex comprises of both a moderately deep (less than 2m deep) retaining basin (Figure 1-10: Coppermine Waterhole) and adjacent floodplain. Coppermine Waterhole begins to fill at approximately 65000 ML day^{-1} (see Figure 1-3 for connection and disconnection dates in relation to the hydrograph of the 2010-11 floods). The complex fills through an ephemeral channel leading from Monomon Creek into the eastern end of the lake (Figure 1-4 and Figure 1-10). During high flows water spills from the waterhole in the northern end into an extensive lignum shrubland and finally flows back into Chowilla Creek (Figure 1-8) through multiple outlets. Coppermine Waterhole received environmental water in February 2005 and November 2008 and both the waterhole and floodplain complex received water in October 2006. In 2009, the waterhole-floodplain complex was rewatered in November. The area inundated with the 2009 environmental flows was estimated to be 325.2 ha.

Figure 1-10: Coppermine Waterhole (MDBA 2010).

1.4.2.3. *Lake Limbra*

Lake Limbra is a temporary lake (approximately 2 m deep), which fills from Chowilla Creek via Hancock Creek (Figure 1-7). Small volumes of water begin to pass over a culvert within Hancock Creek at flows of approximately 35,000 ML day^{-1} over the South Australian border (see Figure 1-3 for connection and disconnection dates in relation to the hydrograph of the 2010-11 floods). The lake begins to fill at flows greater than 45,000 ML day^{-1}. The lake has a nominal capacity of approximately 4500 ML and the area inundated is estimated at 320 ha. Lake Limbra received environmental water in March 2010 and was topped up in June 2010.

Figure 1-11: Lake Limbra.

Table 1-1: Summary of lake features. The features include the nominal water capacity (ML); the area inundated (km^2); the approximate maximum depth (m); the calculated flows into South Australia (ML day^{-1}) required to begin filling the lake (Flow to fill); the approximate salinity range (µS cm^{-1}): the previous dates that watering events took place (Watering Events). km^2 = squared kilometres and the approximate length of time between initial watering to complete evaporation and desiccation (months).

Lake	Nominal capacity (ML)	Area inundated (km^2)	Depth* (m)	Flow to fill (ML day^{-1})	Salinity range* (µS cm^{-1})	Watering Events	Length of time from watering to complete evaporation and desiccation* (months)
Lake Littra	1,000	0.86	1	47,000	260- 3240	September 2005 (topped up in December) March 2008 (topped up in May) October 2009	6
Coppermine Waterhole	265	0.11	2	65,000	180 - 840	February 2005 October 2006 November 2008 November 2009	12
Lake Limbra	4,500	3.2	2	45,000	270 - 750	March 2010 (topped up in June 2010)	12

*** Figures are approximate as there is no long term data available and were obtained either via personal communication and values measured during this study {Wallace, 2014 #610}.**

1.5. The project

The hydrological connectivity of the river and floodplain during the high flow period of 2010-2011 provided the opportunity to investigate the role of a large flood on a large dryland river floodplain and its role in the broader landscape. This thesis aims to investigate some of the key functions in which floods of this magnitude are thought to play. This includes resetting and stimulating successional processes and the transferal of materials such as nutrients and organic material between the floodplain and main channel habitats as described by the FPC. To do this a landscape ecology approach will be undertaken (see heading 1.2.2.4) where the defined region is the section of the River Murray and adjacent floodplain beginning just above the Chowilla Floodplain to just below (i.e. the area depicted in Figure 2-1). The functional units chosen include the five floodplain habitats, Hancock Creek, Chowilla Creek, Lake Littra, Coppermine Waterhole and Lake Limbra and the main river channel of the River Murray (see section 1.4.2 for site descriptions). Hereafter, these functional units will be referred to as ‘habitats’. Hydrological phases of floodplain inundation were defined using the flow hydrograph, corresponding area of the floodplain inundated and habitat connection and disconnection points. These phases of hydrological connectivity will be used throughout the thesis as an indicator of the functional role of hydrology on the patterns and processes being investigated. As a key primary consumer within these habitats, zooplankton are of a key focus.

The first two data chapters investigate general patterns across the landscape during a flood-pulse using methods such as those described in section 1.2.2.4. Firstly, as the physico-chemical environment drives many of the processes within river-floodplain systems, patterns in physico-chemical factors across the landscape in relation to hydrology will be investigated (0). Based on the role of local habitat influences and floodplain connectivity as described in section 1.2.2.1 it is hypothesised that: (a) physico-chemical factors will be most similar at the peak of the flow hydrograph (high connectivity) due to hydrological exchanges and mixing and (b) as flow decreases physico-chemical factors will become increasingly different as local habitat influences become the dominant environmental drivers. Secondly, patterns in zooplankton assemblage structure were investigated and used to identify the key physico-chemical factors driving community succession within these habitats in relation to hydrology (Chapter 3). It was hypothesised that: (a) zooplankton community structure will be most similar when the degree of connectivity between habitats is high and mixing homogenises the zooplankton communities, and (b) as connectivity decreases communities will become increasingly different as habitat heterogeneity re-emerges as the dominant environmental driver.

The following two data chapters will investigate resource exchange between the floodplain and the main river channel to identify the functional role of the floodplain within the broader river landscape. Firstly, the role of the floodplain as a source, sink and transformer of resources to the main channel of the River Murray was investigated (Chapter 4). The resources measured included dissolved organic carbon (DOC), ammonia (NH_4), oxidised nitrogen (NOx) and filterable reactive phosphorus (FRP). Organic particulates include phytoplankton, zooplankton and particulate organic material >1.2µm with phytoplankton and zooplankton subtracted (hereafter termed ‘other particulate organic material’ (O-POM)). Based on the processes described in section 1.2.2.2 it was hypothesised that: (a) the function of the floodplain within the broader river landscape would change over time with: (i) initially high dissolved nutrient concentrations due to mobilisation from sediments and dead organic material; (ii) followed by lowered dissolved nutrient concentrations but elevated particulate nutrients as dissolved nutrients are incorporated into phytoplankton and zooplankton and (2) therefore the floodplain will function as a sink of dissolved nutrients and a source of particulate organic material in accordance with floodplains elsewhere during the study period. Secondly, a closer examination of zooplankton source areas within the floodplain and resulting contributions to the main river channel will be investigated (Chapter 5). Based on the processed described in section 1.2.2.3 it was hypothesised that: (a) the floodplain will make a significant contribution to the riverine zooplankton community during a flood period. To investigate this hypothesis both (1) zooplankton contributions from a single floodplain lake, and (2) zooplankton contributions from the floodplain to the main river channel were examined.

The final data chapter will investigate the effect of flood following an extended drought period on the active egg-bank and active community within two floodplain lakes (Chapter 6). Due to factors that affect the egg bank and processes described in section 1.2.2.3 it was hypothesised that: (a) due to the extended drought the pre-flood egg-banks will be of low diversity, (b) following inundation the active community within each lake will be comprised of both species imported with the floodwaters and those from within the pre-flood egg-bank, and following floodplain desiccation the egg-bank will be comprised of a combination of species from the pre-flood egg-bank and imported species and therefore will be more diverse.

Chapter 2. The role of hydrology and habitat on floodplain physico-chemical heterogeneity

2.1. Introduction

It has been suggested that the natural functioning of Australian arid and semi-arid rivers (hereafter termed ‘dryland rivers’) can be described by a combination of both the River Continuum Concept (RCC) (Vannote 1980) and the Flood Pulse Concept (FPC) (Junk, Bayley *et al.* 1989) (Walker, Sheldon *et al.* 1995). A number of recent studies however have provided evidence that support the applicability of the Riverine Productivity Model (RPM) (Thorp and Delong 1994; Thorp and Delong 2002) (Balcombe, Bunn *et al.* 2005; Bunn, Davies *et al.* 2003; Fellows, Wos *et al.* 2007; Gawne, Merrick *et al.* 2007; Hadwen, Fellows *et al.* 2010; Medeiros and Arthington 2011; Oliver and Lorenz 2013; Oliver and Merrick 2006; Pease, Justine Davis *et al.* 2006). The applicability of each to dryland rivers is dependent upon on rainfall, which varies over seasonal, annual and inter-annual cycles. Regardless of the erratic nature in which floodplain connectivity occurs within dryland systems it is thought to play a major role in the sustainability of resident biota and whole ecosystem processes.

The fluvial dynamics of floodplain connectivity and local habitat influences are a key driver of physico-chemical diversity across habitats. Physico-chemical diversity determines habitat availability for biotic communities such as aquatic plants, microinvertebrates, macroinvertebrates and amphibians and the ecological succession that follows (e.g. Collier 1995; Gillooly 2000; Kutka and Bachmann 1990; Roman, Gauzens *et al.* 1993). Diversity in physico-chemical variables can be influenced by regional processes acting at the catchment scale and/or local processes occurring at the floodplain scale (Thomaz, Bini *et al.* 2007). It has been suggested that during high waters (flood) regional forces are more influential. This inference has been based on findings that hydrological connectivity between floodplain habitats increases the exchange of water, dissolved nutrients, suspended sediments and organic materials (e.g. Tockner, Pennetzdorfer *et al.* 1999). Uniformity is then created between habitats that respond to regional influences such as seasonality. As hydrological connectivity decreases, habitats become isolated, water residence time’s increase and local forces such as water source (e.g. groundwater, ice, etc), flow paths, soil type and morphology become more dominate. These then drive autogenic processes (processes driven form within individual waterholes), which affect the physico-chemical environment of individual water bodies.

The variable flow regime of Australian dryland rivers has been demonstrated to be a key driver of the spatial and temporal patterns and processes within the landscape. Cycles of floodplain expansion and contraction have been found to be linked with similarities and differences respectively in abiotic and biotic components within a number of tropical and temperate rivers (see Thomaz, Bini *et al.* 2007). Prior to the last decade, dryland systems have however received little attention. Recent studies however have demonstrated this general pattern among the biotic community within the Cooper Creek catchment in Central Australia including the phytoplankton (McGregor, Marshall *et al.* 2006), vegetation (Capon 2003), macroinvertebrate (Marshall, Sheldon *et al.* 2006) and fish (Balcombe, Bunn *et al.* 2007) communities and water quality parameters (Sheldon and Fellows 2010) however none are yet to be conducted within other Australian dryland systems such as the River Murray.

The naturally high flow variability of Australian dryland systems such as the River Murray are associated with the atmospheric phenomenon El Niño Southern Oscillation (Leigh, Sheldon *et al.* 2010; Puckridge, Walker *et al.* 2000). The ENSO is “a major see-saw in air pressure and rainfall patterns between the Australian/Indonesian region and the eastern Pacific” (BOM 2014a). This see-saw in air pressure can be related to the temperature of the underlying ocean, otherwise known as *El Niño* and *La Niña* events (BOM 2014a) where *El Niño* events can result in much dryer and *La Niña* much wetter than average conditions (BOM 2014a). From 2001 to 2009 Australia suffered its driest period since 1900 (the ‘Millennium Drought’). This intensified the already severe impacts in which river regulation had caused such as a significant reduction in the flooding frequency of floodplain areas (Dijk, Beck *et al.* 2013). Beginning in autumn 2010 *El Nino* weather conditions transitioned into *La Nina* and continued into 2011 (BOM 2014a). The 2010-11 *La Nina* events combined were one of the strongest on record dominating weather patterns with floods occurring throughout the country (BOM 2014a). The combination of significant flows within both the Darling and the Murray River’s at Wentworth reached its maximum of approximately 93,000 megalitres per day at the South Australian border (DEWNR 2012). Approximately 96% of the floodplain area was inundated between the Hume Dam (near Albury in Victoria) and Wellington (approximately 35 kilometres downstream of Murray Bridge in South Australian) along the River Murray (Overton, McEwan *et al.* 2006).

The primary focus of this thesis is on river floodplain zooplankton communities which are highly sensitive to their direct environment. Their emergence from diapause and subsequent population dynamics are directly influenced by variables including pH (Yin and Niu 2008), temperature (Gillooly 2000), salinity (Nielsen, Brock *et al.* 2003), dissolved oxygen (Roman, Gauzens *et al.* 1993), turbidity (Dejen, Vijverberg *et al.* 2004) and food availability (Peters and Downing 1984). This chapter examines these key physico-chemical variables across habitats of a large River Murray floodplain during the 2010-11 floods. Firstly, hydrological phases of floodplain inundation are defined based on the flow hydrograph, corresponding area of the floodplain inundated and habitat connection and disconnection points. These phases are used as an indicator of hydrological connectivity. These phases are: overbank flows, expansion, contraction, disconnection and evaporation. It is hypothesised that: (1) the physico-chemical characteristics will be most similar between habitats during the expansion phase (high connectivity) due to hydrological exchanges and mixing and (2) that as flow decreases from the contraction phase to the evaporation phase, physico-chemical characteristics will become increasingly different as local habitat influences become the dominant environmental drivers.

2.2. **Sampling sites and procedures**

2.2.1. ***Study site***

The River Murray begins near Mount Kosciuszko in the Australian Alps and meanders across inland Australia for 2530 km before discharging to the Southern Ocean (MDBA 2013) (Figure 2-1: inset). The Chowilla Floodplain (33°57'0.41"S, 140°56'29.64"E) is one of the major floodplains adjoining the River Murray covering 17,700 hectares. It has a semi-arid climate with an annual rainfall of approximately 260 mm (Kearns, Hairston *et al.* 1996). It is one of six ‘Icon Sites’ as part of Australia’s largest river restoration program ‘The Living Murray’, chosen for its high ecological value (MDBA 2013). The natural character of the floodplain is now under threat and of all the Icon Sites is the most affected by flow regulation (MDBA 2013).

The Chowilla floodplain is morphologically complex and once flows breech the banks at approximately 33000 megalitres per day (ML day^{-1}) in the main river channel at the South Australian border (for method of calculation see footnote on page 18) a range of habitats are inundated including, fast and slow meandering creeks, ephemeral depressions, abandoned channels and swales and cut-off meanders (Mackay and Eastburn 1990; Shiel, Green *et al.* 1998). The area contains an array of vegetation types where the most dominate are River Red gum (e.g. *Eucalyptus camaldulensis*), Black box (e.g. *Eucalyptus largiflorens*), River cooba (e.g. *Acacia stenophylla*) and Lignum (e.g. *Muehlenbeckia florulenta*) distributed according to hydrological, soil and salinity gradients (MDBC 2013; Sharley and Huggan 1995). The floodplain consists of a range of soil types with a complex arrangement across the area, which varies from sandy ridges to heavy clay depositional areas that influence the rate of salinisation and leaching of salt during flood (Overton and Doody 2008).

In this study, eight sites were chosen to represent both permanent channel and ephemeral floodplain habitats (Figure 2-1). The four permanent channel habitats (hereafter termed ‘channel sites’) were comprised of one within the main channel of the River Murray (RM) and three within Chowilla Creek (CC-1, CC-2 and CC-3). In some instances, results from the three Chowilla Creek sites are averaged and reported as a single site (CC). The four ephemeral floodplain sites (hereafter termed ‘floodplain sites’) comprised of Hancock Creek (HC) and three lakes including Lake Littra, Lake Limbra and Coppermine Waterhole. The three floodplain lakes chosen to span the range of electrical conductivity (conductivity) normally observed across the floodplain. Hancock Creek is the inlet/outlet for Lake Limbra, a large terminal lake (ca. 1.5 – 2 meters (m) in depth). The creek begins to fill when flows in the main river channel exceed approximately 35000 ML day^{-1} and the lake begins to fill when flows exceed approximately 45000 ML day^{-1} (Figure 2-2). The two additional lakes include Lake Littra, a shallow (ca. 1 m in depth) ephemeral deflation basin that begins to fill at a flow in the main river channel of approximately 47000 ML day^{-1} and Coppermine Waterhole, a moderately deep (ca. 1.5 – 2 m in depth) lake that is connected to an adjacent floodplain depression and begins to fill at a flow in the main river channel of approximately 65000 ML day^{-1} (Figure 2-2).

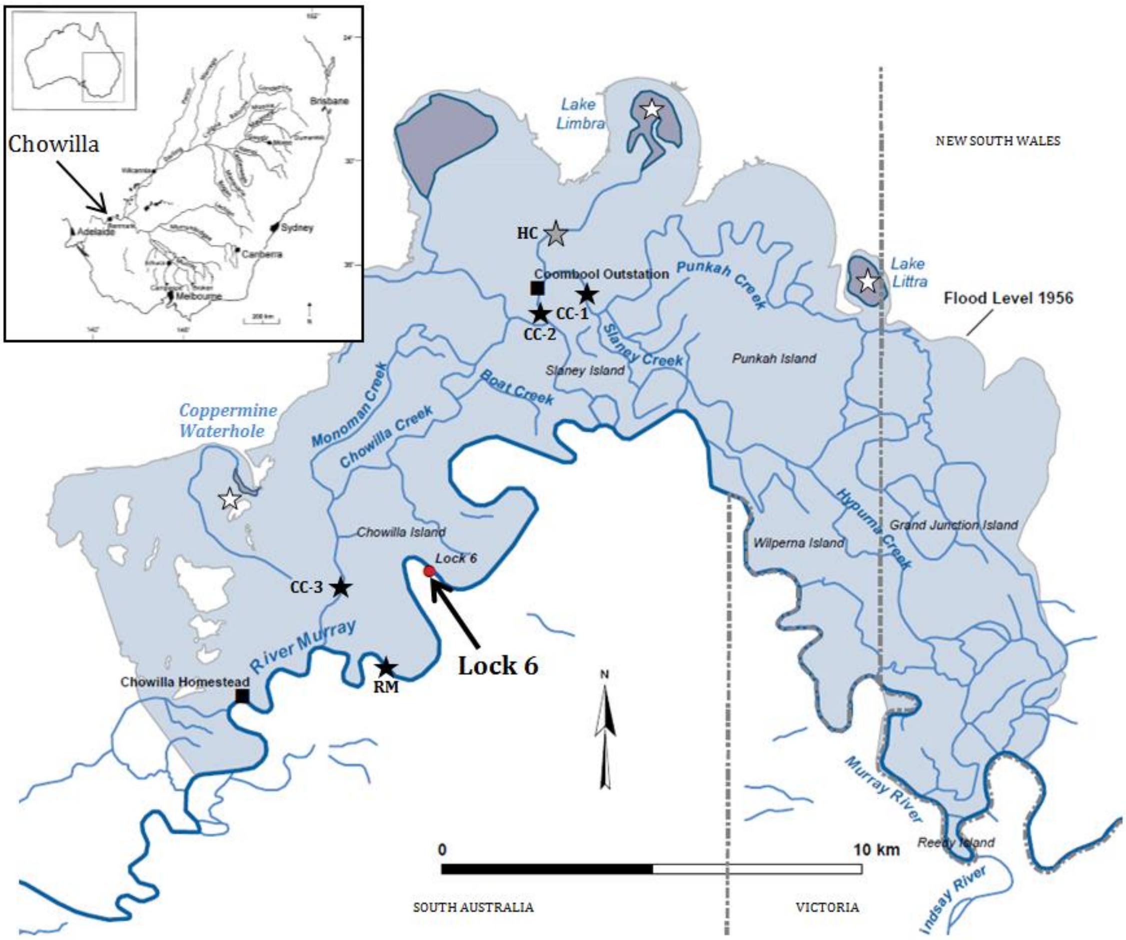


Figure 2-1: The Chowilla Floodplain with study sites (modified from MDBA 2012a). Where Hancock Creek = grey star, lake = open star, permanent creek/river = closed star, Lock 6 = red dot, CC = Chowilla Creek and RM = River Murray. Inset: the Murray Darling Basin (modified from http://tinyurl.com/9cj3jxr).

2.2.2. *Definition of hydrological phases*

The beginning and end of phases were determined using features of the flow hydrograph (calculated flows into South Australia (MDBA 2012)) and connection and disconnection events of the floodplain and major water bodies (see Figure 2-2). It is important to note that these phases represent a continuum and thus the beginning and end of phases are not distinct and have periods of transition between them. The sampling period was divided into 5 hydrological phases of connectivity, as defined by Tockner *et al.*, (1999) (Figure 2-2):

1. The “overbank flows” phase (early November 2010 – 28 January 2011)
2. The “expansion” phase (29 January – 30 March 2011)

3. The “contraction” phase (31 March – 10 June 2011)
4. The “disconnection” phase (11 June – 10 September)
5. The “evaporation” phase (11 September onwards)

Water begun to flow through the majority of the anabranch system during early November and at the beginning and throughout the overbank flows phase remained largely confined within the banks of the creeks and lakes. During the expansion phase, flows began to spill over the banks of creeks and major lakes onto the flatter, less defined areas of the floodplain; significantly increasing the area inundated and lotic habitat and floodplain discharge. During the contraction phase, river flows began to decrease rapidly, resulting in floodplain drawdown and the flatter, less defined areas of the floodplain drying completely. The major lakes disconnected from the permanent creeks. During the disconnection phase the major waterbodies remained isolated yet relatively full. During the evaporation phase, water gradually evaporated and most waterbodies began to or did completely dry.

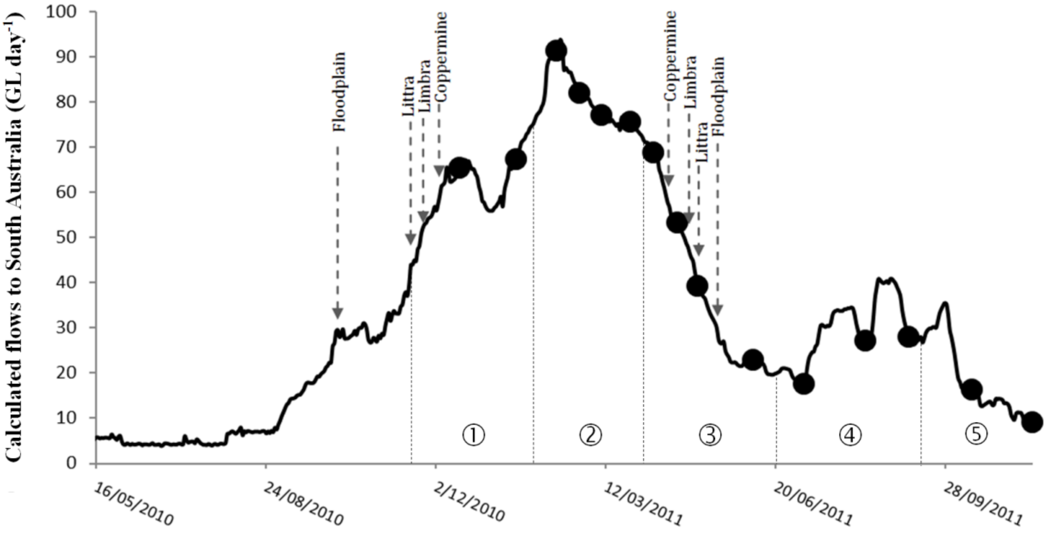


Figure 2-2: Hydrograph of flows to South Australia (data sourced from DEWNR 2012). Connection and disconnection dates of Lake Littra, Lake Limbra, Coppermine Waterhole and the remainder of temporary floodplain habitats (Floodplain) are indicated with broken arrows. Sampling dates are indicted as ●. Broken lines identify the five phases of hydrological connectivity as defined in the text.

2.2.3. ***Water quality: measurement, collection and processing***

Sampling was conducted fortnightly or monthly between 17 December and November 2011 (Figure 2-3 for the dates each site was sampled, Figure 2-2 for sampling dates in relation to the flood hydrograph). Conditions prevented sampling at some sites on 17 December 2010, 18 January 2011 (high river levels) and 6 June 2011 onwards (desiccation) (Figure 2-3). Sampling for each trip was conducted over a two-day period and sites were sampled during the day.

At each site, spot measurements of water temperature, turbidity, pH, electrical conductivity (conductivity) and dissolved oxygen concentration (DO) were taken using a multi-parameter YSI sonde (Model no. YSI-5739, Distributor: YSI Incorporated, Yellow Springs, Ohio). These were taken within the top one metre of the pelagic zone, with 10 measurements within Lake Littra, Lake Limbra and Coppermine Waterhole and three measurements approximately mid channel of HC, CC and the RM. Water samples were taken and placed on ice in the dark in the field for later analysis of chlorophyll-a (Chl-a) and volatile solid (VS) concentrations and analysed according to standard methods (Part 10200: 'Fluorometric Determination of Chlorphyll a' and Part 2540: 'Total, Fixed, and Volatile Solids in Solid and Semisolid Samples' in APHA, AWWA *et al.* 1998). Volatile solid concentration is the concentration of solids in water that are lost on ignition of the dry solids at 550 degrees C. From January until May 2011 three water samples were also taken at the locations in which water quality measurements were taken and placed on ice in the dark in the field for later analysis for total phosphorus (TP), ammonia (NH_4), oxidised nitrogen (NO_x, the sum of nitrate and nitrite), filterable reactive phosphorus (FRP), total nitrogen (TN) and dissolved organic carbon (DOC). Samples were stored in ice in the field and taken back to the laboratory. Water samples for FRP, NH_4, NOx and DOC analysis were filtered through a 0.45 μm filter (M-Millipore MCE Membrane) prior to later analysis at the University of Adelaide. Phosphate, NH_4 and NOx were analysed on a Lachat Quickchem 8200 Flow Injection Analyser (Hach, CO, USA) and DOC on a SGE ANATOC™ Series II Total Organic Carbon Analyser. TP and TN analysis was conducted at the Environmental Analysis Laboratory, Lismore, New South Wales, which is accredited by the National Association of Testing Authorities (NATA according to standard methods (Part 4500-P I: In-line UV/Persulfate Digestion and Flow Injection Analysis for Total Phosphorus and Part 4500-N C: Persulfate Method in APHA, AWWA *et al.* 1998).

Figure 2-3: Sampling dates for each site. Where HC = Hancock Creek, CC = Chowilla Creek, RM = River Murray, - = sampling occurred, H = sampling not possible due to high water levels and D = sampling not possible due to desiccation.

	17.12.2010	11.01.2011	11.02.2011	24.02.2011	09.03.2011	26.03.2011	09.04.2011	02.04.2011	05.05.2011	06.06.2011	12.07.2011	10.08.2011	13.09.2011	13.10.2011	18.11.2011
Littra	-	-	-	-	-	-	-	-	-	-	-	-	-	-	D
Coppermine	-	-	-	H	-	H	-	H	H	-	-	-	-	-	-
Limbra	-	-	-	-	-	-	-	-	-	D	D	D	D	D	D
HC	-	-	-	-	-	-	-	-	-	-	D	D	D	D	D
CC-1	-	-	-	-	-	-	-	-	-						
CC-2	-	-	-	-	-	-	-	-	-	-	-				
CC-3		-	-	-	-	-	-	-	-	-					
RM			-	-	-	-	-	-	-	-					

2.2.4. *Statistical analysis*

For the purpose of this study, site physico-chemical ‘characteristic’ refers to a single type of measurement, e.g. conductivity. Firstly, variance across the landscape over time for each physico-chemical component was examined. This was done by calculating the coefficient of variation (CV) (see Equation 1) using the average EC, turbidity, VS, Chl-a and DO and the standard deviation (SD) of average temperature and SD of the average natural-log transformed average pH values at each site for each date collected from January 2011 up to and including May 2011. Coefficient of variation values were rated as small (< 0.5), moderate (0.5 – 1), large (1 – 3) or very large (>3) (as in Gleason, Euliss *et al.* 2003).

Secondly, to investigate which sites were causing the variation observed and if this changed over time a repeated-measures analysis of variance (RM-ANOVA) was conducted in IBM SPSS Statistics for Windows (SPSS Released 2010) to test for the effects of time on average EC, turbidity, pH, VS, Chl-a, DO and temperature. Due to the availability of data, the RM-ANOVA was performed on the data from January 2011 until and including

May 2011 on all sites (excluding Coppermine Waterhole). If the assumption of sphericity was rejected using Mauchly's criterion, the Greenhouse-Geisser corrected alpha values (e.g. Strecker, Cobb *et al.* 2004; Visman, McQueen *et al.* 1994) were used to determine the statistical significance of site and time effects (Scheiner and Gurevitch 2001).

Thirdly, to investigate how ecological distance between habitats and across the whole landscape change through time due to all of the habitat phsico-chemical characteristics measured a Nonmetric Multidimensional Scaling (NMS) (Kruskal 1964; Shepard 1962a; Shepard 1962b) ordination was conducted in PC-ORD (McCune 2006) including data on VS, Chl-a, turbidity, pH, EC, water temperature and DO for all sites and dates. The distance measure used was Sorensen (Bray-Curtis) (Bray and Curtis 1957) and the rank correlation coefficient was set to 3 (see Chapter 13 in McCune, Grace *et al.* 2002). The corresponding site was overlaid as a categorical variable.

Equation 1: Coefficient of variation (CV)

$$CV = \frac{standard\ deviation}{mean}$$

2.3. Results

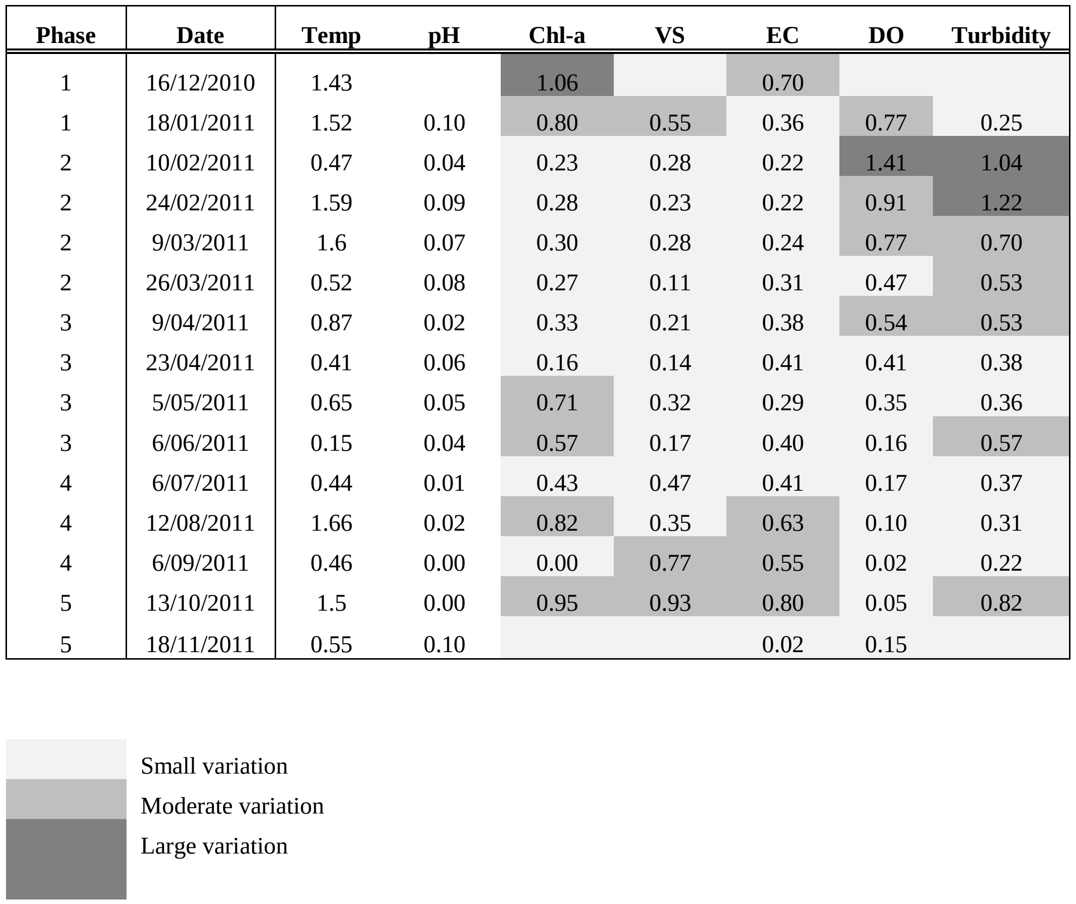
Overall, individual physico-chemical components behaved differently in relation to patterns in between site variability (Table2-2). While sites remained hydrologically connected (phases one, two and three) Chlorophyll-a, volatile solids and conductivity values became less variable between sites (Table2-2). Chlorophyll-a concentrations decreased in Lake Limbra and HC resulting in their convergence with CC and RM causing between site variation to shift from large to moderate during early inundation (overbank flow phase) (Table 2-2 and Figure 2-5: Chlorophyll-a). As lotic habitat increased (the expansion phase) the variation between site chlorophyll-a decreased further (Table 2-2: Chlorophyll a) and the variation in volatile solid concentration between sites was small (Table 2-2 and Figure 2-5: Volatile Solids). Conductivity was initially high in Lake Limbra and Lake Littra and low in Coppermine Waterhole, Chowilla Creek and the River Murray. As connectivity increased (phases one and two) sites converged (except Lake Littra) resulting in variation between sites shifting from moderate to small (Table 2-2 and Figure

2-5: Conductivity). Variation between sites in chlorophyll-a, volatile solids and conductivity all increased, as sites became isolated.

During highest connectivity and floodplain drawdown (phases one and two) the variation in turbidity and DO increased between sites. Between site variation in turbidity was highest (between moderate and large) during highest connectivity (the expansion phase) (Table 2-2: Turbidity). This was largely caused by the much higher turbidity observed in Lake Littra in comparison to the other sites (Figure 2-5: Turbidity). Dissolved oxygen concentrations declined across all sites (Figure 2-5: Dissolved Oxygen Concentration) during highest connectivity (the expansion phase) however to different degrees, which resulted in the highest variation in DO between sites (Table 2-2: DO). Lake Littra decreased to the lowest levels, below 1 mgL^{-1} followed by the River Murray, Chowilla Creek, Lake Limbra and Coppermine Waterhole. Coppermine Waterhole maintained levels above 6 mgL^{-1}. During phases three, four and five the DO concentrations gradually increased and then decreased.

Both temperature and pH maintained small variation between sites throughout the entire study (Table 2-2: Temperate and pH). The pH did however vary more during early inundation and highest connectivity (phases one and two) (Table 2-2 and Figure 2-5: pH). Predictable seasonal patterns in temperature were observed (Figure 2-5: Temperature) and as flow decreased and habitats became isolated (phases three, four and five) pH and dissolved oxygen appeared to be associated.

Figure 2-4: Temporal coefficient of variation between sites of Chl-a, volatile solids (VS), conductivity, dissolved oxygen concentration and turbidity. Temporal standard deviation between sites of temperature and pH (ln transformed). Where light grey = small variation, medium grey = moderate variation and dark grey = large variation between sites.



Phase	Date	Temp	pH	Chl-a	VS	EC	DO	Turbidity
1	16/12/2010	1.43		1.06		0.70		
1	18/01/2011	1.52	0.10	0.80	0.55	0.36	0.77	0.25
2	10/02/2011	0.47	0.04	0.23	0.28	0.22	1.41	1.04
2	24/02/2011	1.59	0.09	0.28	0.23	0.22	0.91	1.22
2	9/03/2011	1.6	0.07	0.30	0.28	0.24	0.77	0.70
2	26/03/2011	0.52	0.08	0.27	0.11	0.31	0.47	0.53
3	9/04/2011	0.87	0.02	0.33	0.21	0.38	0.54	0.53
3	23/04/2011	0.41	0.06	0.16	0.14	0.41	0.41	0.38
3	5/05/2011	0.65	0.05	0.71	0.32	0.29	0.35	0.36
3	6/06/2011	0.15	0.04	0.57	0.17	0.40	0.16	0.57
4	6/07/2011	0.44	0.01	0.43	0.47	0.41	0.17	0.37
4	12/08/2011	1.66	0.02	0.82	0.35	0.63	0.10	0.31
4	6/09/2011	0.46	0.00	0.00	0.77	0.55	0.02	0.22
5	13/10/2011	1.5	0.00	0.95	0.93	0.80	0.05	0.82
5	18/11/2011	0.55	0.10			0.02	0.15	

Small variation
Moderate variation
Large variation

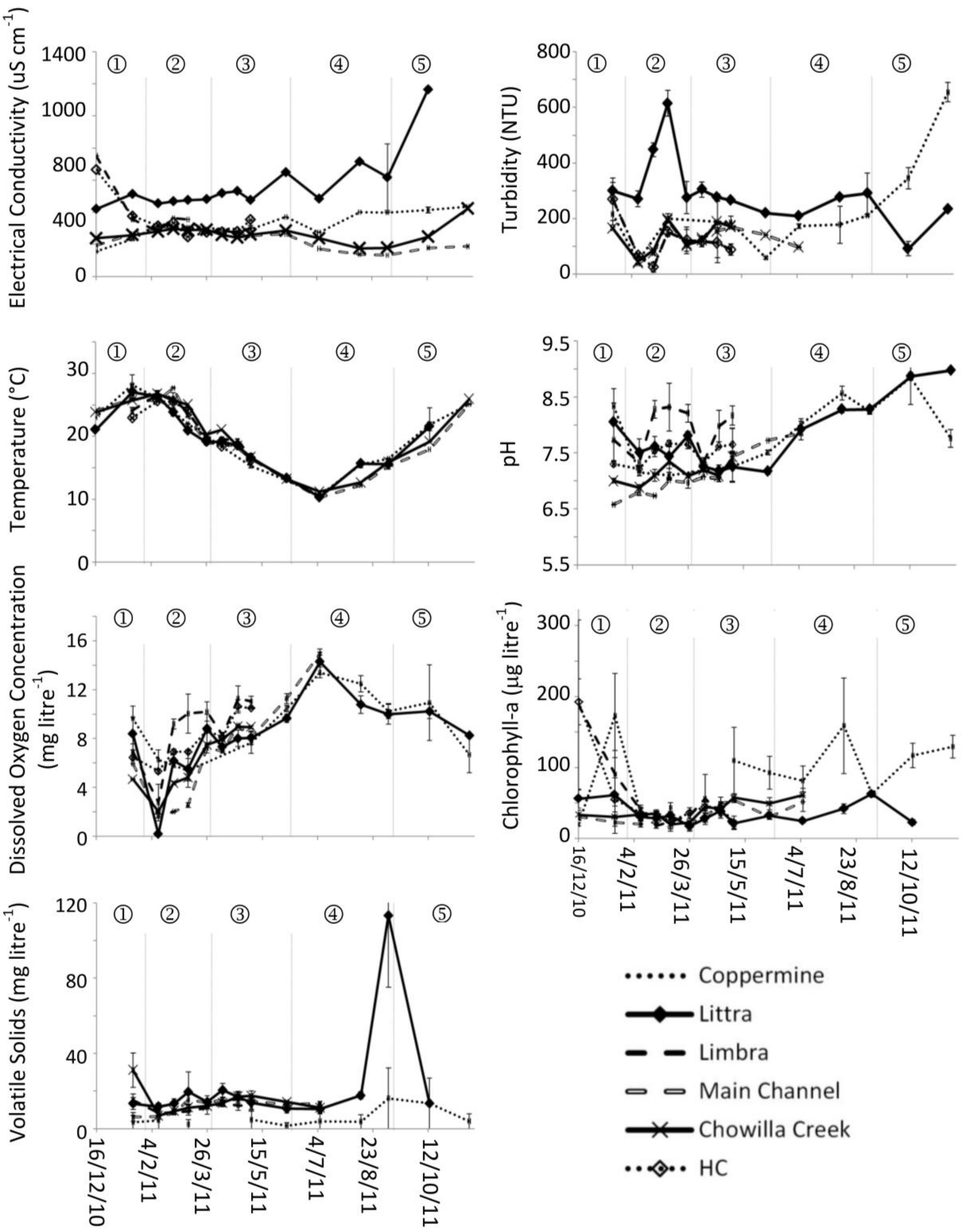


Figure 2-5: Average conductivity (µS cm^{-1}), temperature (°C), dissolved oxygen concentration (mg/L), turbidity (NTU) and pH at Coppermine Waterhole (Copper), Lake Littra (Littra), Lake Limbra (Limbra), the River Murray (RM), Chowilla Creek (CC) and Hancock Creek (HC) over time. Hydrological stages are indicated with broken vertical lines and corresponding number. Error bars represent 1 standard deviation.

Due to the contrasting response of physico-chemical components between sites through time, a significant interaction between site and time was demonstrated for all variables (excluding nutrients which were not tested) (Figure 2-6: P < 0.001).

Figure 2-6: RM-ANOVA testing for the effects of site and time on pH, turbidity, temperature, volatile solids (VS), chlorophyll-a (Chl-a), dissolved oxygen (DO) and conductivity (EC) on Lake Littra, Lake Limbra, Chowilla Creek (CC) and the River Murray (RM) from January until May 2011 Greenhouse-Geisser adjusted probabilities were used for the F statistics.

	Source		***df***	***F***	***P***
Conductivity	Within subjects	*Time*	7	50.3	< 0.001*
		*Time*Site*	21	39.8	< 0.001*
		Error	140		
	Between subjects	*Site*	3	5946.2	< 0.001*
		Error	20		
Turbidity	Within subjects	*Time*	7	115.7	< 0.001*
		*Time*Site*	21	42.6	< 0.001*
		Error	140		
	Between subjects	*Site*	3	722.1	< 0.001*
		Error	20		
Temperature	Within subjects	*Time*	7	1874.5	< 0.001*
		*Time*Site*	21	26.7	< 0.001*
		Error	140		
	Between subjects	*Site*	3	39.3	< 0.001*
		Error	20		
pH	Within subjects	*Time*	7	25.8	< 0.001*
		*Time*Site*	21	22.4	< 0.001*
		Error	140		
	Between subjects	*Site*	3	189	< 0.001*
		Error	20		
Dissolved Oxygen	Within subjects	*Time*	7	378.2	< 0.001*
		*Time*Site*	21	29.8	< 0.001*
		Error	140		
	Between subjects	*Site*	3	229.3	< 0.001*
		Error	20		
Chlorophyll-a	Within subjects	*Time*	7	11.5	< 0.001*
		*Time*Site*	21	8.9	< 0.001*
		Error	140		
	Between subjects	*Site*	3	4.6	0.014*
		Error	20		
Volatile Solids	Within subjects	*Time*	7	19.9	< 0.001*
		*Time*Site*	21	4.9	0.001*
		Error	140		
	Between subjects	*Site*	3	7.3	0.002*

	Error	20

*Statistically significant with α of 0.05

As indicated by the NMS plot, conductivity and turbidity were the major variables driving overall differences between sites (Figure 2-7). The River Murray and Chowilla Creek sites were associated with low turbidity during phases one and two and shifted towards an association with low conductivity into the disconnection phase. Lake Littra was associated with high turbidity during phases one and two yet during the contraction phase a shift occurred and by phases four and five was associated with high conductivity. Coppermine Waterhole was association with high turbidity during the evaporation phase. Overall, the three floodplain lakes appeared to have unique physico-chemical characteristics and greater dispersion through time across hydrological phases in comparison to the channel sites.

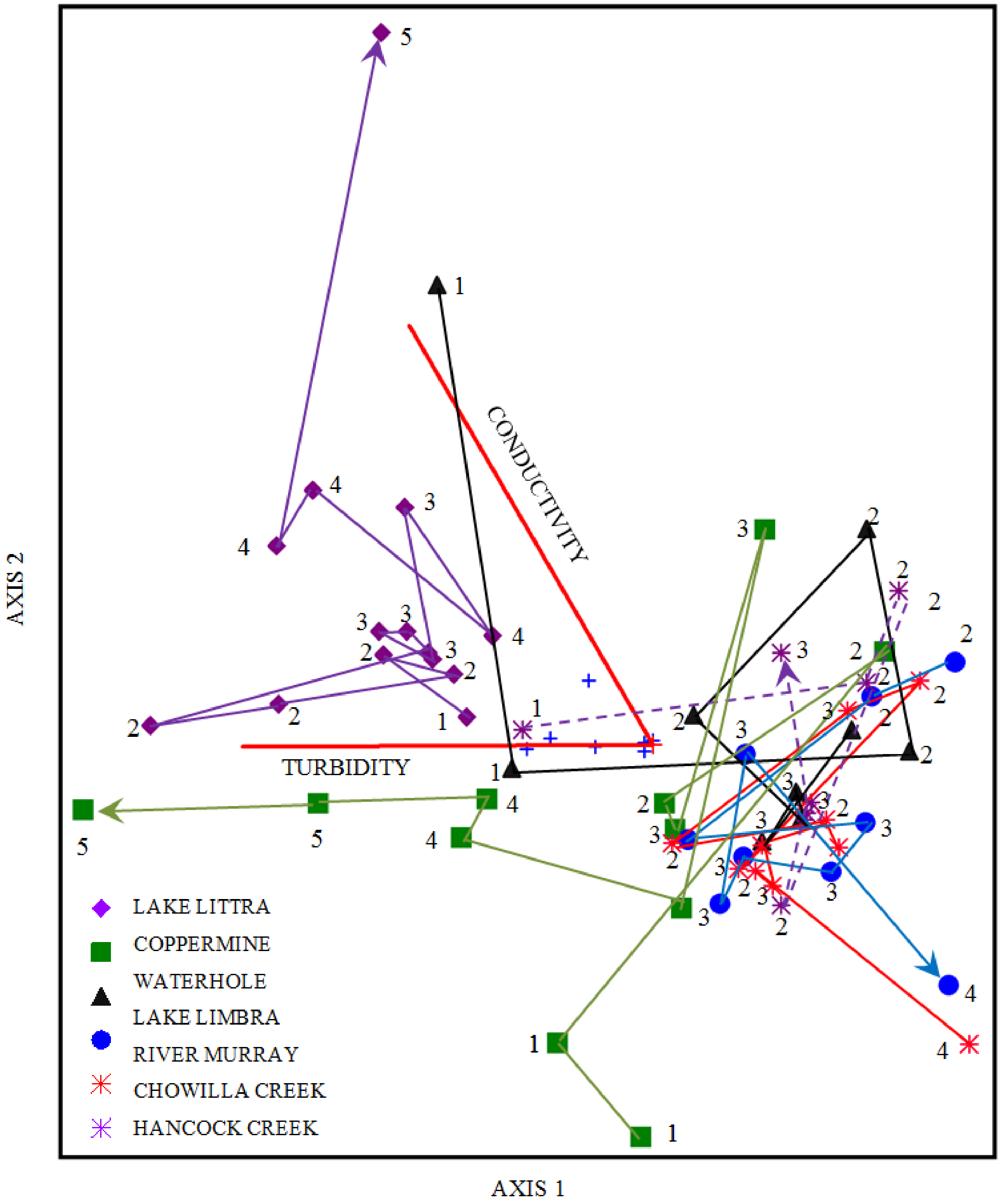


Figure 2-7: A Nonmetric Multidimensional Scaling (NMS) ordination of all water quality parameters across all sites and dates. Various symbols and colours represent different sites. Lines link consecutive samples. Numbers represent hydrological phases where 1 = overbank flows, 2 = expansion, 3 = contraction, 4 = disconnection and 5 = evaporation Final Stress for a 2-dimensional solution = 8.44.

2.4. **Discussion**

2.4.1. ***Landscape variability in physico-chemical response to hydrological phases***

It was hypothesised that physico-chemical variables would be most similar at the peak (the expansion phase) of the flow hydrograph as bulk flow was the dominant process, but as flow decreased (from the contraction through to the evaporation phase) these variables would differ as local, site-specific influences became more dominant. The patterns in conductivity, chlorophyll-a and volatile solids supported this hypothesis. But highest dissimilarity occurred in dissolved oxygen and turbidity during the expansion phase. The variability in dissolved oxygen is likely to be due to typical diel changes in dissolved oxygen however carbon inputs, metabolism and hydrological diversity may also have played a role. Variability in turbidity could be due to possible local affects such as dissolved organic carbon input, metabolism and sediment re-suspension. The most dominant variables associated with site differences were conductivity and turbidity. The regional influence of seasonality was clearly affecting water temperature throughout the entire study and not as expected, seemed to be affecting dissolved oxygen concentrations and pH after peak flow. This demonstrates the importance of floodplain connectivity in driving a succession of variables contributing to spatio-temporal heterogeneity, a precursor to floodplain and thus whole system biological diversity (Ward and Stanford 1995; Ward, Tockner *et al.* 1999).

2.4.2. ***Salinity***

The hydrogeology of the floodplain is complex, influenced by the groundwater and soil type (Overton and Doody 2008). These characteristics strongly influence processes such as salinisation, (Overton and Doody 2008; Salama, Otto *et al.* 1999). The higher conductivities in Lake Littra during peak flood suggest that the shallow and saline groundwater was hydrologically connected to the surface water and influenced lake conductivity. This combined with evapotranspiration probably drove the continual rise in conductivity in both Lake Littra and Coppermine Waterhole. The initial high conductivity of Lake Limbra was probably due to the accumulation of surface salts as capillary action drew the shallow ground water to the surface. However, as flow increased salt was flushed from the soil driving conductivity down. This flushing process is important as salinity affects the dispersal, emergence, reproduction, migration and survival of key biota such as zooplankton and plant communities (e.g. Glenn, Tanner *et al.* 1998; Jensen, Brucet *et al.* 2010; Nielsen and Brock 2009; Snell 1986; Zervoudaki, Nielsen *et al.* 2009). For example, small increases in salinity have been found to affect the species diversity of plants germinating and zooplankton emerging from dry sediment (Nielsen, Brock *et al.* 2003). Processes regulating conductivity across the floodplain play a key role in determining the structural diversity and distribution of the biota (McCoy and Bell 1991; Meerhoff, Mazzeo *et al.* 2003; Nielsen, Brock *et al.* 2003).

2.4.3. ***Dissolved oxygen***

The diel cycle, carbon inputs, metabolism and hydrological diversity, may have contributed to differences in dissolved oxygen during high flow. In early 2011 a large plume of anoxic blackwater, originated upstream of the Chowilla Floodplain and travelled downstream (King, Tonkin *et al.* 2012; SAWater and MDFRC 2010-11). The anoxia was caused by a combination of warm temperatures and the rapid bacterial consumption of high levels of dissolved organic carbon, present due to leaf litter and other forms of organic carbon that had accumulated during the drought. Concentrations dropped to levels low enough (below 1 mgL^{-1}) to have lethal, physiological and behavioural effects on various organisms including zooplankton (e.g. Roman, Gauzens *et al.* 1993; Vanderploeg, Ludsin *et al.* 2009) and fish (e.g. Buentello, Gatlin Iii *et al.* 2000). Some of the variation in dissolved oxygen is due to typical diel changes in dissolved oxygen as measurements were not taken at the same time of day each time. Additional carbon inputs (Wallace, Ganf *et al.* 2008) and the microbial groups present (Holste and Peck 2006) may have had some influence on the variability between sites. Other potential contributors include the effects of hydrology on the extent to which water migrated laterally and flow pathways affecting oxygen transfer from the atmosphere and sediment oxygen demand.

2.4.4. ***Turbidity***

The higher differences observed in turbidity during high flow may have been driven by a combination of geomorphological, hydrological, vegetative and aerial diversity and wind driven mixing. The varying geomorphology and hydrology across the floodplain results in a variable supply of sediment and energy conditions across the floodplain and influences sediment, erosion suspension and accumulation (Thoms, Foster *et al.* 2000). These processes are also related to the existing vegetation structure and vice versa (Bendix and Hupp 2000; Junk, Bayley *et al.* 1989; Puigdefábregas 2005). During the drought the floodplain had shifted towards a more terrestrial vegetation community and areas of bare soil had increased (Gehrig, Marsland *et al.* 2012; Marsland, Nicol *et al.* 2009. For these reasons it is not uncommon for sediment suspension and suspension rates and thus turbidity to differ spatially and temporally across floodplains during flood. This variability in sedimentation has been demonstrated in a River Murray floodplain upstream of Chowilla during a similar magnitude flood event {Thoms, 2000 #601). Turbidity can affect processes such as zooplankton feeding rates (Hart 1988; Robinson, Capper *et al.* 2010), fish feeding (Gardner 1981; Kemp, Sear *et al.* 2011; Sutherland and Meyer 2007) and the light available for photosynthesis (Bilotta and Brazier 2008; Izagirre, Serra *et al.* 2009; Lloyd, Koenings *et al.* 1987).

2.4.5. ***Regional influences***

Despite local influences driving differences in variables between sites at times, similarities between sites also occurred while responding to seasonality. Predictable seasonal trends in temperature occurred throughout the entire study. Temperature can affect zooplankton emergence from and production of diapause states (Bernot, Dodds *et al.* 2006; Snell 1986; Vandekerkhove, Declerck *et al.* 2005a), having significant influences on both current and future populations. It also affects ingestion rates (Nielsen, Podnar *et al.* 2013) and growth {Masclaux, 2009 #624}. Temperature appeared to be affecting dissolved oxygen concentrations after peak flood. Negative correlations between these variables often occur due to the effects of temperature on the solubility of oxygen and biological oxygen demand (Kalff 2002). Additionally, increasing pH appeared to be associated with increasing water temperature as floodwaters receded on the floodplain. Positive correlations often occur between these variables due to the effect of temperature on photosynthesis. These responses to seasonal temperature changes became evident only after peak flow, as the floodplain receded and disconnected from the main river channel. Despite most species being capable of tolerating the range of pH values measured in these study even small changes can affect the zooplankton community. This is because many species have been found to show distinct peak abundance at certain pH levels, especially in cladocera species (Amsinck, Jeppesen *et al.* 2007; Belyaeva and Deneke 2007).

2.4.6. ***Conclusions***

Ecologically river-floodplain systems are in decline worldwide, largely due to anthropogenic interferences to the natural flow regime. The frequencies of floods, especially large ones that promote high connectivity, have been reduced significantly. Large floods are recognised as important for the exchange of propagules, nutrients and organisms between habitats. This study has demonstrated that in addition to this, they are important in the maintenance of habitat heterogeneity. The habitat heterogeneity created by a succession of physico-chemical variables plays an important role in providing the conditions required for biological diversity and over time different successional stages within them. The following chapter aims to investigate what affect this may have on the resident zooplankton communities as they are highly sensitive to their direct environment and play an important role within the ecosystem. Additionally, this study has demonstrated the importance of habitat connectivity in providing access to refuges during events such as the anoxic blackwater event observed in this study.

Chapter 3. Hydrological connectivity and landscape heterogeneity structure zooplankton communities in a river-floodplain system

3.1. Introduction

Within riverine ecology a generalised concept is yet to be developed that accurately describes patterns and processes within lowland rivers of arid or semi-arid climates (hereafter termed dryland rivers) in part due to the extreme hydrological variability. Australian dryland systems are rated amongst the most variable systems throughout the world where their flow variability plays a crucial role in driving ecological processes (Puckridge, Sheldon *et al.* 1998). The river continuum concept (RCC) suggests that ecological processes change predictably along the downstream gradient but overlooks the role of floodplain dynamics. In comparison, the flood pulse concept (FPC: Junk, Bayley *et al.* 1989) emphasises lateral connectivity in river floodplain systems yet is more applicable to tropical rivers with predictable flows. It has been suggested that the functioning of dryland rivers are best described by a combination of both concepts, where high variability plays an additional role in controlling ecological processes (Robertson, Bunn *et al.* 1999; Walker, Sheldon *et al.* 1995). However, a number of recent studies however have provided evidence that support the applicability of the Riverine Productivity Model (RPM) which proposes that most energy assimilated by organisms is sourced from autochthonous production and the riparian zone (Thorp and Delong 1994; Thorp and Delong 2002) (Balcombe, Bunn *et al.* 2005; Bunn, Davies *et al.* 2003; Fellows, Wos *et al.* 2007; Gawne, Merrick *et al.* 2007; Hadwen, Fellows *et al.* 2010; Medeiros and Arthington 2011; Oliver and Lorenz 2013; Oliver and Merrick 2006; Pease, Justine Davis *et al.* 2006).

Floodplains are recognized for their high heterogeneity created by the complex geomorphology and hydrological variability. This results in physical, chemical and biological attributes that vary across spatial and temporal patches and gradients (Walker, Sheldon *et al.* 1995). These patches and gradients move within as well as in and out of the landscape where the transition zones between them are ecotones and connectivity the ease in which organisms and matter move between (Ward, Tockner *et al.* 1999). Floodplain inundation increases connectivity and facilitates mixing and exchange of resources across these patches shifting floodplains towards a more homogeneous landscape (Bonecker and Lansac-Tôha 1996; Fernandes 1997; Tockner, Pennetzdorfer *et al.* 1999). As floodwaters receded habitats become increasingly isolated and the underlying heterogeneity re-emerges affecting the biotic communities residing within them (e.g Mosley 1983; Ward, Malard *et al.* 1999). Within dryland river floodplain systems this generalised concept has been demonstrated in a number of biotic components including phytoplankton (McGregor, Marshall *et al.* 2006), vegetation (Capon 2003), macroinvertebrates (Marshall, Sheldon *et al.* 2006) and fish (Balcombe, Bunn *et al.* 2007) however not in zooplankton (Bozelli 1992; James, Thoms *et al.* 2008).

One of the key opportunistic groups that thrive within the variable and complex environments of dryland river floodplains is zooplankton. Zooplankton cope with hydrological variability through diapause over dry periods and rapid emergence upon wetting. After colonisation, they reproduce rapidly and feed on the bounty of bacteria, phytoplankton and organic material (e.g Desvilettes, Bourdier *et al.* 1997; Jumars, Penry *et al.* 1989; Kobayashi and Church 2003). They themselves are preyed upon by organisms such as other zooplankton, fish, birds, amphibians and macroinvertebrates (Arumugam and Geddes 1988; Crome 1985; Lynch 1979; Meredith, Matveev *et al.* 2003; Ranta and Nuutinen 1985) and thus play a vital role within the function of the ecosystem.

Behavioural characteristics, life history traits and drivers of population dynamics support the premise that the distribution and development of zooplankton is likely to be coupled with the shifts found between homogeneity and heterogeneity in other variables. Homogenisation is likely to occur as the passive dispersal of zooplankton leads to the importation of early colonists to floodplain habitats (Jenkins and Boulton 2003) and are therefore likely to reflect a typical high flow riverine assemblage consisting of primarily rotifers (e.g. Havel, Medley *et al.* 2009; Shiel, Costelloe *et al.* 2006). Rivers are dominated by rotifers during high flows due to the inability of cladocerans and copepods to reproduce in fast flowing water (Obertegger, Flaim *et al.* 2007; Rzoska 1978). In addition, zooplankton are highly sensitive to their direct environment and the abiotic variables and biotic communities that are often homogenised during flood affect emergence and subsequent population dynamics (e.g. turbidity Dejen, Vijverberg *et al.* 2004; e.g. temperature Gillooly 2000; e.g. predation Nagata and Hanazato 2006; e.g. salinity Nielsen, Brock *et al.* 2003; e.g. water residence time (WRT) Obertegger, Flaim *et al.* 2007; e.g. pH Roman, Gauzens *et al.* 1993). As hydrological connectivity decreases, the water residence time on the floodplain increases and favours larger zooplankton species such as crustaceans (e.g. Basu and Pick 1996; Obertegger, Flaim *et al.* 2007). It follows that with a loss of connectivity the influence of flow decreases and local habitat influences (e.g. competition, predation, riparian vegetation cover) play a bigger role in structuring zooplankton communities.

Here the spatial patterns in abundance and assemblage structure of zooplankton during various phases of inundation and drying across a dryland river floodplain system are examined. It is hypothesised that zooplankton community structure will be most similar when the degree of connectivity between habitats is high and mixing homogenises the zooplankton communities. However, as connectivity decreases communities will become increasingly different as habitat heterogeneity re-emerges as the dominant environmental driver. In investigating this hypothesis we also predict that (1) zooplankton assemblage across both the main channel and floodplain habitats will be dominated by rotifers immediately after inundation due to importation from the river channel and higher WRT's and (2) over time assemblages will shift towards a cladoceran and copepod dominated assemblage on the floodplain. This study took place within an Australian dryland river floodplain, the Chowilla Floodplain and adjacent River Murray, during a flood-event in 2010-2011.

3.2. Sampling sites and procedures

3.2.1. *Study site*

The Chowilla Floodplain (Figure 3-1: 33°57'0.41"S, 140°56'29.64"E) is one of the major floodplains adjoining the River Murray in Australia and covers 17,700 hectares. Chosen for its high ecological value the floodplain is one of six 'Icon Sites' as part of Australia's largest river restoration program 'The Living Murray' (MDBA 2013) and is also an internationally important Ramsar site (Ramsar 1971). The climate is semi-arid to arid with an annual rainfall of approximately 260 mm (Kearns, Hairston *et al.* 1996). After the most persistent drought of the 21st century within the Murray-Darling Basin from the year 2001 until 2009 (Bayly 1992), two years of widespread rainfall and flooding dominated weather patterns. Large scale lateral connectivity was generated basin wide and inundated the majority of floodplains adjoining the river, including Chowilla (Figure 3-1).

Chowilla is a complex floodplain and once flows breach the banks at approximately 33000 ML day^{-1}, measured upstream of the main inlet, a range of habitats including low gradients, fast and slow meandering creeks, ephemeral depressions, abandoned channels and swales and cut-off meanders are inundated (Mackay and Eastburn 1990; Shiel, Green *et al.* 1998). The area contains an array of vegetation types where the most dominate are River Red gum (e.g. *Eucalyptus camaldulensis*), Black box (e.g. *Eucalyptus largiflorens*), River cooba (e.g. *Acacia stenophylla*) and Lignum (e.g. *Muehlenbeckia florulenta*) distributed according to hydrological, soil and salinity gradients (MDBC 2013; Sharley and Huggan 1995).

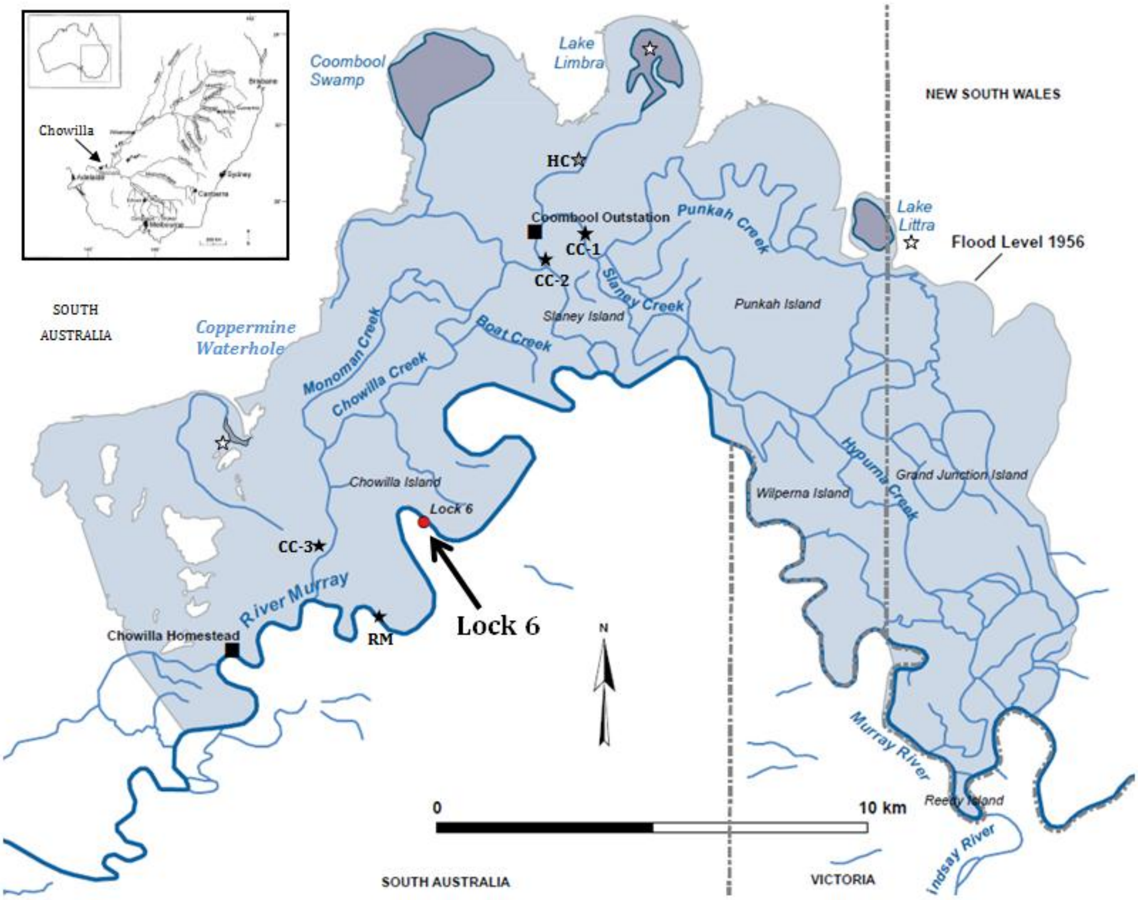


Figure 3-1: The Chowilla Floodplain with study sites Floodplain (modified from Gell, Bulpin *et al.* 2005). Hancock Creek = grey star, lake = white star, permanent creek/river = closed star, Lock 6 = red dot, CC = Chowilla Creek and RM = River Murray. Inset: the Murray Darling Basin (modified from http://tinyurl.com/9cj3jxr) black arrow indicates the location of Chowilla.

3.2.2. ***Sampling periods***

Eight sites were chosen to represent both permanent channel and ephemeral floodplain habitats (Figure 3-1). The four permanent habitats (hereafter termed ‘channel habitats’) were comprised of one within the main channel of the River Murray (RM) and three within Chowilla Creek (CC-1, CC-2 and CC-3). The four ephemeral sites (hereafter termed ‘floodplain sites’) were comprised of Hancock Creek and three lakes: Lake Littra, Lake Limbra and Coppermine Waterhole. Hancock Creek begins to fill when flows exceed approximately 35000 ML day^{-1} and the Lake Limbra when flows exceed approximately 45000 ML day^{-1} into South Australia. Hancock Creek is the inlet/outlet for Lake Limbra, a large terminal lake (ca. 1.5 – 2 m maximum depth), Lake Littra is a shallow (ca. 1 m maximum depth) ephemeral deflation basin which begins to fill at approximately 47000 ML day^{-1} and Coppermine Waterhole is a moderately deep (ca. 1.5 – 2 m) lake connected to an adjacent floodplain depression, which begins to fill at approximately 65000 ML day^{-1}.

3.2.3. ***Definition of hydrological phases***

The beginning and end of phases in this study were determined using features of the flow hydrograph (calculated flows into South Australia; MDBA 2012) and connection and disconnection events of the floodplain and major water bodies (see Figure 3-2). It is important to note that these phases represent a continuum and thus the beginning and end of phases are not distinct and have periods of transition between them. The sampling period was divided into 5 hydrological phases of connectivity, as defined by Tockner *et al.*, (1999)

1. The “overbank flows” phase (early November 2010 – 28 January 2011)
2. The “expansion” phase (29 January – 30 March 2011)
3. The “contraction” phase (31 March – 10 June 2011)
4. The “disconnection” phase (11 June – 10 September)
5. The “evaporation” phase (11 September onwards)

Water begun to flow through the majority of the anabranch system during early November and at the beginning and throughout the overbank flows phase remained largely confined within the banks of the creeks and lakes. During the expansion phase, flows began to spill over the banks of creeks and major lakes onto the flatter, less defined areas of the floodplain; significantly increasing the area inundated and lotic habitat and floodplain discharge. During the contraction phase, river flows began to decrease rapidly, resulting in floodplain drawdown and the flatter, less defined areas of the floodplain drying completely. The major lakes disconnected from the permanent creeks. During the disconnection phase the major waterbodies remained isolated yet relatively full. During the evaporation phase, water gradually evaporated and most waterbodies began to or did completely dry. Zooplankton dynamics will be discussed in relation to these phases and features of hydrological connectivity.

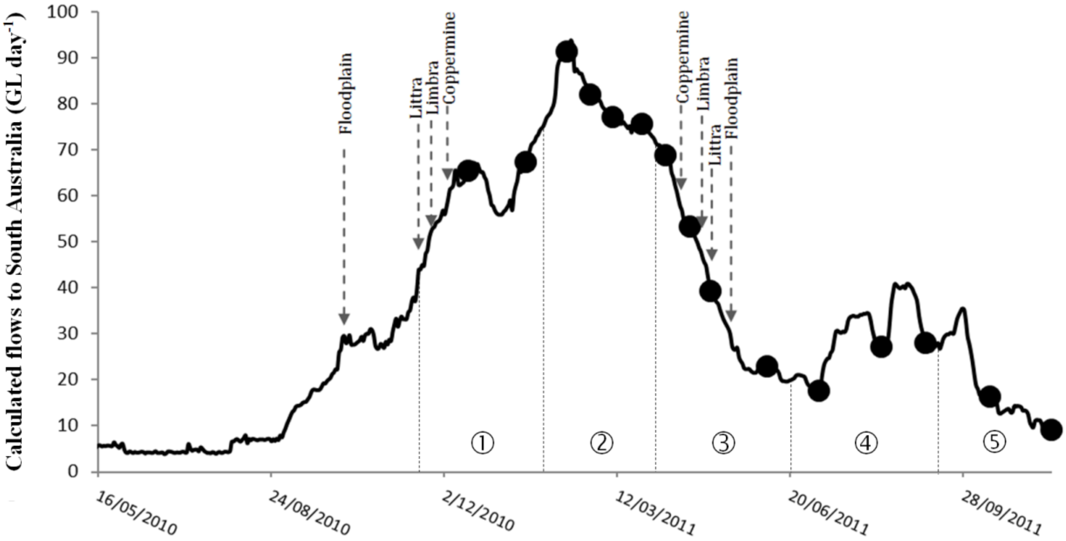


Figure 3-2: Hydrograph of flows to South Australia. Disconnection dates of the floodplain, Lake Littra, Lake Limbra and Coppermine Waterhole are indicated with broken arrows. Sampling dates are indicted as ●. Broken lines identify the five (corresponding numbers indicated) phases of hydrological connectivity.

3.2.4. *Collection and processing of zooplankton*

Zooplankton samples were collected for quantitative counts using a 14 L Schindler trap. Three replicates were taken approximately 50 metres apart from within the top 1 m of water mid channel of Hancock Creek, Chowilla Creek and the river and five replicates within the top 1 m of each lake. Quantitative samples within the lakes were taken from sites evenly distributed across the waterbody. Samples were concentrated to <10 millilitres (mL) using a 35 μm plankton net and returned to the lab in 50 mL falcon tubes. Samples were collected for qualitative analysis with a 35 μm plankton net from within the top 1 m of water within the pelagic (all dates) of all sites and littoral zones (December 2010 and January 2011) of the three lake sites. For the purpose of this study the littoral zone was defined as the region lying along the shore, less than half a metre in depth and more heavily vegetated than the pelagic zone which is the region of open water within lakes at least one and a half meters deep when full. All samples were concentrated, preserved, and returned to the lab.

Quantitative samples were inverted three times and a 1 mL sub-sample was transferred into a pyrex gridded Sedgewick-Rafter cell. The entire sub-sample was counted and zooplankton identified using an Olympus compound microscope at 40 to 100x magnification. This was repeated three times for each sample. Due to the spatial and temporal variability of zooplankton communities using power analysis to calculate the minimum sample size would be inaccurate. Therefore the number of samples taken was the maximum possible in the available time frame. The average number of zooplankton were then calculated and expressed as numbers of individuals per litre (ind. L^{-1}) and number of species L^{-1} and percentages of each major group of the total population were calculated.

The first 200 individuals within the pelagic and littoral qualitative samples collected on December 2011 and January 2011 were counted and identified and converted to a percentage of the population. All zooplankton were identified to species level where possible using published descriptions (Bayly 1992; Koste 1978; Shiel 1995; Smirnov and Timms 1983).

3.2.5. *Water quality: measurement, collection and processing*

At each site, spot measurements of water temperature, turbidity, pH, electrical conductivity (EC) and dissolved oxygen concentration were taken using a multi-parameter YSI sonde (YSI-5739). These were taken within the top metre of the pelagic zone, with 10 measurements within Lake Littra, Lake Limbra and Coppermine Waterhole and three mid channel of Hancock Creek, Chowilla Creek and the river. Water samples were taken from the same locations and placed on ice in the dark in the field for later analysis of chlorophyll-a (Chl-a) and volatile solid (VS) concentrations and analysed according to standard methods (APHA, AWWA *et al.* 1998). Volatile solid concentration is the concentration of solids in water that are lost on ignition of the dry solids at 550 degrees C. From January until May 2011 three water samples were also taken at the locations in which water quality measurements for analysis of filterable reactive phosphorus (FRP), total phosphorus (TP), ammonia (NH_4), oxidised nitrogen (NO_x, the sum of nitrate and nitrite), total nitrogen (TN) and dissolved organic carbon (DOC). Samples were stored in ice in the field and taken back to the laboratory. Water samples for PO_4^{3-}, NH_4, NO_x and DOC analysis were filtered through a 0.45 μm filter prior to analysis at the University of Adelaide. TP and TN analysis was conducted at the Environmental Analysis Laboratory, Lismore, New South Wales, which is accredited by the National Association of Testing Authorities (NATA).

3.2.6. *Statistical analysis*

To investigate how zooplankton communities change through time across the landscape a Nonmetric Multidimensional Scaling ordinations (NMS) (Kruskal 1964; Shepard 1962a; Shepard 1962b) was conducted in PC-ORD (McCune 2006). One ordination was conducted on species abundance data for all sites and dates and corresponding water quality. The distance measure used was Sorensen (Bray-Curtis) (Bray and Curtis 1957) and the rank correlation coefficient was set to 3 (see Chapter 13 in McCune, Grace *et al.* 2002).

To compare differences in abundance between sites and over time repeated-measures analysis of variance (RM-ANOVA) was conducted in IBM SPSS Statistics for Windows (SPSS Released 2010) on average abundance over time. The RM-ANOVA was performed on the data from January 2011 until and including May 2011 on all sites excluding Coppermine Waterhole which is the period for which all sites were sampled. If the assumption of sphericity was rejected using Mauchly’s criterion, the Greenhouse-Geisser corrected alpha values were used to determine the statistical significance of site and time effects (Scheiner and Gurevitch 2001). If a statistically significant effect of site was revealed and no interaction between site and time a post hoc Tukey’s HSD test was conducted.

For each site, species richness (R), evenness (E), Shannon’s diversity index (H) and Simpson’s diversity index (D`) was computed in PC-ORD on average species abundance (ind. L^{-1}) for each hydrological phase (alpha (α) diversity). Each site was compared to all others independently and the number of species unique to a site summed and averaged for each hydrological phase as a measure of species variation between habitats (beta (β) diversity). The total number of species present across the floodplain and channel habitats was summed as a measure of landscape diversity (gamma (γ) diversity).

3.3. **Results**

Within the overbank flow phase the channel sites (CC and RM) were positively correlated with water temperature and flow (Figure 3-3) where species richness was higher (Figure 3-5). Hancock Creek and Lake Limbra were correlated with higher EC and Chl-a (Conductivity: Figure 3-5 and Figure 3-6) and lower abundance than the other floodplain sites during December (Figure 3-4). Due to the contrasting response of zooplankton abundance through time (from the overbank flow to three phase) there was a significant interaction between site and time (Table 3-3: $P=<0.001$). The remaining floodplain sites all exhibited very high abundance on these dates. Overall, the overbank flow phase had the highest landscape diversity (γ) (Figure 3-8).

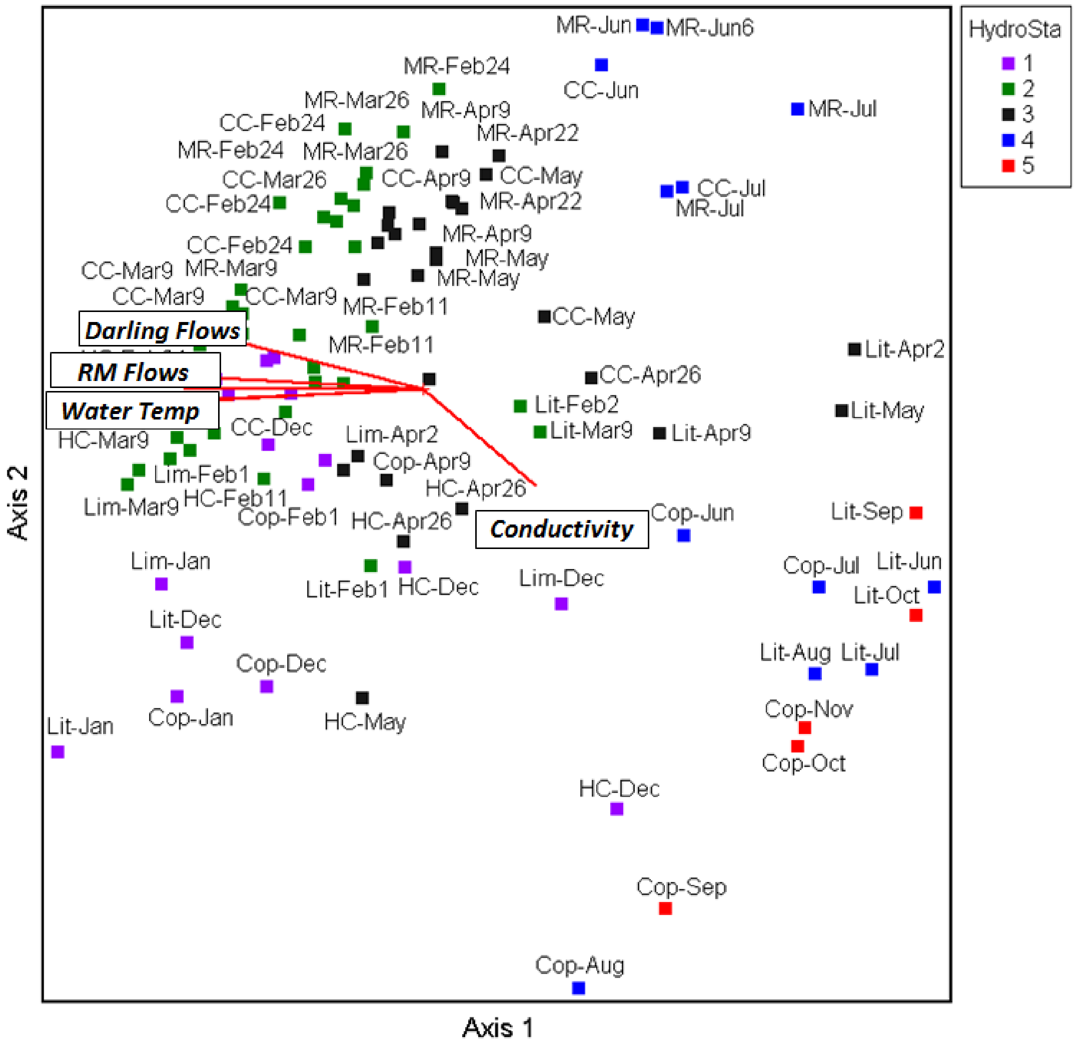


Figure 3-3: A Nonmetric Multidimensional Scaling (NMS) ordination of all zooplankton species across all sites and dates. Numbers 1 – 5 represent the five phases of hydrology. Where Conductivity = electrical conductivity, Darling Flows = Darling River flows, RM Flows = River Murray flows, Water Temp = water temperature, RM = River Murray, CC = Chowilla Creek, HC = Hancock Creek, Cop = Coppermine Waterhole, Lim = Lake Limbra and Lit = Lake Littra.

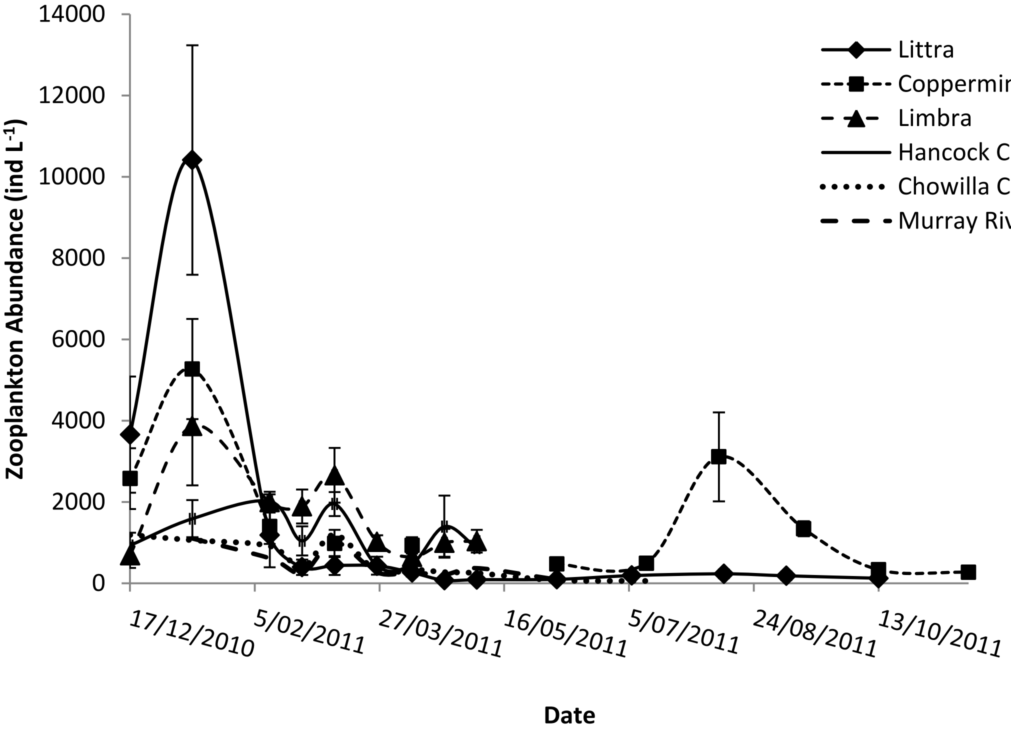


Figure 3-4: Temporal changes in abundance (ind. L^{-1}) for all sites (Chowilla Creek sites combined). Vertical bars represent ± 1 SD.

Within the expansion phase all sites excluding Lake Littra, were weakly positively correlated with water temperature and flow and negatively correlated with conductivity (Figure 3-3). Rotifers dominated (Figure 3-9) and EC converged (Figure 3-6) at these sites. Lake Littra exhibited higher turbidity and EC (Figure 3-6). In comparison to the other sites Lake Littra was less dominated by rotifers, more so by copepods (Figure 3-9) had lower species richness (Figure 3-5) and was weakly correlated with increasing conductivity (Figure 3-3). Overall landscape diversity (γ) remained high (Figure 3-9) and Chl-a converged between sites (Figure 3-6).

Within the contraction phase Coppermine Waterhole, Lake Limbra, Chowilla Creek (excluding CC-1 on 22 April) and the River Murray (Figure 3-3 and Figure 3-4) remained dominated by rotifers (Figure 3-9). Lake Littra had a lower species richness, evenness and Shannon's diversity index (Figure 3-5) and maintained the higher EC observed in the expansion phase (Figure 3-6). Overall, landscape diversity (γ) again remained high (Figure 3-8) EC and Chl-a began to diverge between sites (Figure 3-6).

Figure 3-5: The average species richness (R), evenness (E) and Shannon's diversity index (H) at each site for each hydrological phase. Where RM = River Murray, CC = Chowilla Creek and HC = Hancock Creek.

		R	E	H
Overbank flow	**Littra**	38	0.628	2.283
	Coppermine	46	0.619	2.371
	Limbra	40	0.721	2.658
	RM	56	0.676	2.723
	CC	63	0.628	2.601
	HC	47	0.794	3.056
Expansion	**Littra**	41	0.614	2.28
	Coppermine	56	0.695	2.799
	Limbra	66	0.677	2.835
	RM	64	0.635	2.642
	CC	66	0.665	2.786
	HC	66	0.65	2.724
Contraction	**Littra**	27	0.59	1.943
	Coppermine	38	0.703	2.557
	Limbra	38	0.703	2.557
	RM	53	0.688	2.73
	CC	72	0.632	2.702
	HC	55	0.688	2.758
Disconnection	**Littra**	14	0.496	1.308
	Coppermine	21	0.344	1.047
Evaporation	**Littra**	16	0.672	1.863
	Coppermine	25	0.585	1.883

Within the disconnection phase (Figure 3-3) all samples from both channel sites remained dominated by rotifers until sampling ceased (Figure 3-9). Lake Littra continued to have higher EC (Table 2) and be dominated by copepods (Figure 3-9). Overall, average species variation between habitats (β diversity) was the highest for the study (Table 3-4). Alternatively, species richness, evenness and Shannon's diversity were the lowest (Figure 3-5). Within the evaporation phase Lake Littra remained copepod dominated. Lake Littra and Coppermine Waterhole were positively correlated with conductivity (Figure 3-3). Notably, these were the only two sites samples during this phase. Overall, abundance (Figure 3-4), species richness, evenness and Shannon's diversity were low during the evaporation phase (Figure 3-5) and EC continued to diverge (Figure 3-6).

Figure 3-6: Range of average temperature (˚C), pH, turbidity (NTU), chlorophyll-a (µg l^{-1}), electrical conductance (µg cm^{-1}) and dissolved oxygen at each site throughout the five hydrological phases.

	HYDROLOGICAL PHASE				
	Overbank flow	Expansion	Contraction	Disconnection	Evaporation
TEMPERATURE					
Littra	21 - 27	19 – 26	13 - 19	10 - 16	22 - 27
Limbra	24	19 – 27	17 - 20	-	-
Coppermine	23 - 28	22 – 26	13 - 15	11 - 16	22 - 25
Hancock Creek	23	19 – 26	16 - 19	-	-
Chowilla Creek	25	19 – 19	13 - 19	10 - 10	-
Murray River	26	19 – 20	13 - 20	10 - 10	-
pH					
Littra	8.1	7.4 – 7.8	7.2 – 7.3	7.9 – 8.3	8.9 – 9.0
Limbra	7.7	7.3 - 8.2	7.3 – 8.2	-	-
Coppermine	8.3	7.1 - 7.2	7.3 - 7.5	8 - 8.6	7.8 - 8.9
Hancock Creek	7.3	7.2 – 7.7	7.3 – 7.6	-	-
Chowilla Creek	7	7 - 7.3	7.1 - 7.6	7.5 - 7.8	-
Murray River	6.6	6.8 – 7	7 - 8.3	7.5 - 7.9	-
TURBIDITY					
Littra	299	270 – 615	219 -304	209 - 290	91 - 233
Limbra	269	25 - 151	88 - 118	-	-
Coppermine	216	47 - 200	58 - 186	172 - 211	345 - 655
Hancock Creek					
Chowilla Creek	165	105 - 114	113 - 273	99 - 108	-
Murray River	181	99 - 113	124 - 173	90 - 98	-
CHL-A (µg/L)					
Littra	56 - 61	17 - 32	21 - 39	25 - 63	23
Limbra	91 - 188	18 - 40	18 - 57	-	-
Coppermine	18 - 264	22 - 56	93 - 110	65 - 346	93 - 147
Hancock Creek	55 - 192	24 - 37	23 - 45	-	-

Chowilla Creek	11 - 74	7 - 46	23 - 58	51 - 70	-
Murray River	17 - 27	14 - 49	10 - 66	-	-
EC (µS/cm)					
Littra	420 - 514	454 - 481	476 - 650	485 - 716	1165- 2429
Limbra	354 - 752	275 - 363	271 - 303	-	-
Coppermine	152 - 246	308 - 339	294 - 370	273 - 401	413 - 443
Hancock Creek	377 - 664	245 - 336	278 - 353	-	-
Chowilla Creek	214 - 258	268 - 329	258 - 388	236 - 238	-
Murray River	198 - 264	266 - 309	232 - 271	170 - 178	-
DO (mg/L)					
Littra	8.4	0.20 – 8.8	7.3 – 9.7	10.0 – 14.3	8.3 – 10.2
Limbra	6.9	2.8 – 10.2	8.3 – 11.3	-	-
Coppermine	9.6	6.3 - 5.4	7.7 - 10.5	10.2 - 13.4	6.7 - 10.9
Hancock Creek	6.5	5.3 – 8.7	8.1 – 10.6	-	-
Chowilla Creek	4.7	6.9 - 8.3	6.9 - 12.4	14.8 - 15.3	-
Murray River	6	5.8 - 7.6	6.6 - 12.3	14.7 - 15	-
VS (mg/L)					
Littra	13.34	11.71 - 19.48	10.67 - 20.45	10.45 - 113.32	13.39
Limbra	15.04	8.42 - 11.23	12.04 - 13.28	-	-
Coppermine	17.41	11.59 - 14.57	16.15 - 25.42	25.84 - 33.27	25.84 - 65.09
Hancock Creek	12.34	7.78 - 13.90	12.27 - 17.20	-	-
Chowilla Creek	-	7.37 - 12.42	12.71 - 16.32	-	-
Murray River	-	7.55 - 13.44	10.92 - 15.29	-	-
TP (mg/L)					
Littra	0.16 - 0.29	0.12 - 0.14	0.11 - 0.13	-	-
Limbra	0.21	0.15 - 0.21	0.1 - 0.13	-	-
Coppermine	0.21 - 0.28	0.18 - 0.25	0.14 - 0.74	-	-
Hancock Creek	-	0.139 - 0.216	0.084 - 0.129	-	-
Chowilla Creek	-	0.18 - 0.25	0.11 - 0.13	-	-
Murray River	-	0.161 - 0.26	0.11 - 0.15	-	-
FRP (mg/L)					
Littra	-	0 - 0	0 – 0	-	-
Limbra	-	0.0097 - 0.11	0.0097 - 0.11	-	-
Coppermine	-	0.01 - 0.069	0 - 0	-	-
Hancock Creek	-	0.015 - 0.12	0 - 0.01	-	-
Chowilla Creek	-	0.027 - 0.1	0.012 - 0.016	-	-
Murray River	-	0.011 - 0.045	0.0063 - 0.034	-	-

TN (mg/L)					
Littra	1.36 - 1.63	1.36 - 1.38	1.36 - 1.42	-	-
Limbra	1.78	1.22 - 1.25	0.96 - 1.08	-	-
Coppermine	0.76 - 2.22	1.21 - 1.46	1.45 - 3.51	-	-
Hancock Creek	-	1.2 - 1.67	0.091 - 1.07	-	-
Chowilla Creek	-	1.18 - 1.35	0.99 - 1.03	-	-
Murray River	-	1.05 - 1.4	0.67 - 1.06	-	-
NH4 (mg/L)					
Littra	-	0.14 - 0.74	0.0074 - 0.0097	-	-
Limbra	-	0.0049 - 0.042	0.019 - 0.023	-	-
Coppermine	-	0.017 - 0.028	0.0054 - 0.013	-	-
Hancock Creek	-	0.011 - 0.021	0.013 - 0.016	-	-
Chowilla Creek	-	0.019 - 0.069	0.011 - 0.021	-	-
Murray River	-	0.015 - 0.042	0 - 0.036	-	-
NO_X (mg/L)					
Littra	-	0.07 - 0.28	0.32 - 0.4	-	-
Limbra	-	0.012 - 0.03	0.013 - 0.14	-	-
Coppermine	-	0.017 - 0.024	0 - 0.02	-	-
Hancock Creek	-	0.015 - 0.07	0.091 - 1.07	-	-
Chowilla Creek	-	0.054 - 0.14	0.13 - 0.22	-	-
Murray River	-	0.018 - 0.22	0.21 - 0.33	-	-

Figure 3-7: RM-ANOVA testing for the effects of site and time on abundance on all sites excluding Coppermine Waterhole (from January until May 2011). Greenhouse-Geisser adjusted probabilities were used for the F statistics.

Source	df	MS	F	P
Within subjects				
Time	7	27266812	203.216	< 0.001*
Time*Site	28	11293483	84.169	< 0.001*
Error	140	134177		
Between subjects				
Site	4	14536608	160.546	< 0.001*
Error	20	90544.565		

Figure 3-8: Species variation between habitats (β diversity) and landscape diversity (γ diversity) during each hydrological phase where Overb = Overbank flows, Exp = Expansion, Cont = Contraction and Evap = Evaporation phase. Where β diversity is the number of species unique to each (site) when compared to each other site independently (comparison site).

		Overb	**Exp**	**Cont**	**Disco**	**Evap**
Site	Comparison Site			β diversity		
Littra	Coppermine	32	37	25	19	21
	Limbra	24	31	25		
	RM	40	39	36		
	CC	41	41	57	70	
	HC	31	39	36	53	
Coppermine	Limbra	22	37	0	63	
	RM	46	40	25		
	CC	33	26	44	50	
	HC	22	8	29	23	
Limbra	RM	36	34	25		
	CC	29	28	44		
	HC	19	19	29		
RM	CC	25	24	27		
	HC	31	26	26		
CC	HC	22	8	23		
Average		30	29	30	46	21
γ diversity		101	92	83	83	31

Figure 3-9: Percentage of the total abundance of the three major zooplankton groups, rotifers, cladocerans and copepods during the hydrological phases at each site (Chowilla Creek sites combined).

	HYDROLOGICAL PHASE				
	1	2	3	4	5
LITTRA					
Rotifers	46 - 97	38 - 75	3 - 40	7 - 62	17
Cladocerans	<1 - 4	1 - 7	0 - 6	0 - <1	0
Copepods	3 - 50	23 - 59	54 - 97	38 - 93	83
LIMBRA					
Rotifers	32 - 94	95 - 99	90 - 97		
Cladocerans	1 - 26	0 - 5	1 - 6		
Copepods	5 - 42	<1 - 3	2 - 8		
COPPERMINE					
Rotifers	69 - 81	90 - 98	42 - 89	75 - 90	43 - 47
Cladocerans	1 - 26	< 1	1	1 - 2	1 - 13
Copepods	19 - 22	2 - 10	10 - 57	9 - 24	44 - 52
HANCOCK CREEK					
Rotifers	33 - 88	97 - 98	48 - 96		
Cladocerans	2 - 17	<1 - 1	<1 - 1		
Copepods	10 - 50	1 - 2	3 - 51		
CHOWILLA CREEK					
Rotifers	94 - 98	93 - 99	82 - 98	90	
Cladocerans	1	<1 - 1	<1 - 2	2	
Copepods	1 - 5	0 - 7	1 - 18	8	
RIVER MURRAY					
Rotifers	99	95 - 99	96 - 98		
Cladocerans	<1	<1 - 1	1		
Copepods	1	<1 - 5	1 - 3		

3.4. **Discussion**

As hypothesised zooplankton assemblages were most similar in their composition during the highest degree of connectivity (expansion phase) and became increasingly dissimilar over time. Thus flow acts to mix zooplankton communities across the floodplain but as flow recedes and connectivity decreases the site-specific habitat, emergence from diapause and factors such as dispersal by wind or by birds play a greater role in shaping zooplankton communities. Despite the highest assemblage similarities that occurred during connectivity, sites maintained a high level of uniqueness and floodplain lakes contained highly abundant zooplankton communities in comparison with the channel sites. Furthermore, both habitat diversity (α diversity) and landscape diversity (γ diversity) were higher during floodplain connection. The increasing dissimilarity between sites resulted in the highest species variation between habitats (β diversity) during the disconnection phase. The lower abundance, lower diversity and increasing copepod dominance that developed over time was not only associated with disconnection but also an increasing salinity gradient.

3.4.1. ***The role of river-floodplain connectivity in early community structure***

The results of this and other studies (Bonecker, Da Costa *et al.* 2005; Bozelli 1992; James, Thoms *et al.* 2008) demonstrate that highly connected habitats in comparison to isolated habitats host assemblages that are more similar in composition. High connectivity results in the importation of populations within the floodwaters (Jenkins and Boulton 2003) and mixing within and between floodplain habitats (e.g. Forbes and Chase 2002). This is probably why it is not uncommon (Casanova, Panarelli *et al.* 2009; Jenkins and Boulton 2003; Shiel, Costelloe *et al.* 2006), that laterally connected waterbodies are dominated more strongly by rotifers during connectivity than not, reflecting more riverine than lake assemblages (e.g. Baranyi, Hein *et al.* 2002; Casanova, Panarelli *et al.* 2009; Shiel, Costelloe *et al.* 2006). Nevertheless other studies have shown that laterally connected water bodies are not always similar (e.g. Górski, Collier *et al.* 2013) and most likely reflect the strength of connection as demonstrated by Marshall *et al.*,(2006) in macroinvertebrates.

3.4.2. ***Temporal and spatial variations in abundance during floodplain connection***

3.4.2.1. *Overbank flows*

Regardless of connectivity increasing the similarity in composition between habitats, the variations in abundance during the overbank flows phase, especially between floodplain and river sites highlight the importance of floodplain expansion in providing access to food resources. In comparison to many river systems, zooplankton abundances observed in this study were high (e.g. up to 1136 ind. L-1 in comparison to up to 8 ind. L-1 in the Waikato River floodplain in Górski, Collier *et al.* 2013; 160.6 ind. L-1 in the Danube in Reckendorfer, Keckeis *et al.* 1999) yet comparable to those found in some Australian Rivers (Hawkesbury-Nepean River Kobayashi, Shiel *et al.* 1998; Upper River Murray in 2006 and 2007 and Ovens in 2006 Ning, Gawne *et al.* 2012) and large regulated temperate rivers in the Northern Hemisphere (see Kobayashi, Shiel *et al.* 1998). Those found in the lakes were also very high in comparison to many floodplain lakes (e.g. up to 10409 ind. l-1 in Lake Littra, 5269 in Coppermine Waterhole ind. l-1 and 3867 ind. l-1 in Lake Limbra in comparison to 10-20 ind. l-1, Waikato River floodplain in Górski, Collier *et al.* 2013; 305 ind l-1, Paraná River floodplain, Brazil in Lansac-Tôha, Bonecker *et al.* 2009; approximately 50 ind l-1, Lower Orinoco River in Vasquez and Rey 1989) yet also comparable to some (e.g. up to 11370 ind l-1 in Ehoma Lake, a floodplain lake in Nigeria inOkogwu 2010).

3.4.2.2. *Expansion and contraction*

Significant increases in zooplankton abundance following inundation and then reduction to very low levels during peak flood has previously been reported in floodplain lakes (e.g. Saunders and Lewis 1988a; Tan and Shiel 1993). However, in this study, despite following a similar pattern (i.e. reduction during peak flood) abundance remained very high on the floodplain during floodplain expansion and contraction. Other studies have also reported a sharp decrease in abundance within floodplain lakes following reconnection due to dilution (e.g. Nadai and Henry 2009). Increases in abundance following inundation are most likely due to the hatching of diapause eggs (Tan and Shiel 1993). As temporary waterbodies dry out many zooplankton species produce diapause eggs which sink to the benthos and collectively form an egg bank (Brendonck and De Meester

2003). Hatching in these environments is largely (yet not all) triggered upon inundation (Brock, Nielsen *et al.* 2003) and result in an initial surge in abundance whereas not within permanent or reconnected waterbodies. A combination of the egg bank response, higher food availability and higher water residence times (Obertegger, Flaim *et al.* 2007; Sterner, Kilham *et al.* 1996) common to floodplains in comparison to main channel habitats are the most likely explanation for the high floodplain abundances found in this study.

3.4.3. *The importance of flooding frequency*

Several wetlands and lakes within the Chowilla Floodplain were watered artificially via pumps prior to the 2010-11 floods. The more frequently watered habitats responded with higher abundance during the overbank flow phase. Between 2006 and 2010 Lake Littra was watered five times (abundance peaked at 10409 ind. L-1), Coppermine Waterhole was watered four times (abundance peaked at 5269 ind. L-1) and Lake Limbra was watered once (abundance peaked at 3867 ind.l-1) (watering frequency data from Schultz and Lenon 2010). A study conducted by Boulton and Lloyd (1992) demonstrated the importance of flooding frequency showing a larger response (density and biomass) in emergent zooplankton from sediment collected from frequently flooded areas in comparison to sites less flooded. This is because egg banks are more susceptible to degradation during dry periods due to factors such as senescence, predation, disease and dispersal (Brendonck and De Meester 2003; Caceres and Hairston Jr 1998; De Stasio 1989). This highlights the importance of flooding frequency and floodplain connectivity in opening up pathways to a range of habitats with extremely abundant zooplankton populations.

3.4.4. *The role of connectivity in maintaining biodiversity*

Connectivity and spatio-temporal heterogeneity has frequently been associated with the high biodiversity of river floodplain systems (see Shiel 1995; Ward, Tockner *et al.* 1999). This and other studies (Havel, Eisenbacher *et al.* 2000; Lansac-Tôha, Bonecker *et al.* 2009; Shiel, Costelloe *et al.* 2006) have demonstrated an increase in both habitat and landscape diversity during floodplain connection. However, this is not always the case. For example, using recreated mesocosm metacommunities Forbes and Chase (2002) found that connectivity had no effect on habitat diversity and decreased regional diversity. However this was using sediment collected from a subtropical climate. The high diversity within floodplains is largely due to the ability of zooplankton assemblages to encapsulate the spatial and temporal variability of both the past and present during connectivity. Spatial variability is captured through the importation from upstream locations and the wash out of the littoral and upstream and adjacent ephemeral habitats (e.g. Repsys and Rogers 1982). For example species such as *Keratella tropic*a were identified in high abundance during connectivity and are typically found in tropical and subtropical climates rather than arid ones (Koste 1978). On the other hand, temporal variability is captured through emergence from diapause which was described by Templeton and Levin (1979) as migration from the past. These emergent populations then combine with the present community effecting present species diversity, physiological ability to deal with change and the extent of the genetic variation available (Hairston 1996). Furthermore, the composition of these changing communities then influences nutrient cycling and the pathway by which they are assimilated into the aquatic food-web.

3.4.5. *Water residence time as a driving force of zooplankton structure*

Crustaceans such as cladocerans and copepods generally remain in relatively low numbers until weeks after inundation however then develop into abundant populations on floodplains over time. This is due to the longer inundation time required for the termination of diapause (e.g. Rees 1979) and increasing water residence times that favour them. As predicted copepods became more dominant over time, however the most considerable contributions of cladocerans to communities occurred during the overbank flow phase in Lake Limbra and Coppermine Waterhole yet were rapidly lost. The limitations of food nutritional content have been shown to extend to herbivores and may be one reason for the low success rate of this group (e.g. Ferrao-Filho, Tessier *et al.* 2007; Hill, Smith *et al.* 2010). For example Elser et al., (2001) found that seston enriched with phosphorus stimulated Daphnia growth, in this study phosphate decreased rapidly during February and remained at very low concentrations until May when nutrient analysis stopped. Alternatively, their absence may have been due to the triggering of emergence upon inundation (depleting the egg bank) and loss to advection as lotic conditions persisted (i.e. washout). Cladocerans are also a preferred prey item of planktivorous fish and when these fish are present they can alter the composition of the existing zooplankton community, as well as affect their behaviour. For example the presence of predators can cause confinement to refuges (e.g. Daphnia hyalina migrate vertically to the benthic Ringelberg 1991) or exclusion through selective predation (e.g. reduced representation of Cladocera Brooks and Dodson 1965; Shiel 1982). Spawning in some fish species including golden and silver perch is cued by flow (Humphries, King *et al.* 1999; Mallen-Cooper and Stuart 2003) and correspond to periods of higher zooplankton biomass (e.g. Ning, Gawne *et al.* 2012). Juvenile phases of both of these species are known to feed upon zooplankton (e.g. golden perch Culver and Geddes 1993; e.g. silver perchWarburton, Retif *et al.* 1998). Zampatti and Leigh (2011) found that the abundance of these species increased considerably within Chowilla in 2011 compared to the years 2005 until 2010.

3.4.6. *Drives of community divergence following floodplain disconnection*

Zooplankton assemblages from different sites/habitats showed greater divergence as the degree of connectivity decreased. Water quality between sites and over time appeared to vary little and remained within ranges generally tolerable to most species (Shiel 1982), however conductivity was associated with some of the differences in the assemblages that developed. Relatively small changes in salinity have been shown to affect emergence, population dynamics and species diversity of zooplankton (e.g. Nielsen, Brock *et al.* 2003; Sarma, Nandini *et al.* 2006). This may also explain the lower species richness in Lake Littra during earlier phases as well. Additional factors that could have influenced the direction of community succession include ongoing emergence (e.g. in response to seasonal or hydraulic changes) (e.g. Vandekerkhove, Declerck *et al.* 2005a), predation pressure, the influence of species dispersed via means such as avian or wind (see Havel, 2000) and available food resources (e.g. Vanni 1987).

Increasing pressure on our water resources and diversion away from rivers has caused the degradation of river-floodplain systems worldwide. The delivery of flows for environmental purposes and in some cases the construction of structures which allow localised flow manipulation is now being considered. Numerous authors have highlighted the significance of hydrological connectivity in sustaining river health and the paucity of our understanding of the processes involved (e.g. Bunn and Arthington 2002; Ward, Tockner *et al.* 2002). This study demonstrated that floodplain inundation does not only create and provide access to habitat with highly productive and unique zooplankton communities, but also facilitates a degree of mixing and exchange across spatial and temporal ecotones. High diversity across multiple scales resulted from these exchanges and most likely facilitated egg bank replenishment, improving the ecosystems resistance and resilience. This highlights the importance of maintaining floodplain heterogeneity and also in reinstating connectivity across spatial and temporal gradients when implementing flows for the environment.

Chapter 4. River-floodplain exchange and transformation of organic matter and nutrients in a dryland river system

4.1. Introduction

The flow regime is a principal driver of the way in which resources are sourced, transported and transformed through riverine ecosystems. Resources can be described as being organic, inorganic, gaseous, dissolved or particulate matter (Junk, Bayley *et al.* 1989). The quantity and form of those resources are essential for aquatic food-web structure and system function. Two distinctly influential theoretical concepts have emerged that describe how flow drives resource transport and transformation through lotic ecosystems. These are the River Continuum Concept (RCC) (Vannote 1980) and the Flood Pulse Concept (FPC) (Junk, Bayley *et al.* 1989). The RCC predicts that in lowland rivers, the primary source of organic material is derived from upstream areas. The FPC highlights the significance of hydrology and lateral connectivity in river floodplain ecosystems, suggesting that the majority of a river's productivity comes from the floodplain. A third concept, the Riverine Productivity Model (RPM) has been developed, suggesting that the majority of energy assimilated by organisms is sourced from autochthonous production and the riparian zone (Thorp and Delong 1994; Thorp and Delong 2002).

The importance of floodplains in whole system functioning is well established and intrinsically linked to the flooding regime. Floodplains can act as sources, sinks or transformers of resources however this is dependent upon the frequency, extent, duration and timing of inundation. As water moves across the floodplain and water velocity decreases, sediment particles are often deposited while dissolved nutrients are incorporated into abiotic and biotic complexes (Gurnell 1997). Through these processes the floodplain acts as a sink for suspended sediments and dissolved nutrients (e.g. Tockner, Pennetzdorfer *et al.* 1999). Areas of the floodplain that experience wetting-drying cycles develop into biogeochemical "hotspots" (McClain, Boyer *et al.* 2003) as nutrients are mobilised from the sediment and leached from organic material upon wetting. Combined with warmer water temperatures, longer water residence times (WRT) and elevated nutrients, high primary production within the aquatic area of the floodplain occurs (e.g. Glazebrook and Robertson 1999). These organics are then partially assimilated back into the food-web by both the emerging and colonising aquatic biota (Balcombe, Bunn *et al.* 2005; Bunn, Davies *et al.* 2003). One of the key primary consumers within these habitats are zooplankton. Zooplankton often occur in high abundance on floodplains due to the plentiful food resources, higher water residence times (e.g. Baranyi, Hein *et al.* 2002) and emergence from diapause states within the sediment (e.g. Boulton and Lloyd 1992). These resources may then be transported into the main river channel, fuelling primary production and providing food for higher order consumers downstream (e.g. Bouvet, Pattee *et al.* 1985; Cellot 1996; Eckblad, Volden *et al.* 1984; Fisher 2011; Hein, Baranyi *et al.* 2003).

Through these processes floodplains play a key role in the biogeochemical cycling not only within the floodplain but throughout the entire riverine ecosystem. This however is a simplistic overview of floodplain function. The role that floodplains play in fuelling riverine food-webs, particularly within dryland river systems, is yet to be fully explored and verified. Furthermore, Australian rivers of arid or semi-arid climates (hereafter termed ‘dry-land rivers’) have never clearly been defined by either the RCC or FPC. The extent, duration and frequency in which the high flow conditions necessary occur, have been significantly reduced by river regulation. This most likely has had considerable effects on the role in which autochthonous resources play within the system (Robertson, Bunn *et al.* 1999). Therefore the River Murray is probably best described by a combination of both concepts, but the extent to which floodplains affect in stream productivity remains unclear.

Here, the role of a large dryland river floodplain (Chowilla Floodplain) as a source, sink and transformer of resources to the main channel of the River Murray in Australia is investigated. This study however is not intended to provide a quantitative nutrient budget, rather it represents a preliminary attempt to identify the main sinks and sources. For the purpose of this study the term resources refers only to dissolved nutrients and organic particulates. Dissolved nutrients include dissolved organic carbon (DOC), ammonia (NH_4), oxidised nitrogen (NOx) and filterable reactive phosphorus (FRP). Organic particulates include phytoplankton, zooplankton and particulate organic material other that phytoplankton and zooplankton (hereafter termed ‘other particulate organic material’ (O-POM)) most likely comprising primarily of vegetative matter. It is hypothesised that during a study period the function of the floodplain would change over time with: initially high dissolved nutrient concentrations due to mobilisation from sediments and dead organic material; followed by lowered dissolved nutrient concentrations but elevated particulate nutrients as dissolved nutrients are incorporated into phytoplankton and zooplankton. It is expected that the Chowilla Floodplain will therefore function as a sink of dissolved nutrients and a source of particulate organic material in accordance with floodplains elsewhere. This study however only spans three months of the six in which the floodplain was connected during the falling limb of the flood when the inundated area of the floodplain was contracting and therefore we can only determine whether the floodplain is a source or sink during the study period. In investigating this hypothesis, the partitioning of the three key nutrients (carbon (C) nitrogen (N) and phosphorus (P)) within phytoplankton, zooplankton and O-POM was estimated. In investigating this hypothesis temporal trends will be examined to observe landscape responses to flood while site differences will be used to assess the effect of the floodplain.

4.2. Sampling sites and procedures

4.2.1. *Study site*

The River Murray begins near Mount Kosciuszko in the Australian Alps and meanders across inland Australia for 2530 km before discharging to the Southern Ocean (MDBA 2013) (inset in Figure 4-1). The Chowilla Floodplain (33°57'0.41"S, 140°56'29.64"E) is one of the major floodplains adjoining the River Murray covering 17,700 hectares (Figure 4-1) and is characterised as a semi-arid climate with an annual rainfall of approximately 260 mm (Kearns, Hairston *et al.* 1996). Chowilla is one of six ‘Icon Sites’ as part of Australia’s largest river restoration program ‘The Living Murray’, chosen for its high ecological value (MDBA 2013). The Chowilla Floodplain is complex and once flows breach the banks at approximately 33,000 ML day^{-1}, a mixture of lakes, and lentic and lotic channel forms including anabranches and shallow depressions are inundated (Mackay and Eastburn 1990; Shiel, Green *et al.* 1998). Upstream of Lock 6 (see Figure 4-1) water passes from the River Murray into a network of streams which then converge to form the main anabranch of the floodplain, Chowilla Creek, which flows back into the river below Lock 6 (Jolly, Walker *et al.*

1994). The area contains an array of vegetation types including River Red gum (e.g. *Eucalyptus camaldulensis*), Black box (e.g. *Eucalyptus largiflorens*), River cooba (e.g. *Acacia stenophylla*) and Lignum (e.g. *Muehlenbeckia florulenta*) distributed according to hydrological, soil and salinity gradients (MDBC 2013; Sharley and Huggan 1995).

The natural character of the floodplain is now under threat and of all the Icon Sites is the most affected by flow regulation (MDBA 2013). Due to its low rainfall, Chowilla Floodplain relies on upstream flows from the upper Murray and Darling Rivers(Maheshwari, Walker *et al.* 1995). Significant diversions, primarily for irrigation (MDBMC 1996), have meant that inflows to Chowilla are much less than those that occurred pre-development (Maheshwari, Walker *et al.* 1995; MDBMC 1996). For example, small floods (40,000 ML day^{-1}) that once occurred 91 out of every 100 years now only occur 40 years in 100 years and large floods (110,000 ML day^{-1}) that once occurred 27 out of every 100 years now only occur 5 years in 100 years (DEWNR 2006).

After the most persistent drought of the 21th century within the Murray-Darling Basin, two years of widespread rainfall and flooding dominated weather patterns. Large scale lateral connectivity was generated basin wide and inundated the majority of floodplains adjoining the river, including Chowilla. The Chowilla Floodplain was connected to the main river channel from November 2010 through to May 2011. This study was conducted during this period as it provided the opportunity to assess the mobilisation of resources from the Chowilla Floodplain under high flows.

4.2.2. *Sampling periods*

Sampling began on the 11 February 2011 and continued fortnightly until the 5 May 2011. During this time the Chowilla Floodplain was hydrologically connected to the main river channel of the River Murray (Figure 4-2). Eight sites were chosen representing both permanent channel and ephemeral floodplain habitats (Figure 4-1). To investigate the role of the Chowilla Floodplain as a source or sink of resources and the partitioning of nutrients between them, two sites were chosen within the main channel of the River Murray (RM-1 and RM-2). To investigate changes in the partitioning of nutrients between dissolved forms, phytoplankton, zooplankton and O-POM throughout the floodplain three sites were chosen within the main anabranch of the floodplain (permanent creek), Chowilla Creek (CC-1, CC-2 and CC-3). In addition, one site was chosen in each of three ephemeral lakes, Lake Littra, Lake Limbra and Coppermine Waterhole. Lake Limbra is a large terminal lake (ca. 1.5 – 2 m maximum depth) which begins to fill at approximately 45000 ML day^{-1} (measured upstream of the Chowilla Floodplain inlet). Lake Littra is a shallow (ca. 1 m maximum depth) ephemeral deflation basin, which begins to fill at approximately 47000 ML day^{-1}. Coppermine Waterhole is a moderately deep (ca. 1.5 – 2 m) lake connected to an adjacent floodplain depression, which begins to fill at approximately 65000 ML day^{-1}.

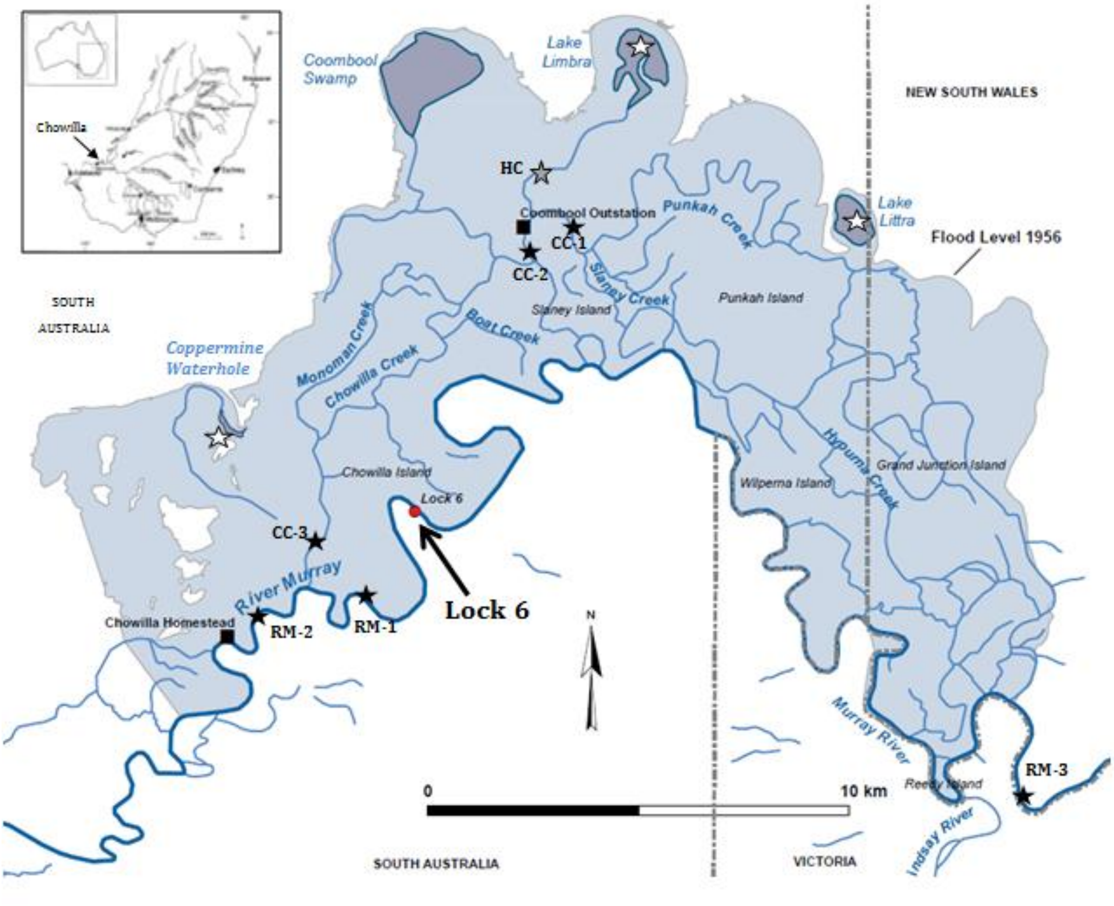


Figure 4-1: The Chowilla Floodplain with study sites Floodplain (modified from Gell, Bulpin *et al.* 2005). Hancock Creek = grey star, lake = open star, permanent creek/river = closed star, Lock 6 = red dot, CC = Chowilla Creek and RM = River Murray. Inset: the Murray Darling Basin (modified from http://tinyurl.com/9cj3jxr) white square indicates the location of Chowilla.

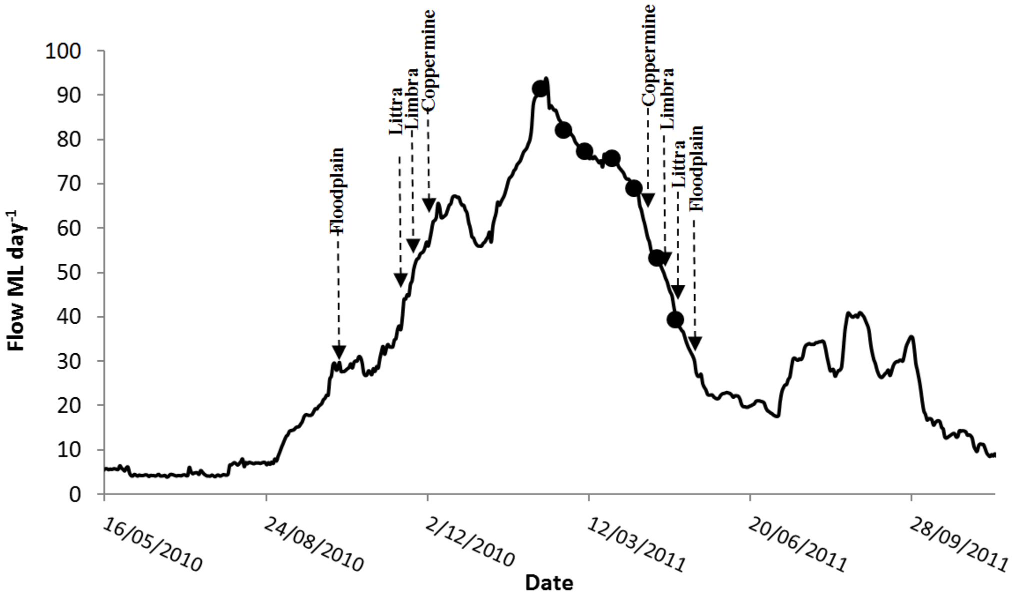


Figure 4-2: Hydrograph of flows to South Australia. Disconnection dates of the floodplain, Lake Littra, Lake Limbra and Coppermine Waterhole are indicated with broken arrows. Sampling dates are indicted as (●).

4.2.3. *Collection and processing of zooplankton*

Zooplankton samples were collected for quantitative counts using a 14 L Schindler trap. Three replicates were taken approximately 50 m apart from within the top 1 m of water mid channel of Hancock Creek, Chowilla Creek and the river and five replicates within the top 1 m of each lake. Replicates for quantitative samples within the lakes were evenly distributed across the waterbody. Samples were concentrated to < 10 millilitres (mL) using a 35 μm plankton net and returned to the lab in 50 mL falcon tubes. Samples were also collected for qualitative analysis with a 35 μm plankton net from within the top 1 m of water within the pelagic (all dates) of all sites of the three lake sites. The pelagic zone was considered to be the region of open water at least 1.5 m deep at lake capacity and less heavily vegetated than the surrounding littoral zone. All samples were concentrated, preserved, and returned to the lab.

Quantitative samples were inverted three times and a 1 mL sub-sample was transferred into a pyrex gridded Sedgewick-Rafter cell. The entire sub-sample was counted and zooplankton identified using an Olympus compound microscope. The number of zooplankton were then calculated and expressed as numbers of individuals per litre (ind. litre^{-1}) and number of species per litre (litre^{-1}) and percentages of each major group of the total population were calculated. Zooplankton biomass was calculated by multiplying the average number of each species per volume by the species dry weight. Dry weight estimates were obtained from the literature for the identified species (Dagne, Herzig *et al.* 2008; Dumont, Velde *et al.* 1975; Masundire 1994; Pauli 1989; Sendacz, Caleffi *et al.* 2006). If estimates were not available for a particular species, a species of similar size and/or genus was used.

4.2.4. ***Temporal and spatial changes in the concentration of dissolved and particulate resources***

Water samples were taken for later analysis of chlorophyll-a (Chl-a) and volatile solid (VS) concentrations which were analysed according to standard methods (Part 10200: 'Fluorometric Determination of Chlorphyll a' and Part 2540: 'Total, Fixed, and Volatile Solids in Solid and Semisolid Samples' in APHA, AWWA *et al.* 1998). Volatile solid concentration is the concentration of solids in water that are lost on ignition of the dry solids at 550 degrees C. Three replicates were taken approximately 50 m apart from within the top 1 m of water mid channel of Hancock Creek, Chowilla Creek and the river and five replicates within the top 1 m of each lake. Replicates for quantitative samples within the lakes were evenly distributed across the waterbody. An estimate of phytoplankton biomass (dry weight) was also calculated from Chl-a biomass according to standard methods (Part 10200 I. Determination of Biomass (Standing Crop) in APHA, AWWA *et al.* 1998). The biomass of other particulate organic material (O-POM) was estimated by subtracting the zooplankton and phytoplankton biomass from the VS concentration. This is expected to consist of primarily terrestrial and aquatic plant material.

From January until May 2011 water samples were taken at all Chowilla Creek, River Murray and lake sites. These were analysed for total phosphorus (TP), ammonia (NH_4), oxidised nitrogen (NO_x, the sum of nitrate and nitrite), total nitrogen (TN), filterable reactive phosphorous (FRP) and dissolved organic carbon (DOC). Samples were stored in ice in the field and taken back to the laboratory. Water samples for FRP, NH_4, NOx and DOC analysis were filtered through a 0.45 μm filter (M-Millipore MCE Membrane) prior to later analysis at the University of Adelaide. FRP, NH_4 and NOx were analysed on a Lachat Quickchem 8200 Flow Injection Analyser (Hach, CO, USA) and DOC on a SGE ANATOC™ Series II Total Organic Carbon Analyser. TP and TN analysis was conducted at the Environmental Analysis Laboratory, Lismore, New South Wales, which is accredited by the National Association of Testing Authorities (NATA according to standard methods (Part 4500-P I: In-line UV/Persulfate Digestion and Flow Injection Analysis for Total Phosphorus and Part 4500-N C: Persulfate Method in APHA, AWWA *et al.* 1998). Total organic carbon (TOC) was estimated by summing O-POM(C), Phyto(C), Zoop(C) and DOC (see 'Partitioning of nutrients between resources' on page 75 and Figure 4-4). Additionally nitrogen and phosphorus concentrations within O-POM, phytoplankton, zooplankton and dissolved fractions were subtracted from TN and TP. This was to estimate other sources of nitrogen (Other-N) and phosphorus (Other-N) that were not accounted for within the other estimates and expected to be largely colloidal nutrients but some bacteria.

4.2.5. *Calculation of nutrient loads*

The study period was broken up into multiple periods, with the sampling dates being the midpoint for each period (see Figure 4-3). The total flow above and below the Chowilla Floodplain within the River Murray was calculated by summing daily flow into South Australia for each day for each period.

Figure 4-3: The total flow volume (megalitres: ML) for each period and the date in which the representative sample was taken. Where RM = River Murray (at RM-2 & RM-3) and CC = Chowilla Creek (at CC-3).

		Total Flow (ML)	
Date sampled	**Period**	RM	CC
11/02/2011	27/01/2011 - 17/02/2011	1872766	604294
24/02/2011	18/02/2011 - 2/03/2011	1080125	419504
9/03/2011	3/03/2011 - 16/03/2011	1078904	411725
26/03/2011	17/03/2011 - 1/04/2011	1200020	457999
9/04/2011	2/04/2011 - 15/04/2011	953852	367787
22/04/2011	16/04/2011 - 28/04/2011	696817	227568
5/05/2011	29/04/2011 - 12/05/2011	558840	148583

Changes in resources within the main channel of the River Murray due to discharge from the Chowilla Floodplain were determined by calculating load at RM-2 (Figure 4-1) and subtracting the estimated load above the floodplain (hereafter RM-3) (Figure 4-1). The load above the floodplain was estimated by multiplying the total discharge by concentration, with the concentration being that at RM-1 (Figure 4-1), with the assumption that this was representative of that upstream of floodplain.

4.2.6. *Partitioning of nutrients between resources*

Nutrient partitioning between resources were calculated using a combination of estimates of carbon (C) as a percentage of biomass and C:N:P ratios collected from the literature (Figure 4-4). Nutrient partitioning is expressed as concentrations at each site over time.

4.2.7. *Statistical analysis*

Due to financial limitations only one sample was taken per site for nutrient analysis and therefore the statistical analyses available were limited. Therefore the analysis undertaken is descriptive and is used simply to provide additional evidence to general patterns that are observed in the data. Nutrient concentrations including TOC, TN, TP, NH_4, NOx and FRP and biomass concentrations including O-POM, phytoplankton and zooplankton were analysed with linear mixed-effects models with site and time as random effects. In addition to random fluctuations in nutrient concentrations over time, it was assessed whether there was a linear or nonlinear (i.e. quadratic polynomial) trend over time. Evidence for these trends was investigated using likelihood ratio tests, comparing the models with fixed effects to the null models with only the random effects. Results in which the model including fixed effects did not differ significantly from the null model were rejected.

Conditional on the fixed trend model, estimates of the mean (hereafter termed the ‘conditional mean’) and partial deviations from the conditional mean were calculated and graphed for both site and time. The precent of variation from this model (% variation) due to the effects of site and time were then calculated using the following equation:

$$\% \, variation_{x} = \frac{V_x}{V_{site} + V_{time} + V_{residual}} \text{ X } 100$$

where:

V = variance

x = effect (site or time)

Normality and homogeneity of residuals were checked by visual inspections of plots of residuals against fitted values. All data were analysed using R (Team 2012) and the R package 'lme4' (Bates, Maechler *et al.* 2012).

Figure 4-4: Summary of methods used to estimate the mass of carbon (C), nitrogen (N) and phosphorus (P) within each resource including phytoplankton (phyto), zooplankton (zoo) and O-POM. Where TM = total mass, C = carbon, N = nitrogen and P = phosphorus.

	Acronym	*Formula*	*Additional information*	*Reference*
Phytoplankton	*Phyto(C)*	$\mathrm{C_{Phyto}} = \frac{\mathrm{TM_{Phyto}}}{2}$	*C = 50% of biomass*	*(Reynolds 1984)*
	Phyto(N)	$\mathrm{N_{Phyto}} = \mathrm{P_{Phyto}} \times 7.1$	*N:P = 7.1:1 (mass) = 16:1 (atomic)*	*(Redfield 1958)*
	Phyto(P)	$\mathrm{P_{Phyto}} = \frac{\mathrm{C_{Phyto}}}{41.1}$	*C:P = 41.1:1 (mass) = 106:1 (atomic)*	*(Redfield 1958)*
Zooplankton	*Zoop(C)*	$\mathrm{C_{Zoo}} = \frac{\mathrm{TM_{Zoo}}}{2}$	*C = 51% of mass (average of multiple species)*	*(Walve and Larsson 1999).*
	Zoop(N)	$\mathrm{N_{Zoo}} = \mathrm{P_{Zoo}} \times 10.1$	*N:P = 10.1:1 (mass) 22.3:1 (atomic)*	*(Elser, Fagan et al. 2000)*
	Zoop(P)	$\mathrm{P_{Zoo}} = \frac{\mathrm{C_{Zoo}}}{48.1}$	*C:P = 48.1:1 (mass) 124:1 (atomic)*	*(Elser, Fagan et al. 2000)*
O-POM	*O-POM(C)*	$\mathrm{C_{OM}} = \frac{\mathrm{TM_{OM}}}{2}$	*C = 49% of mass (average of multiple species)*	*(Bocock 1964)*
	O-POM (N)	$\mathrm{N_{OM}} = \mathrm{P_{OM}} \times 12.7$	*N:P = 12.7:1 (mass) = 28:1 (atomic)*	*(Elser, Fagan et al. 2000)*
	O-POM (P)	$\mathrm{P_{OM}} = \frac{\mathrm{C_{OM}}}{375}$	*C:P = 375:1 (mass) = 968:1 (atomic)*	*(Elser, Fagan et al. 2000)*

4.3. **Results**

4.3.1. *Temporal trends across the landscape*

Evidence of linear and non-linear temporal trends occurred in TN, TP, Other-N, NOx, DOC and O-POM (Figure 4-5). Time explained between 40 and 73% of variation from the conditional means of these nutrients (Figure 4-6).

Both TN and TP generally decreased over time (Figure 4-7). The decreasing concentration of TN was largely due to decreasing concentrations of the primary contributor Other-N as flow decreased (Figure 4-8 and Figure 4-9). The trend in TP was primarily due to decreasing concentrations in Other-P (Figure 4-9) and FRP (Figure 4-10 and Figure 4-7).

Nutrients within organic material increased over time including phytoplankton from the 26 March and O-POM (Figure 4-8, Figure 4-11, Figure 4-12 and Figure 4-13). Phytoplankton biomass was highest during the period in which zooplankton was lowest from 26 March until the 5 May (Figure 4-12).

Dissolved organic carbon concentrations increased from February 11 until 9 March and then decreased and concentrations in NOx increased over the entire study (excluding the 9 April) (Figure 4-10).

Figure 4-5: Likelihood ratio tests comparing models. Polynomial (Poly), linear (Linear) and no trends (None) were tested. The best fit model, degrees of freedom (df), F-statistic (F) and p-values (P) reported. Where fitted models are significantly different, *** = $P < 0.001$, ** = $P < 0.01$, * = $P < 0.05$.

			df	F-statistic	p-value	Trend
Total organic carbon	Quadratic					Random
		]	1,6	8.4532	0.09588	
	Linear					
		]	1,5	9.7768	0.2795	
	No trend					
Total nitrogen	Quadratic					Linear
		]	1,6	0.0108	0.9174	
	Linear					
		]	1,5	9.5763	0.001971 **	
	No trend					
Total phosphorus	Quadratic					Non-linear
		]	1,6	9.2155	0.0024 **	
	Linear					
		]	1,5	8.2417	0.004094 **	
	No trend					
Other nitrogen	Quadratic	]	1,6	1.1273		

	Linear No trend	1,5	20.687	0.2883 5.409e-06 ***	Linear
Other phosphorus	Quadratic Linear No trend	1,6 1,5	1.588 10.632	0.2076 0.001111 **	Linear
Dissolved organic carbon	Quadratic Linear No trend	1,6 1,5	1.8156 7.0635	0.1778 0.007867 **	Linear
Oxidised nitrogen	Quadratic Linear No trend	1,6 1,5	0.0722 13.296	0.7882 0.000266 ***	Linear
Ammonia	Quadratic Linear No trend	1,6 1,5	0.4094 2.7206	0.5223 0.09906	Random
Filterable reactive phosphorus	Quadratic Linear No trend	1,6 1,5	4.955 11.962	0.02602 * 0.000543 ***	Non-linear
Other particulate organic material	Quadratic Linear No trend	1,6 1,5	8.4532 9.7768	0.003644 ** 0.001767 **	Non-linear
Phytoplankton	Quadratic Linear No trend	1,6 1,5	5.9916 4.8398	0.01437 * 0.02781 *	Non-linear
Zooplankton	Quadratic Linear No trend	1,6 1,5	0.3641 3.6105	0.5463 0.05742	Random

Figure 4-6: The percentage of variation from the fixed trend due to the effects of site and time.

	Site	Time
Total organic carbon	3.8%	22%
Total nitrogen	25%	50%
Total phosphorus	8.8%	65%
Other nitrogen	0	73%
Other phosphorus	6%	26%
Oxidised nitrogen	28%	48%
Ammonia	1%	32%
Filterable reactive phosphorus	17%	40%
Dissolved organic carbon	0%	48%
Other particulate organic material	21%	62%
Zooplankton	54%	15%
Phytoplankton	0%	33%

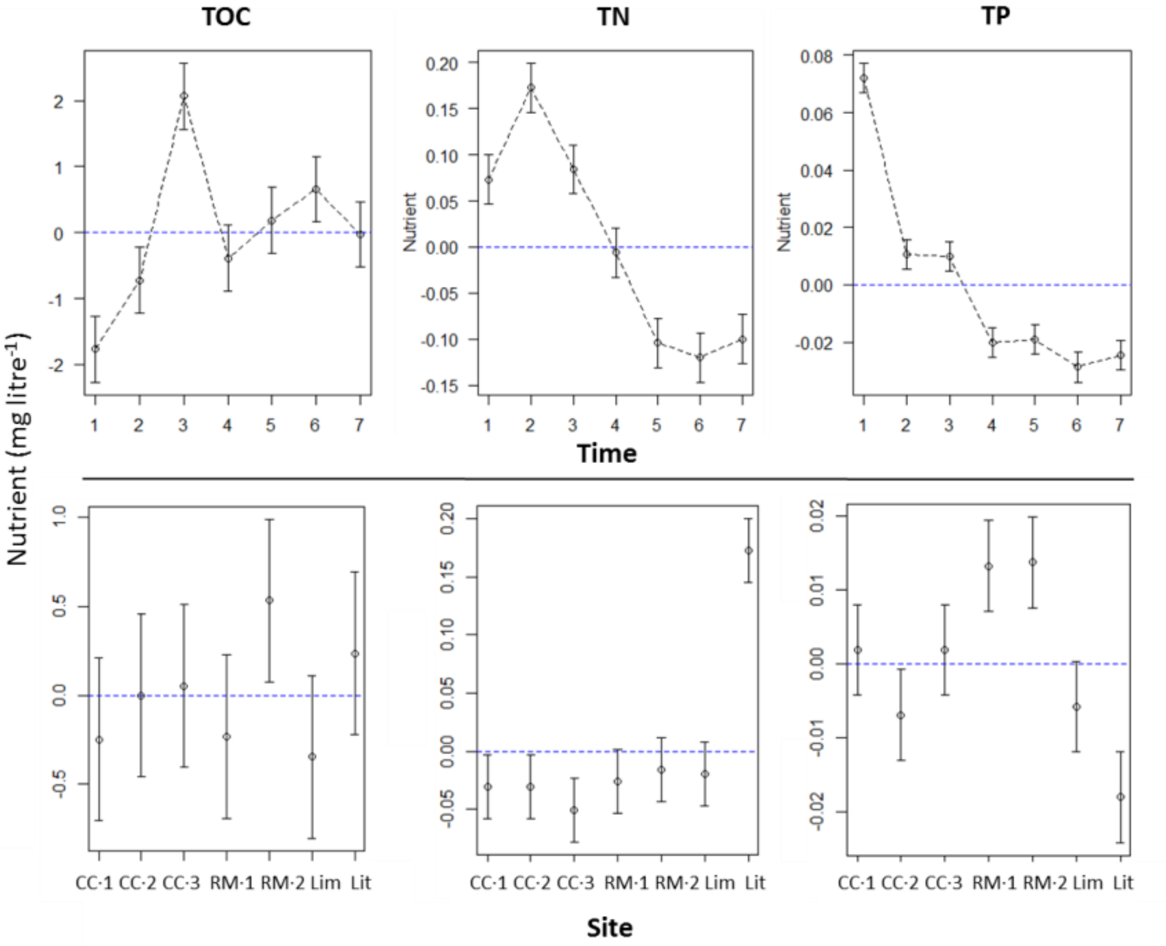


Figure 4-7: Conditional partial deviations from the conditional mean (across all sites and time) for TC, TN and TP (mg litre^{-1}) where the conditional mean has been set to zero and is indicated with the broken blue line. Graphs on the top row are the means (across sites) for each sampling date and the bottom row are the means (across dates) for each site. Date 1 = 11 February 2011, 2 = 24 February 2011, 3 = 9 March 2011, 4 = 26 March 2011, 5 = 9 April 2011, 6 = 22 April 2011 and 7 = 5 May 2011. Site Lim = Lake Limbra and Lit = Lake Littra.

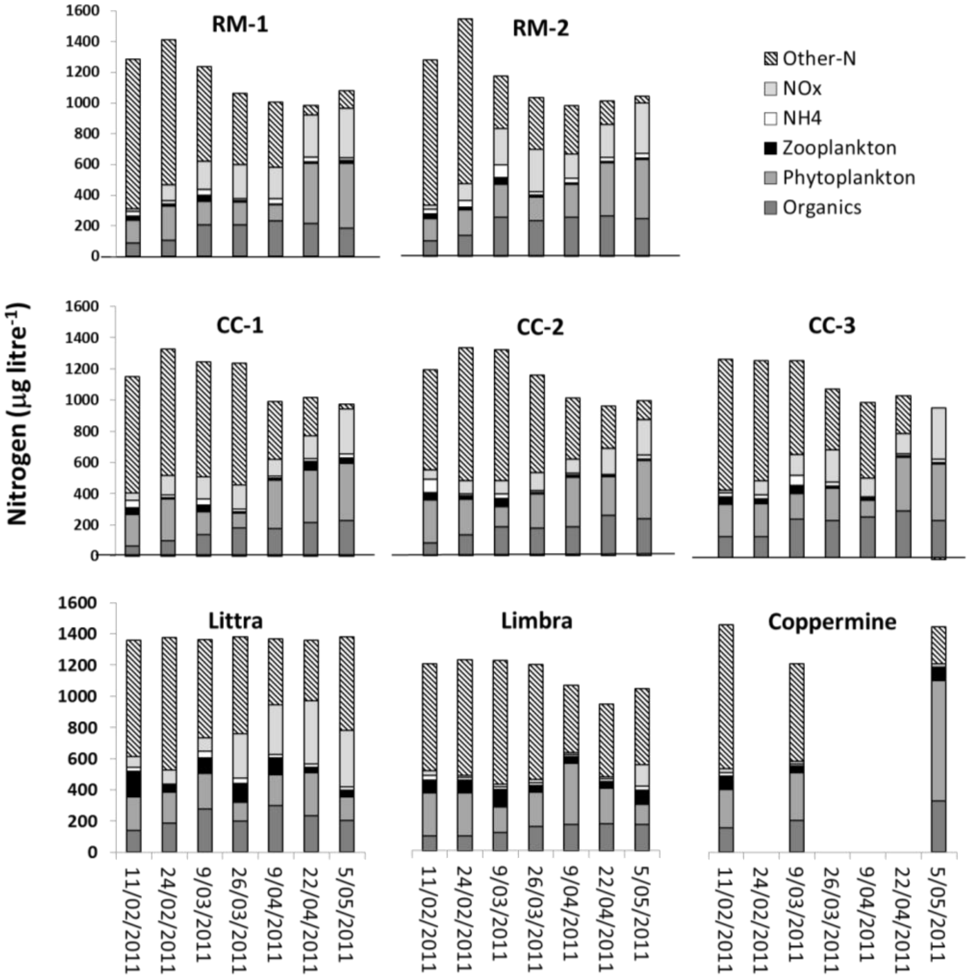


Figure 4-8: Temporal changes in the concentration of nitrogen estimated within other organic material (O-POM), phytoplankton, zooplankton, NH4 and NOx at the sites CC-1, CC-2, CC-3, Littra, Limbra and Coppermine Waterhole.

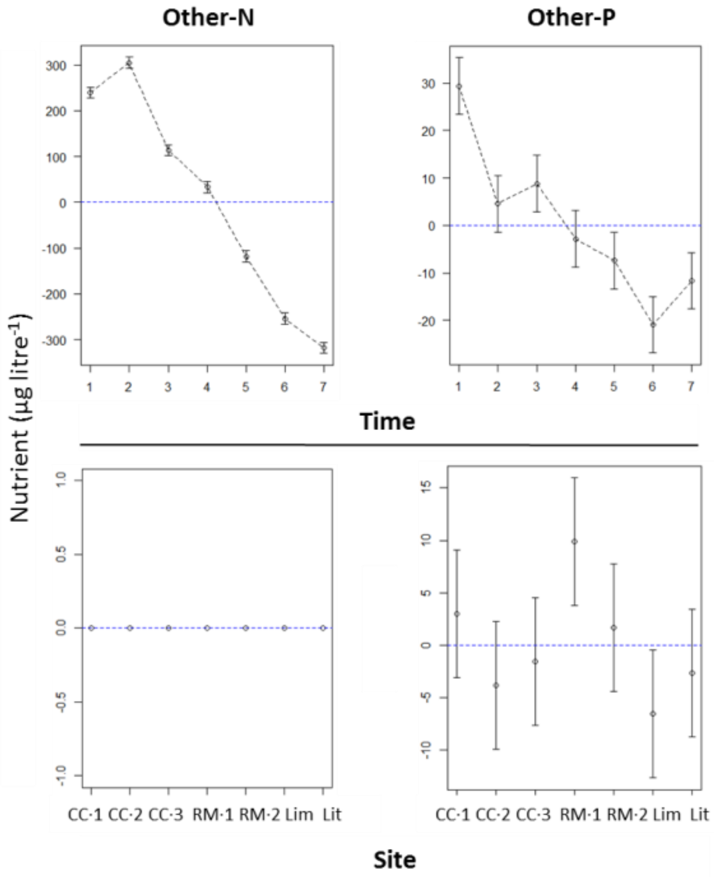


Figure 4-9: Partial deviations from the conditional mean (across all sites and time) of Other-N and Other-P (µg litre^{-1}) where the conditional mean has been set to zero and is indicated with the broken blue line. Graphs on the top row are the means (across sites) for each sampling date and the bottom row are the means (across dates) for each site. Date 1 = 11 February 2011, 2 = 24 February 2011, 3 = 9 March 2011, 4 = 26 March 2011, 5 = 9 April 2011, 6 = 22 April 2011 and 7 = 5 May 2011. Site Lim = Lake Limbra and Lit = Lake Littra.

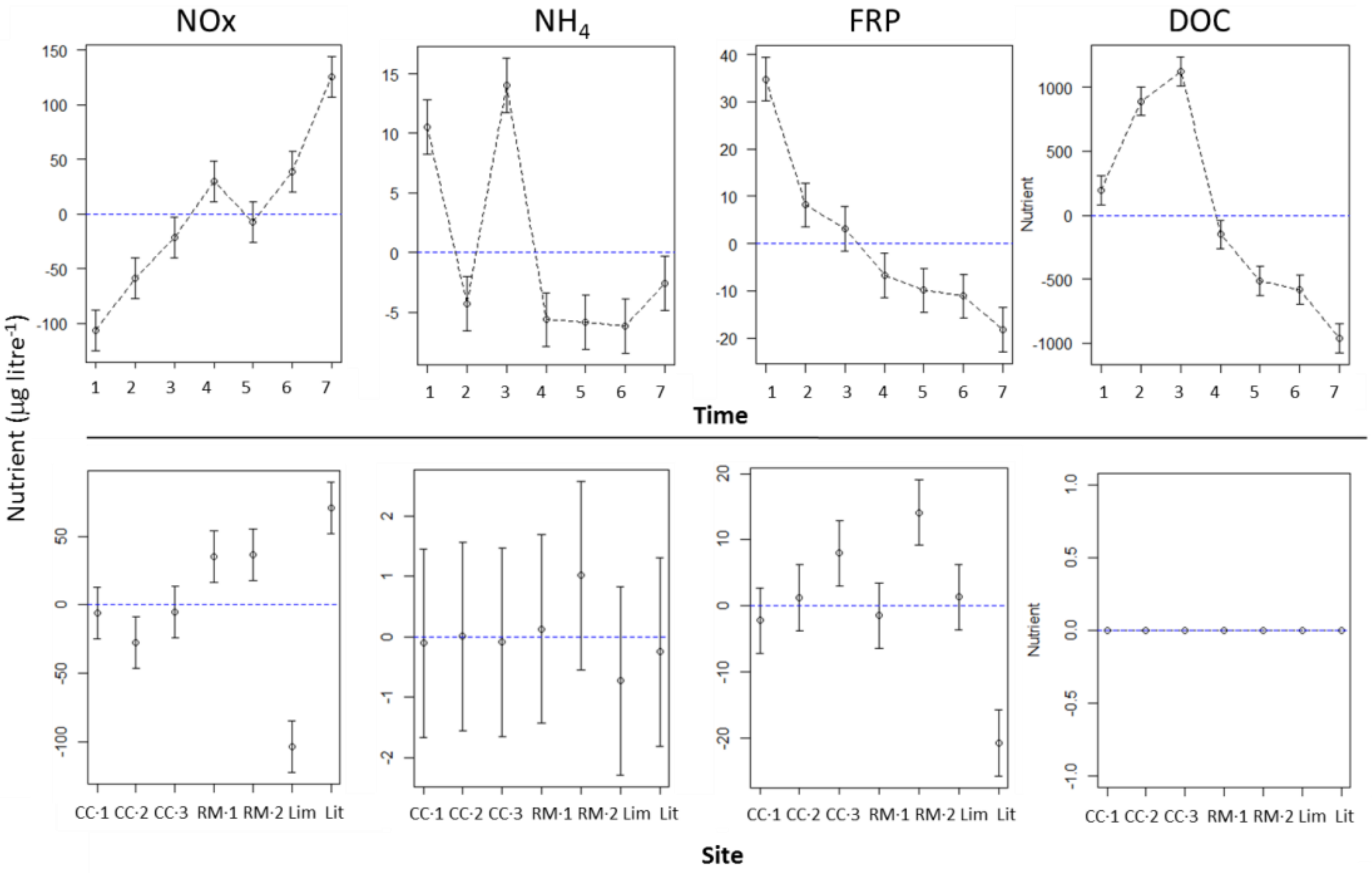


Figure 4-10: Partial deviations from the conditional mean (across all sites and time) for NOx, NH_4, FRP and DOC (µg litre^{-1}) where the conditional mean has been set to zero and is indicated with the broken blue line. Graphs on the top row are the means (across sites) for each sampling date and the bottom row are the means (across dates) for each site. Date 1 = 11 February 2011, 2 = 24 February 2011, 3 = 9 March 2011, 4 = 26 March 2011, 5 = 9 April 2011, 6 = 22 April 2011 and 7 = 5 May 2011. Site Lim = Lake Limbra and Lit = Lake Littra.

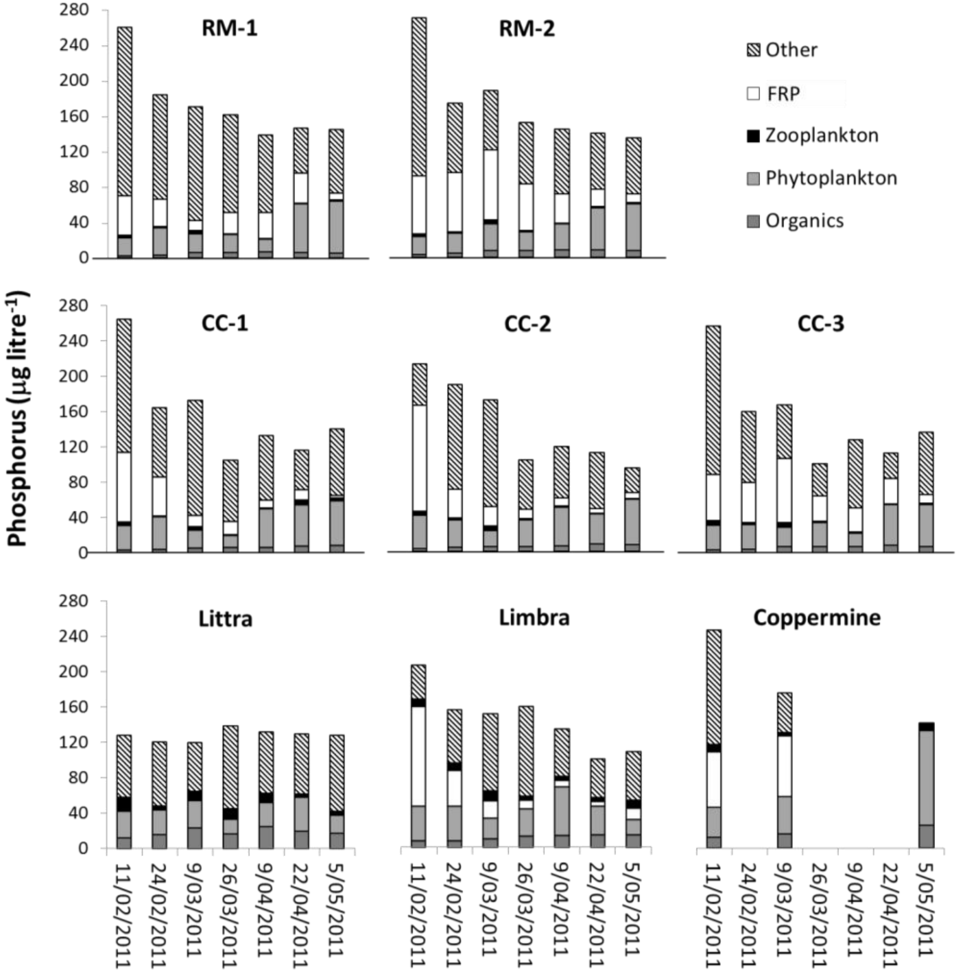


Figure 4-11: Temporal changes in the concentration of phosphorus estimated within t-POM, phytoplankton, zooplankton and PO_4^{3+} at the sites CC-1, CC-2, CC-3, Littra, Limbra and Coppermine Waterhole.

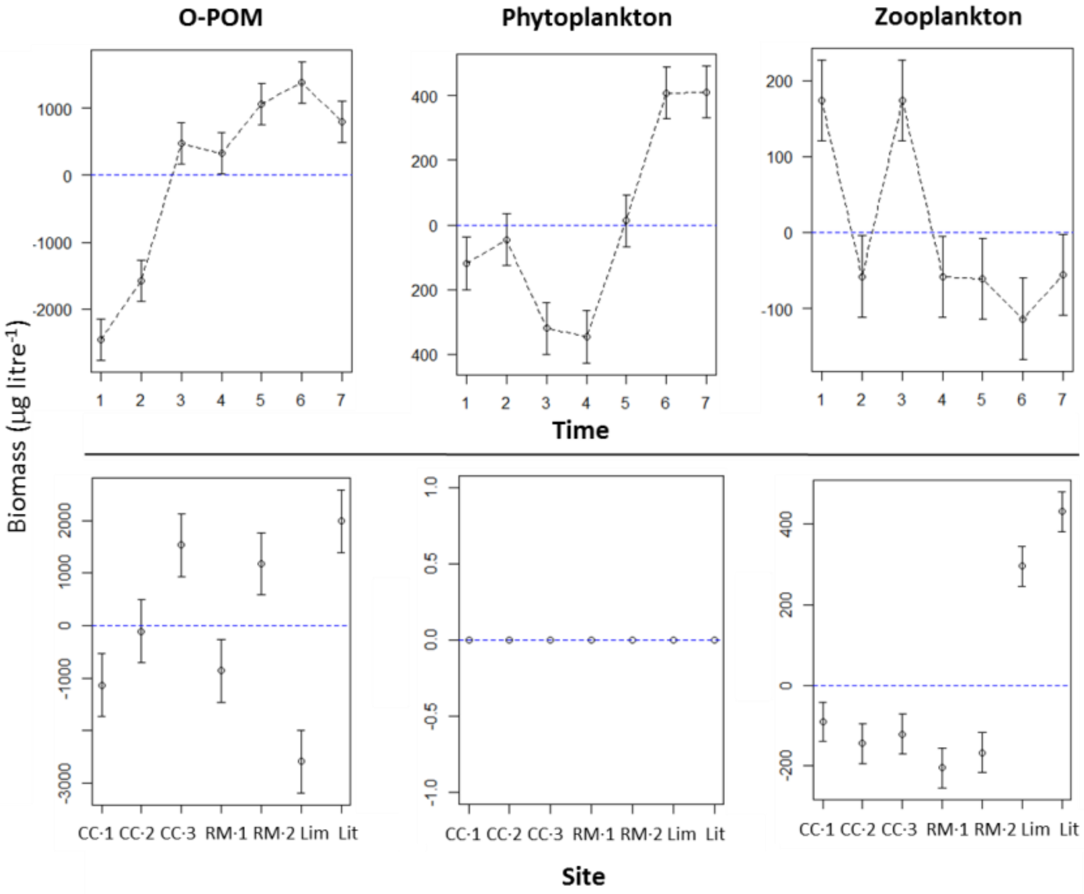


Figure 4-12: Partial deviations from the conditional mean (across all sites and time) for O-POM, phytoplankton and zooplankton (µg litre^{-1}) where the conditional mean has been set to zero and is indicated with the broken blue line. Graphs on the top row are the means (across sites) for each sampling date and the bottom row are the means (across dates) for each site. Date 1 = 11 February 2011, 2 = 24 February 2011, 3 = 9 March 2011, 4 = 26 March 2011, 5 = 9 April 2011, 6 = 22 April 2011 and 7 = 5 May 2011. Site Lim = Lake Limbra and Lit = Lake Littra.

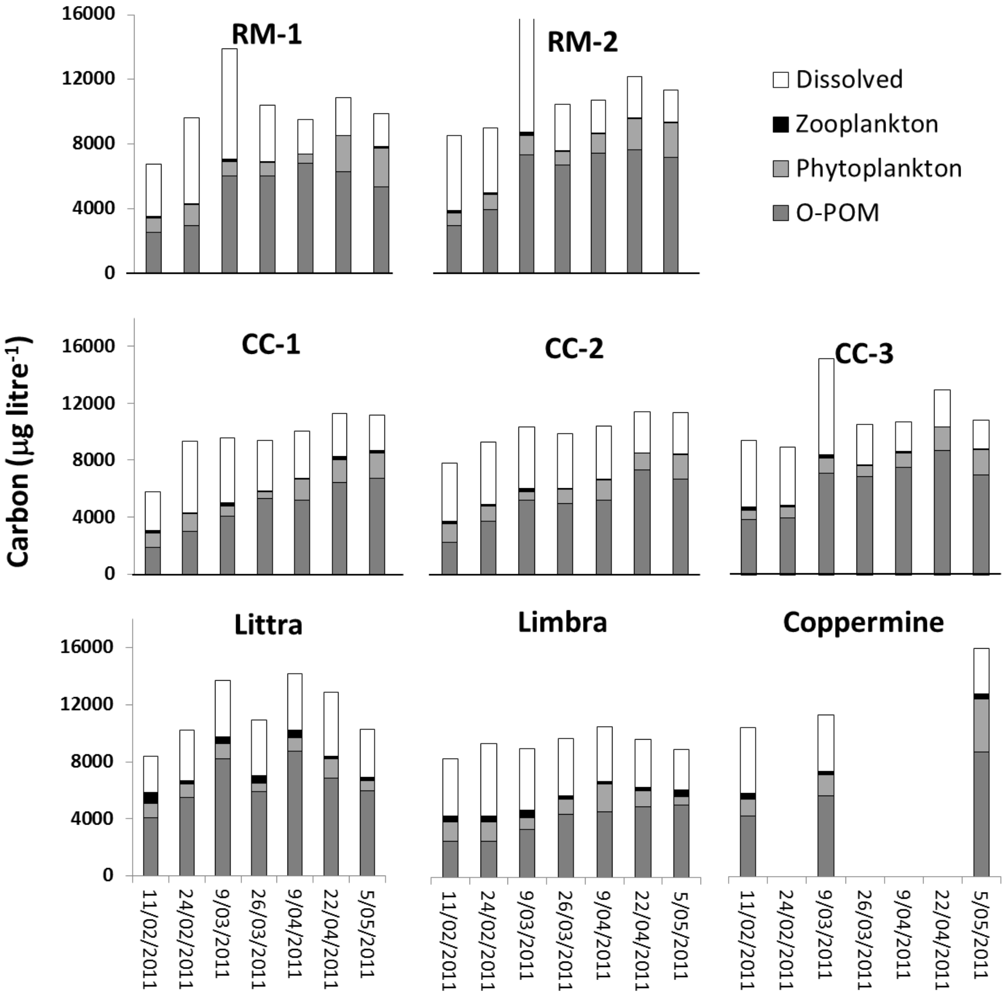


Figure 4-13: Temporal changes in the concentration of carbon estimated within phytoplankton, zooplankton, O-POM and DOC at the sites CC-1, CC-2, CC-3, Littra, Limbra and Coppermine Waterhole.

4.3.2. *Floodplain transformations*

4.3.2.1. *Dissolved nutrients*

In addition to evident temporal trends in NOx and FRP, site explained 28 and 17% of the variation from their conditional means, respectively (Figure 4-6). Site differences in NH_4 and DOC concentrations were negligible (Figure 4-6).

There were distinct site differences in NOx where Lake Limbra consistently had the lowest and Lake Littra the highest concentrations (Figure 4-4 and Figure 4-10).

Concentrations in FRP varied between sites where concentrations consistently increased as water flowed through the floodplains main anabranch Chowilla Creek from CC-1 to CC-2 to CC-3 (Figure 4-10). These increases appeared to be increasing concentrations within the main river channel with concentrations at RM-1 consistently more similar to CC-1 and RM-2 more similar to CC-3 (Figure 4-10). These increases in FRP did not appear to be coming from the floodplain lakes that were sampled as Lake Littra consistently had much lower concentrations and Lake Limbra only slightly higher than CC-1 and RM-1 (Figure 4-10).

4.3.2.2. *Particulate organic material*

Biomass concentrations in O-POM consistently increased as water flowed through the floodplains main anabranch Chowilla Creek from CC-1 to CC-2 to CC-3 (Figure 4-12). These increases appeared to be increasing concentrations within the main river channel with concentrations at RM-1 consistently more similar to CC-1 and RM-2 more similar to CC-3 (Figure 4-12). These increases could have been due to contributions from floodplain habitats such as Lake Littra which consistently had higher biomass concentrations than all other sites yet not Lake Limbra which consistently had the lowest (Figure 4-12). The conditional mean in phytoplankton did not vary between sites (Figure 4-12). Zooplankton biomass was consistently higher within the two floodplain lakes than all other sites (Figure 4-12).

4.3.3. *The floodplain as a sink or source of resources during the receding limb of the hydrograph*

The Chowilla Floodplain was a source of nutrients in both the particulate and dissolved forms (Figure 4-14). Nutrients in the particulate forms, O-POM and zooplankton were consistently exported from the floodplain. Whilst, overall the floodplain was a source of phytoplankton bound nutrients, this was primarily as the floodwaters receded (Figure 4-14). Nutrients in the dissolved forms, FRP, NH4 and NOx were consistently exported from the floodplain during the first four periods, but the floodplain fluctuated between a sink and source during the later periods (Figure 4-14).

Figure 4-14: Loads of particulate and dissolved material from Chowilla Floodplain to the River Murray Channel, 27th of January to 12th of May 2012. Loads are shown for O-POM, phytoplankton, zooplankton, DOC, NH_4, NOx and FRP in tonnes (t). Quantities shown are the total differences in load between RM-2 (downstream of the Chowilla Floodplain) and RM-3 (upstream of the Chowilla Floodplain) for each period (Period) and for the whole sampling study.

Period	Particulate			Dissolved			
	O-POM (t)	**Phytoplankton biomass (t)**	**Zooplankton biomass (t)**	**DOC (t)**	**NH_4 (t)**	**NOx (t)**	**FRP (t)**
27th Jan – 17th Feb	2231	-74	102	2747	0	11	39
18th Feb – 2nd Mar	755	-630	79	-1350	25	0	39
3rd Mar – 16th Mar	2101	631	88	13562	42	60	74
17th Mar – 1st Apr	747	74	65	-768	6.0	6.5	35
2nd Apr – 15th Apr	865	1006	43	0	-5.7	-4.8	29
16th Apr -28th Apr	263	-309	13	186	-7.0	-4.0	-10
29th Apr – 12th May	553	-232	-21	-30	7.8	1.1	1.8
TOTAL	**7515**	**466**	**368**	**14346**	**68**	**50**	**182**

4.4. Discussion

4.4.1. *General findings*

Floodplains have long been recognised for their ability to alter the quantity and form of resources within riverine habitats. Within dryland river systems some debate still remains surrounding the role in which floodplains play. It was expected that the function of the floodplain would change over time with dissolved nutrient concentrations decreasing as they were increasingly incorporated into phytoplankton and zooplankton. The function of the floodplain was more complex than predicted where the hypothesis was upheld for FPP and DOC however not for nitrogen. This could have been due to factors such as groundwater influences, nitrogen fixation and fluxes between organics via consumption and production within the food web. The hypothesis was in part supported by the conversion of nutrients into zooplankton via a number of possible pathways including the consumption of (a) O-POM, (b) bacteria that utilize O-POM or (c) phytoplankton that have incorporated dissolved nutrients. The floodplain acted as both a sink and a source of resources, dependent upon the parameter of interest and time. As expected, due to transformation and resource mobilisation, the floodplain functioned as a source of particulate organic resources including O-POM, phytoplankton and zooplankton. Not as expected the floodplain was also a source of FRP. Additionally, despite little to no difference observed between sites within the River Murray, marginally elevated concentrations meant that there was a load contribution of NOx, NH_4, and DOC.

4.4.2. *The floodplain as a nutrient sink during floodplain contraction*

Contrary to the general view that riverine floodplains function as nutrient sinks, the floodplain was overall a source of dissolved nutrients during floodplain contraction. At times it did however function as a sink, primarily during April and May as the floodwaters were receding rapids. Other studies have also demonstrated variation in the retention or exportation of dissolved nutrients (e.g. el Moghraby 1977). Unfortunately this study missed the initial period of floodplain inundation and it is unknown whether the floodplain also initially functioned as a source. Tockner *et al.*,(1999) also investigated nutrient transport during floodplain connection and found that the floodplain was initially a nutrient sink and later, a nutrient source. It is possible that the Chowilla Floodplain also functioned in this way. Concentrations can be influenced by a range of factors including the decomposition of organic material, conversion by bacteria, uptake through primary production, mobilisation from floodplain soils and associations with suspended sediments (e.g. Briggs, Maher *et al.* 1993; Gunnison, Engler *et al.* 1985). Significant quantities of leaf mass is estimated to leach from litter within days following inundation (e.g. Boulton 1991; Wallace, Ganf *et al.* 2008). This includes the release of DOC and FRP and possible why both of these nutrients were highest at the beginning of the study and also why the floodplain was increasing FRP concentrations the further downstream. Over time the decrease in these nutrients could have been due to utilisation by phytoplankton (which increased in biomass over time from the 26 March), association with sediment as it settled (Forsberg, Devol *et al.* 1988) or microbial metabolism (Havel and Shurin 2004). The floodplains effect on NOx concentrations appeared more complex and is expected to be due to the complex nature of ground and surface water interactions across the area (Overton and Doody 2008). Despite considerable quantities of these dissolved nutrients being exported with the floodwaters, some underwent transformation before transportation as phytoplankton and zooplankton.

4.4.3. *The floodplain as a transformer of nutrients during floodplain contraction*

The floodplain was transforming nutrients through their incorporation into zooplankton through a number of possible pathways. Two of these include the direct grazing of zooplankton on particulate organic materials such as leaf litter and aquatic vegetation or on the bacteria that utilize organic material. Both bacteria and vegetative matter are not uncommon food sources for zooplankton and have been shown to contribute a substantial portion of their diet (Arndt 1993; Cole, Carpenter *et al.* 2011). Concentrations of O-POM, which is expected to include primarily leaf litter and aquatic vegetation, was high and increased over the study in part due to its increasing mobilisation due to decomposition across the floodplain. Therefore the high O-POM and often highly abundant bacteria communities that accompany organic material suggest that there were plentiful food resources available in these forms. Another preferred food item of zooplankton is phytoplankton (Brett, Kainz *et al.* 2009). There was no evidence of site differences in phytoplankton biomass. However, phytoplankton productivity may still have been higher within the floodplain lakes (and explain the lower FRP concentrations) yet biomass concentrations maintained at similar levels to the main river channel and creek due to zooplankton grazing. These elevated food resources in combination with higher water residence times (Baranyi, Hein *et al.* 2002) and emergence from eggs within the floodplain soils (e.g. Boulton and Lloyd 1992) are why, as in this study, zooplankton thrive within floodplain habitats. Zooplankton development is largely confined to these areas of longer water residence and thus their role in nutrient movement is strongly influenced by hydrology. The high flow during the study period is probably why a considerable load of zooplankton was transferred to the main river channel. Other studies investigating the transfer of zooplankton from floodplain to main channel habitats have produced contrasting results. This includes several showing little or no contribution from floodplains (e.g Gigney, Petrie *et al.* 2006; Saunders and Lewis 1989) and others, as with this study (see Chapter 5 for a more thorough investigation), identified significant contributions (e.g. Eckblad, Volden *et al.* 1984; Ning, Gawne *et al.* 2012; Saunders and Lewis 1988a).

4.4.4. *Factors affecting the function of the floodplain as a sink or source*

4.4.4.1. *The temporal changes in floodplain inundation*

The role that floodplains play as a sink or source of resources depends on factors such as flooding regime, features of the flood hydrograph, floodplain topography and sediment loads. This study demonstrated that the Chowilla Floodplain was a major source of organic material. The exportation of organic material from floodplains in terrestrial forms (e.g. leaf litter in the Ogeechee River, Georgia inCuffney 1988) and as phytoplankton (e.g. algae biomass in the River Danube, Austria in Tockner, Pennetzdorfer *et al.* 1999) has also been demonstrated in other systems. Yet floodplains have also been shown to act as a sink (e.g. particulate organic material inTockner, Pennetzdorfer *et al.* 1999). These studies however cover the whole temporal frame of floodplain inundation whereas this study only covered floodplain connection and may in fact explain some of the variable results.

4.4.4.2. *Flooding history*

The flood in this study followed years of drought (2001 – 2009 in Dijk, Beck *et al.* 2013) and significant accumulation of leaf litter had probably occurred during this time. This accumulated leaf litter is most likely primary source of O-POM which was the major contributor of organic carbon. Factors such as the timing and frequency of inundation have been shown to be crucial in determining the role in which floodplains play (e.g. Lucena-Moya and Duggan 2011; Tockner, Pennetzdorfer *et al.* 1999). For example in the River Danube exportation of coarse particulate organic material occurred from the floodplain after the accumulation of leaf litter during autumn, yet not when a second flood occurred two months later (Tockner, Pennetzdorfer *et al.* 1999). Concentrations of O-POM also increased over time. This was probably due to the progressive fragmentation of leaf litter due to the abrasion and shear stress caused by flowing water and biotic processes such as the feeding of shredders. These organics are likely to provide an important carbon source for bacteria and grazing and herbivorous zooplankton within the main channel downstream.

4.4.5. ***Conclusions***

These resources from the floodplain play an important role in aquatic energy and nutrient cycling within the river channel. Native aquatic species are likely to have evolved life history traits that occur in direct response to these inputs. This includes responses such as the spawning of native fish in response to higher flows that coincide with zooplankton transfer (an important food resource) from floodplains. The most severe threat to these processes is modification of the natural flow regime (Bunn and Arthington 2002). Within the River Murray, river regulation has significantly reduced the frequency of higher flows that result in widespread inundation (Walker and Thoms 1993) for example the magnitude of flow that occurred in this study at the Chowilla Floodplain naturally occurred every 37 years out of every 100 yet now only occurs every 11 (DEWNR 2006). This study suggests that this does not only affect the availability of highly productive floodplain habitat but the flow of resources throughout the entire riverine food-web. This study however is strictly a preliminary investigation to identify the main sources and sinks which are difficult to quantify, especially in large systems.

Based on these preliminary findings some of the next steps may be to identify the primary nutrient sources (e.g. leaf litter or groundwater) and the areas of the floodplain and the hydrological conditions that promote their mobilisation and utilisation by aquatic biota while conducting a more exhaustive budget analysis.

Chapter 5. Floodplain connectivity facilitates significant export of zooplankton to the main River Murray channel during a flood event.

5.1. Introduction

Within riverine ecology the river continuum concept (RCC) suggests that ecological processes change predictably along the downstream gradient. Despite being one of the most fundamental concepts to date the RCC overlooks the role of floodplain dynamics. The flood pulse concept (FPC) (Junk, Bayley *et al.* 1989) addressed this, highlighting the importance of lateral exchange of organic matter within river-floodplain systems. The FPC however was developed on systems with predictable flood pulses such as those within tropical regions and not those within arid or semi-arid (hereafter termed 'dryland' rivers) where the flow pulse is variable and unpredictable. Therefore its applicability to dryland river-floodplain systems is currently debated. Some authors have suggested that they are perhaps best described by a combination of both the RCC in upland and the FPC in lowland reaches (Robertson, Bunn *et al.* 1999; Walker, Sheldon *et al.* 1995).

A number of studies followed the development of the FPC, demonstrating that floodplains and their conduits transfer a substantial proportion of their biotic production back to the river channel (e.g. Bouvet, Pattee *et al.* 1985; Cellot 1996; Eckblad, Volden *et al.* 1984; Fisher 2011; Hein, Baranyi *et al.* 2003; Tockner, Pennetzdorfer *et al.* 1999). This includes the transfer of zooplankton, which provide a critical link within riverine food-webs. They provide this link through the ingestion and processing of bacteria, phytoplankton and organic material (e.g Desvilettes, Bourdier *et al.* 1997; Jumars, Penry *et al.* 1989; Knisely and Geller 1986; Kobayashi and Church 2003; Lampert, Fleckner *et al.* 1986; Vanderploeg and Scavia 1979) and as a food source for fish (e.g. golden perch Arumugam and Geddes 1996; Meredith, Matveev *et al.* 2003), waterbirds (e.g. waterfowl Crome 1985), amphibians (e.g. Ranta and Nuutinen 1985) and macroinvertebrates (e.g. Chaoborus Lynch 1979).

The degree and direction in which zooplankton are assimilated into the aquatic food-web depends on both the composition and abundance of the community. The composition affects the range of morphological and behavioural characteristics often restricted to predators (e.g. Ranta and Nuutinen 1985; Schael, Rudstam *et al.* 1991) whereas zooplankton abundance can affect the rate at which predator-prey encounters occur (Cooper and Goldman 1980; Vinyard 1980). It follows that an increase in the diversity of prey options coupled with more abundant zooplankton communities will increase the range of available resources to support a variety of higher trophic organisms through various life history stages. Communities at particular points in time and space have been extensively explored yet despite their essential role, rarely has the occurrence and extent to which they are transported from floodplains been similarly studied.

Floodplains and other off-channel habitats are known to contain diverse and abundant zooplankton communities (Lancaster and Hildrew 1993; Reckendorfer, Keckeis *et al.* 1999; Reynolds, Carling *et al.* 1991; Wallis, Young *et al.* 1989). Whilst several biotic (O'Brien, Slade *et al.* 1976; Rothhaupt 1990) and abiotic (Bailey, Duggan *et al.* 2004; Schallenberg, Hall *et al.* 2003) factors are important in determining the community composition and abundance, the longer water residence time (WRT) of floodplain habitats is a key factor that determines the zooplankton community structure and abundance. Water residence time has a strong positive relationship with zooplankton abundance and biomass and there is generally a shift in assemblage from rotifer to crustacean dominated communities in systems with longer residence time (e.g. Baranyi, Hein *et al.* 2002; Basu and Pick 1996; Obertegger, Flaim *et al.* 2007). Zooplankton also have the ability to produce a resting stage and there are often abundant and species rich egg banks in the ephemeral off channel sites (Brendonck and De Meester 2003; Chesson and Warner 1981; Warner and Chesson 1985) adding to the significance of these habitats.

With the combined effects of higher WRT’s and egg bank emergence, floodplain habitats host highly abundant and unique zooplankton communities. Whilst these habitats are thought to act as zooplankton sources for faster flowing environments, very little direct evidence has been produced. The few studies that have investigated this have produced contrasting results including several showing little or no contribution from floodplains (e.g Gigney, Petrie *et al.* 2006; Saunders and Lewis 1989) and others identifying significant contributions (e.g. Eckblad, Volden *et al.* 1984; Ning, Gawne *et al.* 2012; Saunders and Lewis 1988a). Here the contribution of zooplankton from a large floodplain (Chowilla Floodplain) to a long, lowland river, the River Murray is investigated. Given the size of the floodplain and relatively low discharge of the river, we hypothesise that the floodplain will make a significant contribution to the riverine zooplankton community during a flood period. Floodplain zooplankton contributions will be quantified by testing zooplankton abundances upstream of the floodplain to those below. Lowland rivers within dryland regions such as the River Murray are neither best described by the RCC nor the FPC. Rather, it has been suggested that they could be best described by a combination of both, the RCC during low flow periods and the FPC during high flow periods (Walker, Sheldon *et al.* 1995). To investigate this hypothesis both (1) zooplankton contributions from a single floodplain lake, and (2) zooplankton contributions from the floodplain to the main river channel were examined. This study took place during the 2010-11 River Murray floods, during which measurements of zooplankton species composition, species richness and abundance were taken.

5.2. **Sampling sites and procedures**

5.2.1. ***Study site***

The River Murray begins near Mount Kosciuszko in the Australian Alps and meanders across inland Australia for 2530 km before discharging to the Southern Ocean (MDBA 2013) (Figure 5-1). The Chowilla Floodplain (33°57'0.41"S, 140°56'29.64"E) is one of the major floodplains adjoining the River Murray covering 17,700 hectares and is characterised as a semi-arid climate with an annual rainfall of approximately 260 mm (Kearns, Hairston *et al.* 1996). Chowilla is one of six ‘Icon Sites’ as part of Australia’s largest river restoration program ‘The Living Murray’, chosen for its high ecological value (MDBA 2013). The natural character of the floodplain is now under threat and of all the icon sites is the most affected by flow regulation (MDBA 2013).

Due to its low rainfall the floodplain relies on upstream flows from the upper Murray and Darling Rivers which together once averaged 13,400,000 megalitres per year (ML year^{-1}) (Maheshwari, Walker *et al.* 1995). Flows have always been highly variable however now due to the diversion of an average of 9,801,000 ML year^{-1} primarily for irrigation (MDBMC 1996) flows to Chowilla are much less than occurred pre-development (Maheshwari, Walker *et al.* 1995; MDBMC 1996). Small floods (40,000 ML day^{-1}) that once occurred 91 out of every 100 years now only occur 40 years in 100, and large floods (110,000 ML day^{-1}) that once occurred 27 out of every 100 years now only occur 5 years in 100 (DEWNR 2006). After the most persistent drought of the 20th century within the Murray-Darling Basin, two years of widespread rainfall and flooding dominated weather patterns. Large scale lateral connectivity was generated basin wide and inundated the majority of floodplains adjoining the river, including the Chowilla Floodplain.

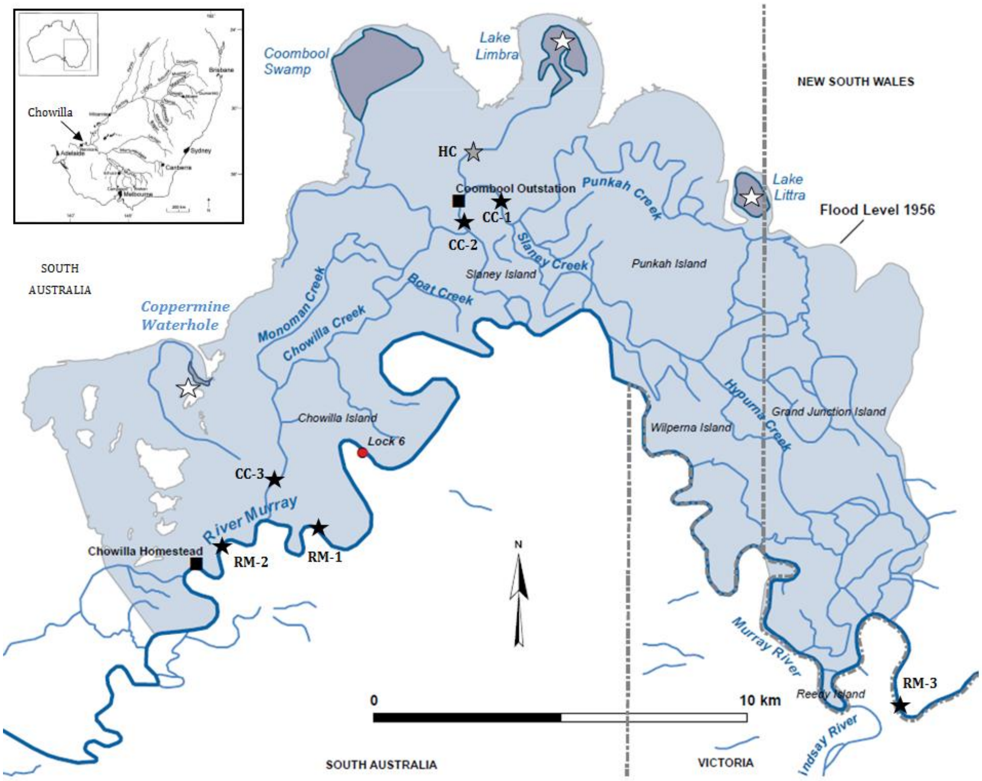


Figure 5-1: The Chowilla Floodplain (modified from Gell, Bulpin *et al.* 2005). Hancock Creek = grey star, lake = white star, permanent creek/river = closed star, HC = Hancock Creek, CC = Chowilla Creek and RM = River Murray. Inset: Murray-Darling Basin (modified from Humphries, King *et al.* 1999).

The floodplain is complex and comprises a mixture of lakes, and lentic and lotic channel forms including anabranches and shallow depressions. Upstream of Lock 6 water is diverted from the River Murray into a network of streams which then converge to form the main anabranch of the floodplain, Chowilla Creek, which flows back into the river below Lock 6 (Jolly, Walker *et al.* 1994). Immediately downstream of the formation of Chowilla Creek is an ephemeral stream, Hancock Creek, which fills and drains a large terminal lake (ca. 1.5 – 2m) Lake Limbra when flow exceeds approximately 45,000 ML day^{-1}.

5.2.2. *Collection and processing of zooplankton*

Contributions from the floodplain to the main river channel were determined and discussed as increases in species richness and/or increases in abundance in the main river channel during a major flooding event. Species richness is used as a guide to the available diversity of morphological and behavioural characteristics within a community and individuals per litre used as the measure of abundance.

Sampling began on 17 December as this was the earliest that I could reach the site. Both the abundance and species composition of zooplankton can change rapidly and therefore ultimately sampling would have continued up to twice or three times weekly. However due to the distance to the site, associated costs and the time required to process samples, sampling continued at the most frequent intervals possible which was fortnightly from February until April 2011 and monthly thereafter until June 2011 (see Table 2-1 for dated each site was sampled, Figure 5-1 for site locations and Figure 5-2 for sampling dates in relation to the flood hydrograph). Conditions prevented sampling at some sites on 17 December 2010, 18 January 2011 (high river levels) and 6 June 2011 (desiccation). Sites were sampled during the day within two-days.

Figure 5-2: Sampling dates for each site. Where HC = Hancock Creek, CC = Chowilla Creek and RM = River Murray.

	17.12.2010	11.01.2011	11.02. 2011	24.02. 2011	09.03. 2011	26.03. 2011	09.04. 2011	02.04. 2011	05.05. 2011	06.06. 2011
HC	-	-	-	-	-	-	-	-	-	-
CC-1	-	-	-	-	-	-	-	-	-	-
CC-2	-	-	-	-	-	-	-	-	-	-
CC-3		-	-	-	-	-	-	-	-	-
RM-1			-	-	-	-	-	-	-	-
RM-2		-	-	-	-	-	-	-	-	-

Sampling sites were located near the confluence of Chowilla Creek and Hancock Creek (hereafter termed the anabranch-tributary confluence) to establish the magnitude of the zooplankton contribution from Lake Limbra and surrounding floodplain to downstream waterbodies. At the anabranch-tributary confluence there were two sites within Chowilla Creek (CC), one upstream (CC-1) and one downstream (CC-2) of the confluence and an additional site within Hancock Creek (HC) (Figure 5-1). To establish the zooplankton contribution from the Chowilla Floodplain to the River Murray sampling sites were located near the confluence of the River Murray and Chowilla Creek (hereafter termed the river-anabranch confluence). Two sites were located in the River Murray, one upstream (RM-1) and one downstream (RM-2) of the river-anabranch confluence with an additional site within Chowilla Creek (CC-3) (Figure 5-1).

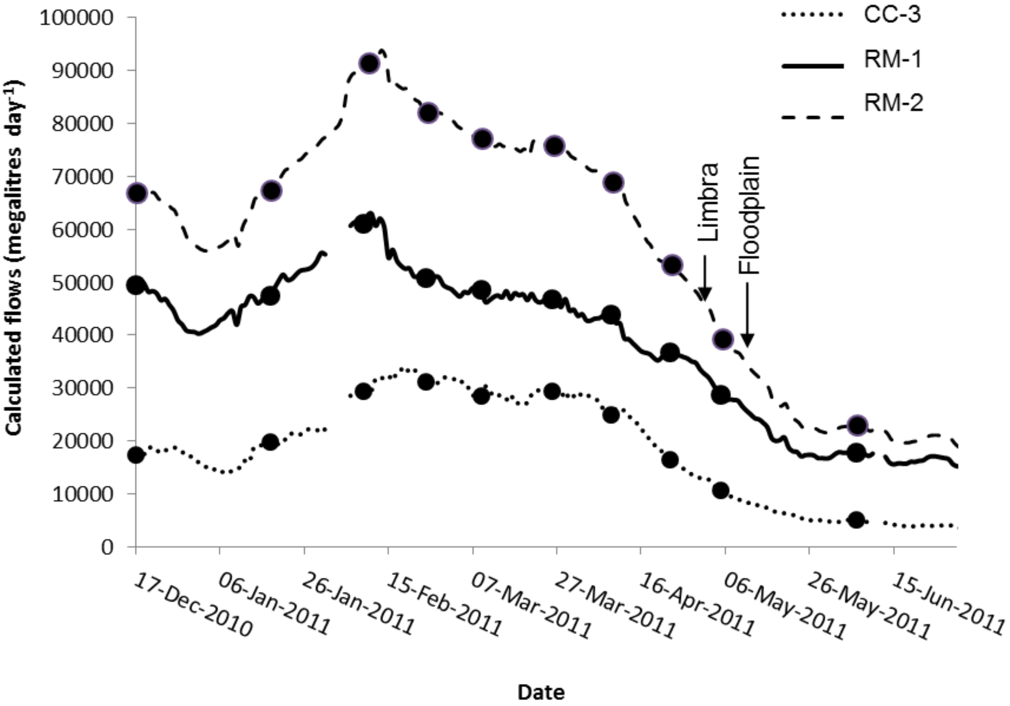


Figure 5-3: Hydrograph of flows in and adjacent to the Chowilla Floodplain. Flows shown are discharge exiting Chowilla Creek (CC-3), flows to South Australia excluding discharge to the Chowilla Floodplain (RM-1) and discharge of the River Murray downstream of the Chowilla Floodplain (RM-2). Disconnection dates of the floodplain and Hancock Creek/Lake Limbra are indicated with arrows. Sampling dates are indicated as •. Gaps in lines represent missing data.

Zooplankton samples were collected for quantitative counts using three 14 litre Schindler trap samples taken from within the top one metre of water within the pelagic zone (roughly the centre of the channel). Samples were concentrated to <25 mL, preserved, and returned to the lab in 50 mL falcon tubes. Samples were inverted three times and a 1 mL sub-sample transferred into a pyrex gridded Sedgewick-Rafter cell. The entire sub-sample was counted and zooplankton identified using an Olympus compound microscope. All zooplankton were identified to species level where possible using published descriptions (Koste 1978, Shiel 1995). The number of zooplankton were then calculated and expressed as numbers of individuals litre^{-1} (ind litre^{-1}) and number of species litre^{-1} (sp. litre^{-1}). The average zooplankton abundance at the upstream and downstream sites at both confluences was compared and differences were assumed to be due to contributions from the floodplain.

5.2.3. *Flow rate calculations*

A STARFLOW model 6526C Ultrasonic Doppler Instrument with Micrologger (Unidata, Australia) was placed in Hancock Creek on 11 March 2011 which measured and recorded water velocity and depth every 30 minutes from which daily average flow were calculated. Measurements on the 11 March 2011 were used as an estimate of flow on the 9 March 2011 to correspond with a zooplankton sampling event. A profile of Hancock Creek was surveyed with a GPS and was used to determine the cross sectional area of Hancock Creek at varying water depths at the location of the flow meter. Daily discharge was then calculated.

Daily average discharge for Chowilla Creek and daily average calculated flows into South Australia were obtained from the Murray Darling Basin Authority (MDBA 2011). The discharge for RM-1 was calculated by subtracting the Chowilla Creek discharge from the calculated discharge into South Australia.

Evaporation which ranged from 1.4 to 15.7 millimetres per day (mm day^{-1}) from the 17th of December 2010 to the 5th of May 2011 (a total of 822 millimetres) was not taken into account when calculating flow budgets and therefore there is some associated error. The associated error was estimated using the estimated areas of the floodplain inundated under different flows (DEWNR 2006) and daily evaporation at Renmark (BOM 2014b) to calculate the daily volume lost to evaporation from 17 December 2010 until 12 May 2011. These daily volumes were then summed to calculate an estimate of total volume lost.

5.2.4. *Area inundated estimates*

The area of Lake Limbra inundated was estimated using Google Earth Pro. The areas of the whole floodplain inundated under various flows within the River Murray were taken from the literature (DEWNR 2006). Areas of the floodplain inundated were only given for specific flows; those most accurately representing the actual flows were used. The area of Lake Limbra was then expressed as a percentage of the total floodplain under inundation.

5.2.5. *Calculation of expected downstream zooplankton abundances*

To determine if the observed zooplankton abundance at the downstream site could be attributed to the combination of the Chowilla Creek and upstream abundances, the expected downstream abundance, was calculated for each date using Equation 2. If the expected downstream abundance fell within the actual average downstream abundance ± 1 SD the measured differences between the upstream and downstream sites were considered to be due to contributions from the floodplain.

Equation 2:

$$Expected\ C_{(DS)} = \frac{\left(C_{(CC)} \times V_{(CC)}\right) + \left(C_{(US)} \times V_{(US)}\right)}{V_{(CC)} + V_{(US)}}$$

Where,

C = Concentration of zooplankton (i.e. individuals per litre)
V = Daily discharge volume (ML)
DS = Downstream
CC = Chowilla Creek
US = Upstream

5.2.6. *Zooplankton biomass calculations*

Zooplankton biomass was calculated by multiplying the average number of each species per volume by the species dry weight. Dry weight estimates were obtained from the literature for the identified species (Dagne, Herzig *et al.* 2008; Dumont, Velde *et al.*

1975; Masundire 1994; Pauli 1989; Sendacz, Caleffi *et al.* 2006). If estimates were not available for a particular species, a species of similar size and/or genus was used.

Total daily loads of zooplankton biomass were then estimated by multiplying the biomass per volume by daily discharge. The total daily contributions from Lake Limbra and into Chowilla Creek were estimated by calculating the daily load at HC (Figure 5-1). From approximately 9 February until 15 April 2011 water was flowing into Lake Limbra from the eastern side, through the lake and out through Hancock Creek. As the lake was full the assumption was made that the volume entering the lake was equivalent to the outflow volume. Biomass concentrations from CC-1 were used as an estimate of those entering the lake and subtracted from those measured at HC on those days.

Increases in zooplankton biomass within the main channel of the River Murray due to discharge from the Chowilla Floodplain were determined by calculating daily load at RM-2 (Figure 5-1) and subtracting the estimated daily load above the floodplain (hereafter RM-3) (Figure 5-1). The daily load above the floodplain was estimated by assuming that the measured abundance and composition at RM-1 (Figure 5-1) was representative of that above the formation of the floodplain and multiplying by the daily flow into South Australia.

5.2.7. ***Statistical analysis***

To compare differences in species richness and abundance between sites and over time at each confluence repeated-measures analysis of variance (RM-ANOVA) were conducted in IBM SPSS Statistics for Windows (SPSS Released 2010), on the average abundance and average species richness over time for each of the confluences and the three sites within Chowilla Creek. Depending upon the availability of data the RM-ANOVA's analysis was performed on the data from 11 February until and including 6 June at the river-anabranch confluence and from 11 January until and including 5 May at the anabranch-tributary confluence. If the assumption of sphericity was rejected using Mauchly's criterion, the Greenhouse-Geisser corrected alpha values (e.g. Strecker, Cobb *et al.* 2004; Visman, McQueen *et al.* 1994) were used to determine the statistical significance of site and time effects (Scheiner and Gurevitch 2001). If a statistically significant effect of site was revealed and no interaction between site and time a post hoc Tukey's HSD test was conducted.

To test for a correlation between river discharge and species richness, a linear regression analysis was conducted in IBM SPSS Statistics for Windows (SPSS Released 2010) on each site independently and all sites combined after visual inspection of the data.

To determine whether contributions from Chowilla Creek were affecting the species composition within the River Murray a Nonmetric Multidimensional Scaling (Kruskal 1964; Shepard 1962a; Shepard 1962b) ordination was conducted in PC-ORD. This was done on average zooplankton species abundances at the three river-anabranch confluence sites where the distance measure used was Sorensen (Bray-Curtis) (Bray and Curtis 1957).

5.3. Results

5.3.1. *Lake contributions: anabranch-tributary confluence*

Average daily discharge from Hancock Creek fluctuated between approximately 2250 and 3000 ML day^{-1} from early March until early April before steadily decreasing until early May before flow ceased and it became completely desiccated (Figure 5-3).

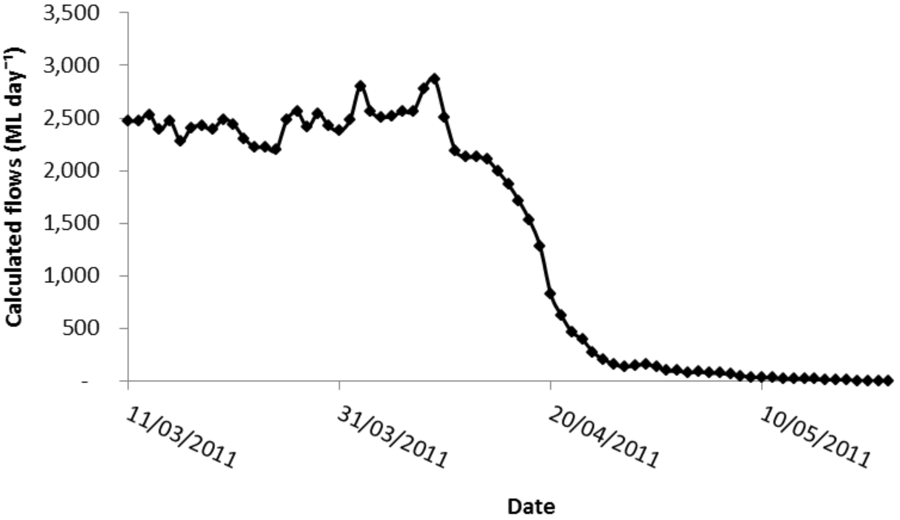


Figure 5-4: Flow in Hancock Creek (ML day^{-1}) from 11 March 2011 until 10 May 2011.

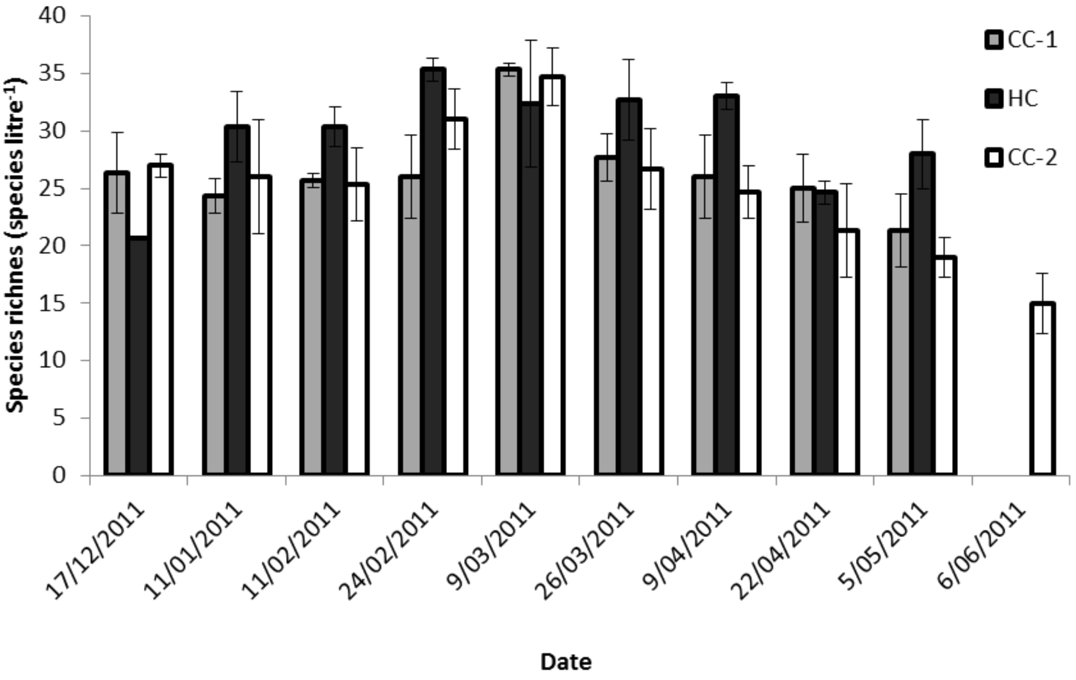


Figure 5-5: Temporal changes in species richness (species litre^{-1}) for the anabranch-tributary confluence. Sites shown are CC-1, CC-2 and HC for each sampling date. Vertical bars represent ± 1 SD.

Species richness (Figure 5-5) was similar at all sites (CC-1, CC-2, & HC) and showed a general upward trend from the beginning of sampling up until the 9 March 2011 followed by a decline to June 2011 (Figure 5-5, Figure 5-6: P=0.008). Linear regression analysis showed that species richness was significantly positively correlated with discharge at CC-2 (R^2=0.658, P=0.004).

Figure 5-6: RM-ANOVA testing for the effects of site and time on species richness and abundance on the anabranch-tributary confluence sites (CC-1, CC-2 & from December 2010 until May 2011, the Chowilla Creek sites (CC-1, CC-2 & CC-3) from January until May 2011 and the river-anabranch confluence sites (RM-1, RM-2 & CC-3). Greenhouse-Geisser adjusted probabilities were used for the F statistics.

	Source	df	MS	F	P
Anabranch-tributary confluence					
Species richness	Within subjects				
	Time	8	80	7.1	0.008*
	Time*Site	16	24	2.2	0.1
	Error	48	11		
	Between subjects				
	Site	2	69	3.3	0.1

	Error	6	21		
Abundance	Within subjects				
	Time	8	1501546	82.1	< 0.001*
	Time*Site	16	367165	20.1	< 0.001*
	Error	48	18293		
	Between subjects				
	Site	2	4006046	271.7	< 0.001*
	Error	6	14742		
River-anabranch confluence					
Species richness	Within subjects				
	Time	7	276	23.38	< 0.001*
	Time*Site	14	15	1.259	0.341
	Error	42	12		
	Between subjects				
	Site	2	41	14.71	0.05*
	Error	6	3		
Abundance	Within subjects				
	Time	7	943228	79.47	< 0.001*
	Time*Site	14	28858	2.43	0.101
	Error	42	11868		
	Between subjects				
	Site	2	272726	65.46	< 0.001*
	Error	6	4182		

*Statistically significant with α of 0.05

The average abundance at CC-1 and CC-2 followed a similar trend through time showing a general decrease until February before a rapid rise and fall in March. Differences between upstream and downstream sites seemed apparent on the 24 February and the 9 March 2011 (Figure 5-7), however post-hoc comparison showed no significant difference (Figure 5-8: P= 0.062). Hancock Creek showed a similar pattern from late February until March however in contrast, abundance was much higher than CC-1 (Figure 5-8: P=<0.001) and CC-2 (Figure 5-8: P=<0.001) and increased from December until February and from late March onwards. Due to the contrasting response of zooplankton abundance at Hancock creek (HC) through time in comparison to the other sites there was a significant interaction between site and time (Figure 5-6: P=<0.001).

Substantial contributions of zooplankton biomass were exported from Lake Limbra during connectivity and ranged between 125 to 914 kg day^{-1}. The highest contributions of 914 kg day^{-1} (Figure 5-10) occurred on 22 April 2011. Over the total sampling period the area of Lake Limbra was between 5 and 11 % of the total area of the floodplain inundated (Figure 5-10).

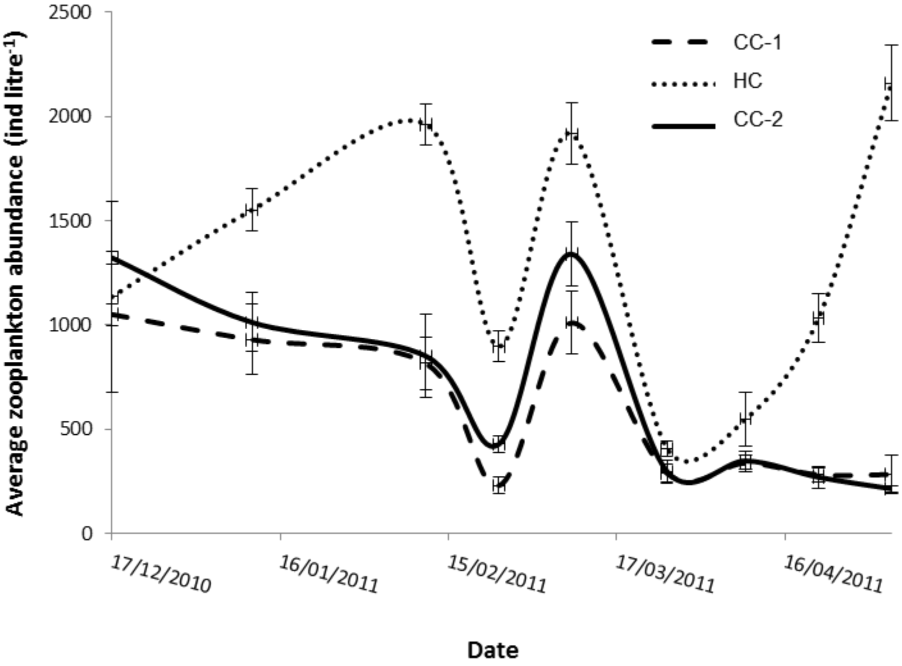


Figure 5-7: Temporal changes in abundance (ind litre^{-1}) for the anabranch-tributary confluence. Sites shown are CC-1, CC-2 and HC for each sampling date. Vertical bars represent ± 1 SD.

Figure 5-8: Post hoc comparisons on zooplankton abundance and species richness using the Tukey HSD test. Sites were compared from January until June 2011.

	Site (I)	Site (J)	Mean Difference (I-J)	Std. Error	Sig. (P)
Anabranch-tributary confluence					
Abundance	CC-1	CC-2	-96	33	0.062
		HC	-710	33	< 0.001*
	CC-2	CC-1	96	33	0.062
		HC	-614	33	< 0.001*
	HC	CC-1	710	33	< 0.001*

		CC-2	614	33	< 0.001*
River-anabranch confluence					
Species richness	CC-3	RM-2	0.583	0.482	.272
		RM-1	2.5	0.482	.002*
	RM-2	CC-3	-0.583	0.482	.272
		RM-1	1.917	0.482	.007*
	RM-1	CC-3	-2.5	0.482	.002*
		RM-2	-1.917	0.482	.007*
Abundance	CC-3	RM-2	98	19	.005*
		RM-1	213	19	.000*
	RM-2	CC-3	-98	19	.005*
		RM-1	115	19	.002*
	RM-1	CC-3	-213	19	.000*
		RM-2	-115	19	.002*

* The mean difference is significant at the 0.05 level.

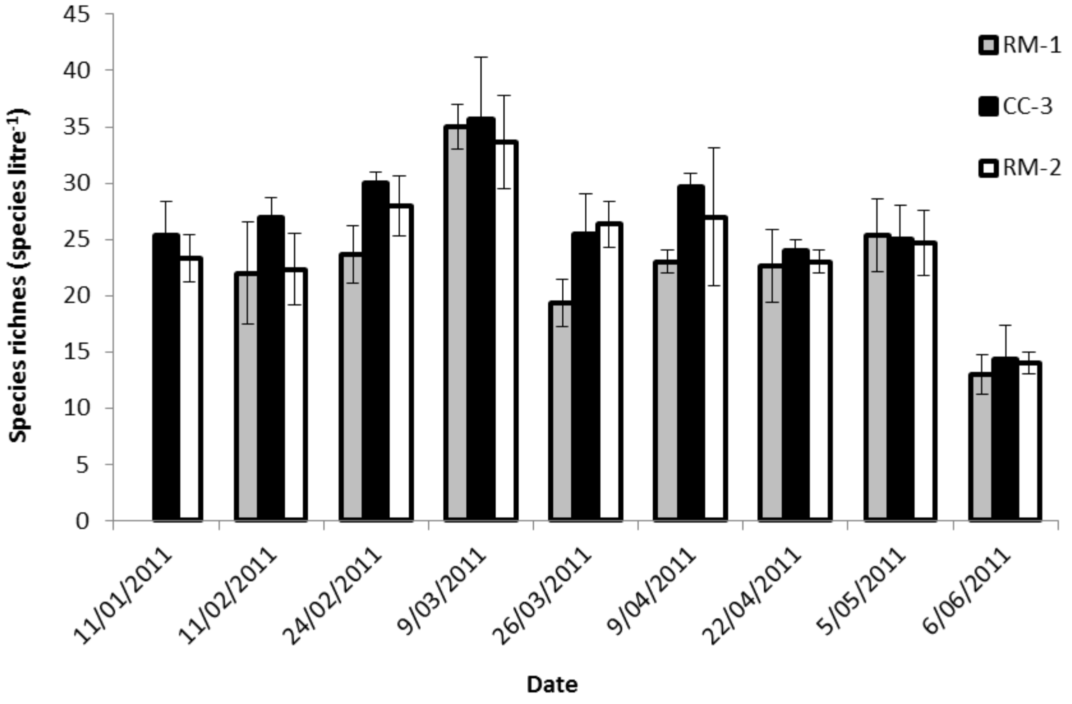


Figure 5-9: Temporal changes in species richness (species litre^{-1}) for the river-anabranch confluence. Sites shown are RM-1, RM-2 and within CC-3 for each sampling date. Vertical bars represent ± 1 SD.

Figure 5-10: Summary of the estimated zooplankton biomass being transferred to Chowilla Creek from Lake Limbra via Hancock Creek in kilograms per day (kg d^{-1}) and the area of the lake as a percentage of total area inundated. Estimates based on average daily flow (ML day^{-1}) and zooplankton biomass concentrations in micrograms per litre (µg l^{-1}). Where In = entering Lake Limbra, Out = exiting Lake Limbra, Out-In = the difference, Lim = Lake Limbra, FP = floodplain and Lim/FP = Limbra as a proportion of the floodplain.

	Flow		Zooplankton biomass			Area Inundated		
	In	Out	In	Out	Out-In	Lim	FP	Lim/FP
	ML day^{-1}	ML day^{-1}	µg l^{-1}	µg l^{-1}	kg day^{-1}	km²	km²	%
9 March	2474	2474	376	704	811	3.2	67	5
26 March	2479	2479	87	138	125	3.2	67	5
9 April	2868	2868	117	297	516	3.2	48	7
22 April	0	466	0	1961	914	3.2	31	10
5 May	0	75	0	4230	316	1.6	14	11

5.3.2. *Floodplain contributions: river-anabranch confluence*

Species richness (Figure 5-9) again showed a general upward trend from the beginning of sampling up until the 9 March 2011 followed by a decline until June 2011. Linear regression analysis showed that species richness was significantly positively correlated with discharge at CC-3 (R^2=0.579, P=0.017). Species richness at all sites combined (including the anabranch-tributary confluence sites) was significantly positively correlated with discharge (R^2=0.375, P<0.005).

Species richness was significantly different between sites (Figure 5-6: P=0.05), often lower at RM-1 than CC-3 (Figure 5-8: P=0.002) and RM-2 (Figure 5-8: P=0.007), however there was no significant difference between CC-3 and RM-2 (Figure 5-8: P=0.3). The most evident dates in which the floodplain was contributing to species richness (increases between RM-1 and RM2) occurred from 24 February up until and including the 9 April 2011 (excluding the 9 March) (Figure 5-9).

There were significant temporal differences in abundance with a general decrease during the study period, but with a rapid increase and subsequent decrease in February-March (Figure 5-12, Figure 5-6: P=<0.001). All sites were significantly different (Figure 5-12: Figure 5-6: P=<0.001) where CC-3 generally had the highest abundances (Figure

5-8: P=0.005 & P=<0.001), RM-1 the lowest (Figure 5-8: P=<0.001 & P=0.002) and RM-2 between CC-3 and RM-1(Figure 5-8: P=0.005 & P=0.002). The most evident dates in which the floodplain was contributing to abundance (increases between RM-1 and RM-2) occurred from 24 February up until and including the 9 April 2011 (excluding the 9 March). The majority of the floodplain was disconnected from Chowilla Creek by approximately 5 May when zooplankton abundance at all three sites converged (Figure 5-12).

The differences in abundance between the upstream and downstream sites were attributed to Chowilla Creek (the floodplain) since the calculated expected downstream zooplankton abundances fell within ± 1 SD (notably within the lower bound of the average ± SD on 26 March, 9 April and the 26 April) on all occasions excluding the 6 June (Figure 5-11). The estimated volume of water lost to evaporation from 17 December 2010 until the 12 May 2011 on the floodplain was 16.7 megalitres.

Whilst there was considerable temporal variation in the zooplankton community composition as indicated by the ordination on all occasions the downstream species composition was positioned between RM-1 and CC-3 (Figure 5-13). On a number of occasions, the downstream composition was more related to that of Chowilla Creek than upstream.

The Chowilla Floodplain contributed a large zooplankton biomass to the River Murray, peaking in February-March (6013 and 6265 kg day-1) (Figure 5-14). Thereafter, the contribution fell as flow receded.

Figure 5-11: Summary of the zooplankton abundances at site six (Average Abundance), the associated standard deviation (SD), the calculated expected (Expected) and whether or not the expected fell within ± 1 SD.

	11 Feb	**24 Feb**	**9 Mar**	**26 Mar**	**9 Apr**	**22 April**	**5 May**	**6 June**
Average abundance	696	330	1026	334	300	226	368	97
SD	83	110	119	50	40	69	14	11
Expected	703	293	1036	291	281	195	364	87
Within ± 1 SD	YES	YES	YES	YES	YES	YES	YES	NO

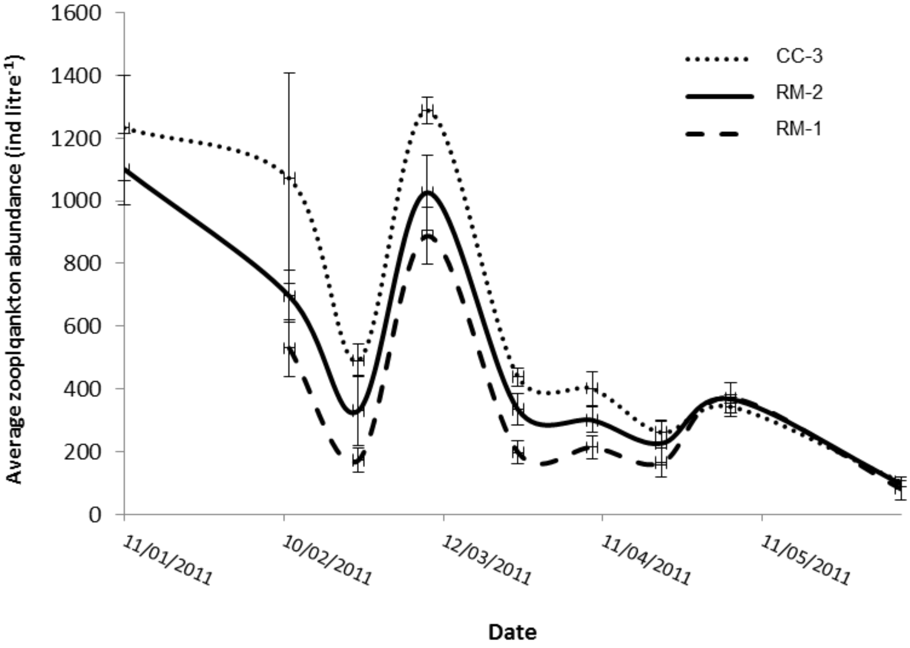


Figure 5-12: Temporal changes in abundance (ind litre^{-1}) for the river-anabranch confluence. Sites shown are CC-3, RM-1 and RM-2 for each sampling date. Vertical bars represent ± 1 SD.

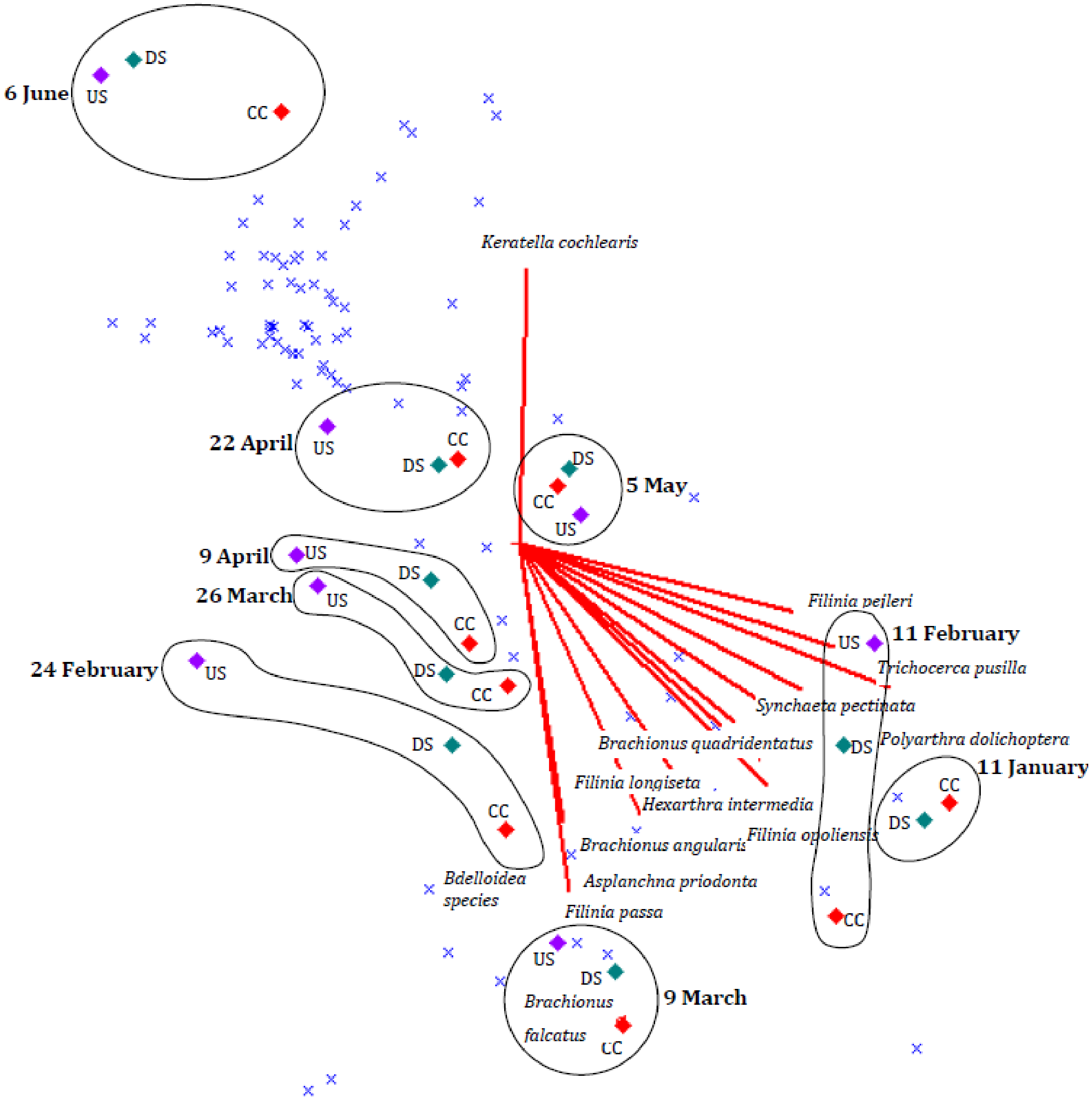


Figure 5-13: A Nonmetric Multidimensional Scaling (NMS) 2 dimensional ordination conducted in PC-ORD on species assemblage (R2 = 4). Characteristic species are written in black and blue crosses represent all species. Purple diamonds represent upstream (US), green downstream (DS) and red Chowilla Creek (CC). Community from the same date are circled with the corresponding date adjacent.

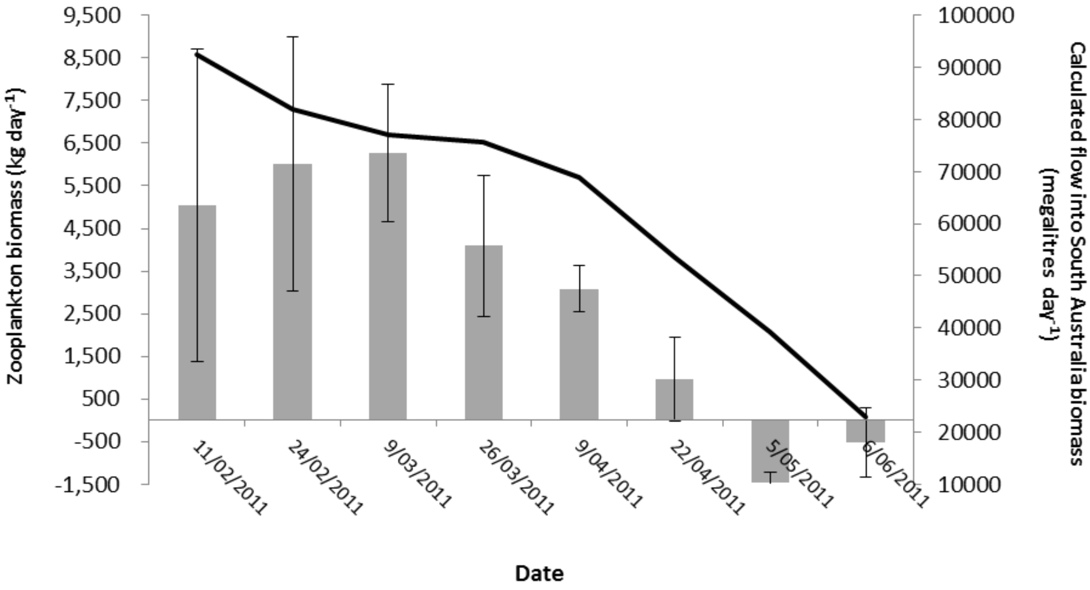


Figure 5-14: The estimated total zooplankton biomass (kg day^{-1}) coming from the Chowilla Floodplain (grey bars). Secondary x-axis shows the calculated flows into South Australia (black line). Vertical bars represent ± 1 SD.

5.4. Discussion

It has become increasingly acknowledged that in channel habitats with low flushing rates and off-channel habitats act as a source of zooplankton for faster flowing environments. Few studies have been able to directly quantify this, however, this study demonstrated that there was significant export of zooplankton from the Chowilla Floodplain, contributing to zooplankton communities within the main river channel. These exports resulted in increased abundances and altered assemblages downstream, with daily contributions of up to approximately six tonnes of resources (zooplankton dry weight) to the riverine food-web per day. This supports the theory suggested by Walker *et al.*, (1995) that during floods in Australian dryland rivers, riverine animal biomass is derived largely from production within the floodplain as described in the FPC (Junk, Bayley *et al.* 1989).

5.4.1. *Floodplain zooplankton communities*

There are a number of factors likely to be contributing to the increases in abundance and changes to the zooplankton assemblages downstream of the Chowilla Floodplain. These include (a) washout of benthic and periphytic species from usually isolated habitats (e.g. Lansac-Tôha, Bonecker *et al.* 2009), (b) emergence from floodplain egg banks (e.g. Boulton and Lloyd 1992) and (c) an increase in available floodplain habitat and food resources, followed by draining of these areas (e.g. Saunders and Lewis 1988a). Early increases could partially have been due to washout, however as sampling began some weeks after initial inundation, the contributions were most likely due to egg bank emergence and reproduction on the floodplain associated with favourable habitat and food availability. Indeed, it has been shown that significant numbers of zooplankton emerge the Chowilla Floodplain egg bank within days after initial inundation (Boulton and Lloyd 1992). Considerable export of zooplankton from the floodplain to the river during late March and early April occurred as flow subsided and large areas of the floodplain drained back into the river channel.

5.4.2. *Floodplain lakes as an important source of zooplankton*

Habitats across the Chowilla Floodplain vary significantly in morphology (Mackay and Eastburn 1990; Shiel, Green *et al.* 1998) as well as in their position along gradients in groundwater influences, inundation history, soil type, vegetation abundance and composition, salinity and elevation. Due to shallow groundwater (Jolly, Walker *et al.* 1993; Overton and Doody 2008) and higher elevation, Lake Limbra is commonly one of the more saline and less frequently flooded habitats on the floodplain. Despite higher flooding frequencies being shown to increase the abundance of organisms emerging from egg banks (Boulton and Lloyd 1992), substantial contributions of zooplankton biomass were detected originating from Lake Limbra. These results highlight the importance of lake habitats, among the many types that exist, as source areas of zooplankton especially when considering that the area of the lake made up only between five and 11 % of the total area of the floodplain inundated.

5.4.3. *Patterns in species richness*

After lake disconnection, species richness decreased within Chowilla Creek below the anabranch-tributary confluence, which may have been due to increased predation and a reduction in the availability of source areas. Increases in predation is expected as spawning in several native fish species, including golden and silver perch, is cued by flow (Humphries, King *et al.* 1999; Mallen-Cooper and Stuart 2003) and juvenile stages of both of these species are known to feed considerably upon zooplankton (e.g. golden perch Culver and Geddes 1993; e.g. silver perchWarburton, Retif *et al.* 1998). The abundance of both these species of fish increased considerably within Chowilla in 2011 compared to 2005-2010 (Zampatti and Leigh 2011).

Species richness across both the floodplain and river showed a significant positive relationship with the flood amplitude. Similar positive correlations between species richness and either connectivity or flood amplitude is evident in a range of different river systems (Missouri River, USA Havel, Eisenbacher *et al.* 2000; Lansac-Tôha, Bonecker *et al.* 2009; Lake Eyre Basin, Australia Shiel, Costelloe *et al.* 2006). These correlations may be due to increasing extent and variability of habitats and exchange amongst them. During this study, species richness was high, generally between 20 and 40 species per litre, compared to approximately 10 to 20 taxa per sample in the upper River Murray from 2006 until 2010 (Ning, Gawne *et al.* 2012), a period characterised by low flow. The absolute species richness, the overall increase in species richness as well as the influence of the floodplain on assemblage within the main river channel highlights the importance of floodplains in structuring riverine zooplankton communities.

5.4.4. ***Riverine zooplankton communities***

The floodplain zooplankton communities contributed significantly to the abundance of zooplankton in the riverine communities, highlighting the importance of hydrological connectivity in facilitating community fluxes across ecotones. In comparison to many river systems, zooplankton abundances observed in this study were high (e.g. 160.6 ind litre-1 in the DanubeReckendorfer, Keckeis *et al.* 1999; 138 ind litre-1 in the Apure Saunders and Lewis 1988b). These measured values are however comparable to those found in other Australian Rivers (Hawkesbury-Nepean River Kobayashi, Shiel *et al.* 1998; Upper River Murray in 2006 and 2007 and Ovens in 2006 Ning, Gawne *et al.* 2012). Similarly, as highlighted by Kobayashi et al., (1998), large regulated temperate rivers in the Northern Hemisphere show similar densities (e.g. maximum densities of 2200 ind litre-1 in the River Rhine De Ruyter Van Steveninck, van Zanten *et al.* 1990). One of the key factors known to control zooplankton abundance within river systems is water residence time and when sufficient (under 0.4 metres second-1 (ms-1) Rzoska 1978), reproduction can occur at rates that allow substantial growth in numbers in both lentic and lotic habitats (Pourriot, Rougier *et al.* 1997; Talling and Rzoska 1967). With water velocity ranging between 0.43 and 0.61 ms^{-1} on average (measurements taken at Lyrup approximately 50 kilometres downstream of ChowillaDEWNR 2012) from December 2010 until May 2011 it is unlikely that significant reproduction occurred within the main river channel during this study. A number of studies have shown that increases in abundance within the river channel correspond to periods of higher flows and floodplain connection (Ning, Gawne *et al.* 2012; Saunders and Lewis 1988a). It is likely that the high zooplankton abundance observed in the main river channel upstream of Chowilla floodplain during higher flows in this study were due to importation from the upstream connected floodplains.

5.4.5. ***Floodplain zooplankton contributions to main river channel habitats***

The importation of zooplankton from floodplains within the upper River Murray has been investigated on a number of previous occasions but the prevailing biogeochemical conditions varied considerably, primarily due high dissolved organic matter input and resulting hypoxia. Ning *et al.,* (2012) observed an increase in abundance of zooplankton in two unregulated tributaries of the River Murray, the Ovens and the Kiewa Rivers, during the 2011 flood period in comparison to 2006-2010, however, no change was observed in the Murray itself. This short-term and/or reduced response within the Murray was attributed to the occurrence of a hypoxic blackwater event (Ning, Gawne *et al.* 2012) which is known to affect zooplankton egg production, hatching success and viability (e.g. Ekau, Auel *et al.* 2010; Invidia, Sei *et al.* 2004; Stalder and Marcus 1997). The dissolved oxygen (DO) concentrations were much lower and hypoxia persisted for longer near the Barmah forest (e.g. Barmah Lake SAWater and MDFRC 2010-11) than occurred closer to Chowilla (e.g. Renmark and Loxton SAWater and MDFRC 2010-11). Despite the lower Murray being less severely affected, these conditions are possibly what reduced zooplankton abundance in early February, as this period coincided with the lowest DO concentrations in this area.

5.4.6. ***Conclusions***

Rivers worldwide are becoming increasingly regulated and flooding extent, frequency and duration of floodplain inundation have been significantly altered, if not completely eliminated. In response, management authorities are now aiming to restore these floodplains that were once vibrant and resourceful habitats e.g. the Amazon (McGrath, Castro *et al.* 1993) and the Danube floodplains (Tockner, Pennetzdorfer *et al.* 1999). A number of studies have demonstrated the importance of floodplains as highly productive areas that export food and nutrient resources to main channel habitats (e.g. POC Hein, Baranyi *et al.* 2003; fish Jardine, Pusey *et al.* 2012; DOC and algae Tockner, Pennetzdorfer *et al.* 1999; DOC and bacteria Wainright, Couch *et al.* 1992). Adding to these, this study has estimated up to six tonnes per day of zooplankton is exported from the Chowilla Floodplain during a large flood period. This suggests that floods of this size and duration have the ability to provide significant quantities of food to main channel habitats. Assuming a 10% transfer of these resources to consumers (Lindeman 1942), this equates to approximately 36 tonnes of zooplankton passed to consumers (eg. fish) during floodplain connection. This is comparable with estimates of fish biomass within the South Australian Lower Lakes and Coorong in 2011-12 including fish species such as golden perch, greenback flounder, pipi and bony bream of approximately 56, 31, 374 and 450 tonnes respectively (Ferguson 2012). Furthermore, this does not consider the feeding that would have occurred within the floodplain during this expansion of floodplain productivity. Therefore it is not only essential to consider the maintenance of vegetation within these habitats but also to reinstate connectivity and flow through environments to facilitate resource and energy exchange.

Chapter 6. The effect of imported and emergent zooplankton communities within a dryland river floodplain on egg-bank diversity

6.1. Introduction

Flow varies over seasonal, annual and inter-annual cycles within rivers of arid or semi-arid climates (hereafter termed ‘dryland rivers’). Primarily flows remain confined within the banks of the main river channel, yet intermittently flood pulses stream across the vast floodplain, driving a surge in productivity. One of the first to colonise and exploit the abundant resources on the floodplain are zooplankton. Many zooplankton species are imported with the floodwaters (Jenkins and Boulton 2003) while others emerge from diapause eggs within the sediment (Boulton and Lloyd 1992). These diapause eggs are produced to bridge periods of unfavourable conditions including physical (e.g., salinity, desiccation) and biological factors (e.g. limited food availability, predation, competition) (Brendonck and De Meester 2003; Green, Jenkins *et al.* 2008). Within ephemeral habitats the majority of hatching occurs within hours to days following inundation due to cues that identify suitable growth and reproduction such as temperature, osmotic potential and oxygen concentrations (Brendonck 1996). Not long after colonisation (i.e. within days to weeks) the active zooplankton community begin to produce diapause eggs, most of which sink to the benthos (Hairston 1996) where they collectively form an ‘egg-bank’. These egg-banks are thought to play an important role in future populations and communities of zooplankton and thus are important for the functioning of aquatic ecosystems.

Embryo dormancy is recognised as an important life history trait, yet its contribution to the active community is not well understood (e.g. Green, Jenkins *et al.* 2008; Hairston 1996). The active community includes all organisms within any life stage excluding diapause. Within ephemeral floodplains only a fraction of the organisms within the egg-bank emerge and combine with those imported with the floodwaters (hereafter termed the ‘imported community’). This fraction is the ‘active egg-bank’ (as defined by Caceres and Hairston Jr 1998), while the remaining eggs supplement the ‘persistent egg-bank’ (see Brendonck and De Meester 2003). The persistent egg-bank provides an important buffer against periods when the active egg-bank becomes depleted due to factors such as mortality and displacement. Due to this tendency for eggs to accumulate, the egg-bank can store a diverse array of organisms from past floods and those that lack the ability to survive within other environments. For example crustaceans have a longer generation time than smaller zooplankton such as rotifers and therefore they are susceptible to advective loss in short residence habitats such as the main river channel (e.g. Pace, Findlay *et al.* 1992). They also have a competitive advantage in exploiting resources in higher residence habitats such as the floodplain (Obertegger, Flaim *et al.* 2007) and consequently are likely to be more highly represented within floodplain egg-banks than within the communities imported with the floodwaters. The mixing of emergent and imported species determines the structure of the early pelagic community. The succession that follows depends upon which species are best adapted to the physical and chemical environment in which they are in (Gyllström, Lakowitz *et al.* 2008).

Despite the ecological significance of zooplankton communities and the assumed influence of diapause eggs on the active community, few studies have investigated the relationship between them (Evans and Dennehy 2005; Gyllström and Hansson 2004; Vandekerkhove, Declerck *et al.* 2005b). This study investigates the effect of a single flood event that followed an extended drought period on the active egg-bank and active community within two floodplain lakes. For the purpose of this study the term ‘pre-flood egg-bank’ refers to the egg-bank prior to floodplain inundation and the term ‘post-flood egg-bank’ refers to the egg-bank after floodplain inundation. It is hypothesised that due to the extended drought the pre-flood egg-banks will be of low diversity. Following inundation the active community within each lake will be comprised of both species imported with the floodwaters and those from within the pre-flood egg-bank. Following floodplain desiccation the egg-bank will be comprised of a combination of species from the pre-flood egg-bank and imported species and therefore will be more diverse.

6.2. Sampling sites and procedures

6.2.1. *Study site*

The Chowilla Floodplain (33°57'0.41"S, 140°56'29.64"E) is one of the major floodplains adjoining the River Murray in Australia and covers 17,700 hectares (Figure 6-1). The climate is semi-arid to arid with an annual rainfall of approximately 260 mm (Kearns, Hairston *et al.* 1996). Due to its low rainfall, the floodplain relies on upstream flows from the upper Murray and Darling Rivers, which together once averaged 13,400,000 megalitres year^{-1} (ML year^{-1}) (Maheshwari, Walker *et al.* 1995). Flows have always been highly variable, but recent flows to Chowilla are considerably less than the historical natural flows (Maheshwari, Walker *et al.* 1995; MDBMC 1996) due to the diversion of water primarily for irrigation. An average of 9,801,000 ML year^{-1} of water is now diverted from rivers of the Murray Darling Basin (MDBMC 1996). Small floods (40,000 ML day^{-1}) that once occurred 91 out of every 100 years, now only occur 40 years in 100. Large floods (110,000 ML day^{-1}) that once occurred 27 out of every 100 years, now only occur 5 years in 100 (DEWNR 2006).

For this study, one site within the River Murray was chosen to estimate the species assemblage of imported communities. This site was upstream of the outlet of Chowilla Creek, where water from the Chowilla Floodplain returns back to the River Murray (Figure 6-1). Two ephemeral lakes were chosen to investigate the aims of the study including Lake Littra and Lake Limbra, while one lake, Coppermine Waterhole was sampled opportunistically. Whilst all are categorised as being freshwater, Lake Limbra is commonly the most saline and Coppermine Waterhole is the least saline. Lake Littra is a shallow, ephemeral deflation basin that fills from Salt Creek. The Coppermine Waterhole is a moderately deep lake and fills through an ephemeral creek channel leading from Monomon Creek into the eastern end of the lake (Figure 6-1**:** Monomon Creek). During high flows water spills from the waterhole in the northern end into an extensive lignum shrubland and finally flows back into Chowilla Creek (Figure 6-1**:** Chowilla Creek) through multiple outlets. Lake Limbra is a temporary lake which fills from Chowilla Creek via Hancock Creek (Figure 6-1**:** HC). Due to the extensive drought which resulted in no natural flooding of the lakes environmental water (see General Introduction, page **Error! Bookmark not defined.** for definition) was pumped from permanent creeks into the lakes (hereafter termed ‘watering event’) between 2005 and 2010. The water was retained within the lake using artificial embankments. Lake characteristics and watering event history are summarised in (Table 6-1).

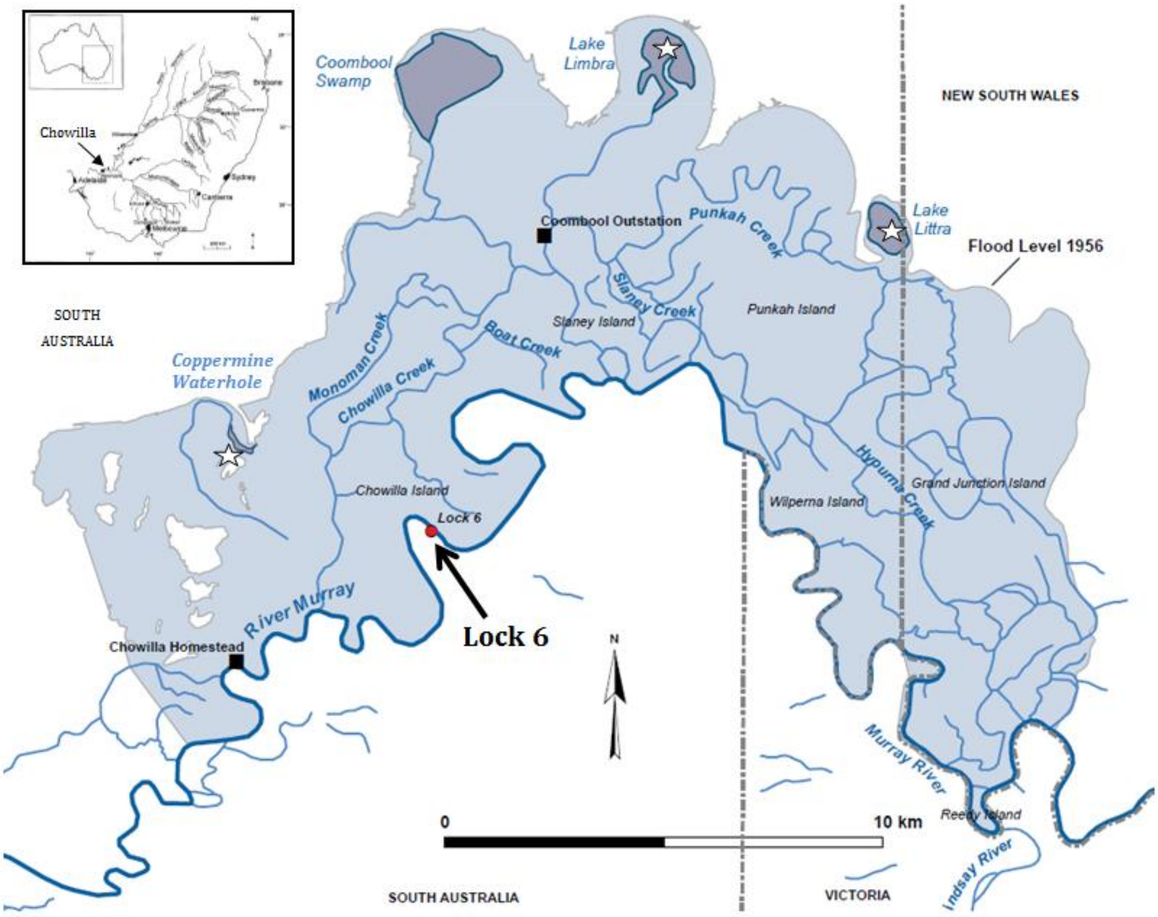


Figure 6-1: The Chowilla Floodplain with study sites (modified from MDBA 2012a). Lake = open star, the main river channel = closed star, Lock 6 = red dot, RM = River Murray and HC = Hancock Creek. Inset: the Murray Darling Basin (modified from http://tinyurl.com/9cj3jxr).

Table 6-1: Summary of lake features. The features include the nominal water capacity (ML); the area inundated (km^2); the approximate maximum depth (m); the calculated flows into South Australia (ML day^{-1}) required to begin filling the lake (Flow to fill); the approximate salinity range (µS cm^{-1}): the previous dates that watering events took place (Watering Events). km^2 = squared kilometres and the approximate length of time between initial watering to complete evaporation and desiccation (months).

Lake	Nominal capacity (ML)	Area inundated (km^2)	Depth* (m)	Flow to fill (ML day^{-1})	Salinity range* (µS cm^{-1})	Watering Events	Length of time from watering to complete evaporation and desiccation* (months)
Lake Littra	1,000	0.86	1	47,000	260- 3240	September 2005 (topped up in December) March 2008 (topped up in May) October 2009	6
Coppermine Waterhole	265	0.11	2	65,000	180 - 840	February 2005 October 2006 November 2008 November 2009	12
Lake Limbra	4,500	3.2	2	45,000	270 - 750	March 2010 (topped up in June 2010)	12

*** Figures are approximate as there is no long term data available and were obtained either via personal communication and values measured during this study (Wallace, Stokes *et al.* 2014).**

6.2.2. *Collection and processing of the active egg-bank*

Sediment samples were collected pre and post the 2010-11 (see page 20, Chapter 1) floods. The sediment core was 2 cm deep and was considered to represent the 'active' egg-bank. Lake Limbra was sampled on the 11 March 2010 (pre flood) and 16 December 2011 (post-flood). Lake Littra was sampled on the 24 September 2010 (pre-flood) and 9 February 2012 (post-flood). Coppermine Waterhole was sampled on the 24 September 2010 only (pre-flood). At the time of pre-flood sampling of Lake Littra and Coppermine Waterhole both lakes held water from previous watering events and sediment was taken from a single spot using a pole with a small shovelling apparatus attached at a water depth of approximately 1 m. At Lake Limbra pre and post flood and Lake Littra post flood, a composite sample was made from between 15 and 20 individual samples of dry sediment.

On return to the laboratory, all sediment samples were oven dried at 50°C, lightly crushed and mixed to homogenise the eggs throughout the sediment. Three 500 millilitre (mL) mesocosms were then filled with 150 grams (g) dry weight of sediment for each site and date and inundated with reverse osmosis water. Mesocosms were then incubated at 21°C and a 12 hour light-dark cycle. Each container was checked every third day for 24 days under a dissecting microscope. All zooplankton were identified to species level where possible, using published descriptions (Koste 1978; Shiel 1995).

6.2.3. *Collection and processing of the active zooplankton community*

Sampling began on 17 December 2010 and continued fortnightly from February 2011 until April 2011 and monthly thereafter until November 2011 (see Table 6-2 for dates each site was sampled). The River Murray was only sampled during the period in which it was connected to the floodplain lakes. Conditions prevented sampling at some sites between the 17 December 2010 and the 22 April due to high river levels and from 6 June 2011 onwards due to desiccation. Sites were sampled during the day within two-days.

Table 6-2: Sampling dates of the active zooplankton community at each site. RM = River Murray. Dashes indicate that the site was sampled on that date. Where H = not sampled due to high water levels and D = did not sampled due to desiccation.

	17/12/201	11/01/2011	11/02/2011	24/02/2011	09/03/2011	26/03/2011	09/04/2011	02/04/2011	05/05/2011	06/06/2011	12/07/2011	10/08/2011	13/09/2011	13/10/2011	18/11/2011
Littra	-	-	-	-	-	-	-	-	-	-	-	-	-	-	D
Coppermine	-	-	-	H	-	H	-	H	H	-	-	-	-	-	-
Limbra	-	-	-	-	-	-	-	-	-	D	D	D	D	D	D
RM		-	-	-	-	-	-	-	-						

Zooplankton samples were collected for quantitative counts using a 14 L Schindler trap. Three replicates were taken approximately 50 metres apart from within the top 1 m of water mid channel of Hancock Creek, Chowilla Creek and the river and five replicates within the top 1 m of each lake. Quantitative samples within the lakes were taken from sites evenly distributed across the waterbody. Samples were concentrated to <10 millilitres (mL) using a 35 µm plankton net and returned to the lab in 50 mL falcon tubes. Samples were inverted three times and a 1 mL sub-sample was transferred into a pyrex gridded Sedgewick-Rafter cell. All zooplankton within each sub-sample were identified using an Olympus compound microscope. All zooplankton were identified to species level where possible, using published descriptions (Koste 1978; Shiel 1995). The number of each zooplankton species were then calculated and expressed as numbers of individual litre^{-1} (ind litre^{-1}).

6.2.4. *Statistical analysis*

A Nonmetric Multidimensional Scaling ordination (NMS) (Kruskal 1964; Shepard 1962a; Shepard 1962b) was conducted in PC-ORD (McCune 2006). It was conducted on species presence and absence data for the active and egg-bank communities for each site. The distance measure used was Sorensen (Bray-Curtis) (Bray and Curtis 1957) and the rank correlation coefficient was set to 3 (see Chapter 13 in McCune, Grace *et al.* 2002). Due to the different methods used to collect egg-bank samples comparisons between samples are not definitive and are to be interpreted cautiously.

6.3. **Results**

Overall, there were 68 species of rotifer, 11 species of cladocera and four species of copepod observed on the Chowilla Floodplain in both the active and diapause communities (Table 6-3). The active communities (Table 6-3: between 79 and 85 species) were far more diverse that both pre and post-flood egg-banks (Table 6-3: between 4 and 14 species). The active communities were comprised of some species within the pre-flood egg-bank however they were primarily comprised of species that were also observed within the River Murray (Table 6-3). This is in agreement with the ordination with active communities strongly associated with imported species (Figure 6-2) suggesting that the active community was imported with the floodwaters. The pre-flood egg-banks within all three lakes were the least closely associated with the imported communities (Figure 6-2) and appear to be partially due to the larger proportion of crustacean species (Table 6-3). The post-flood egg-banks were comprised primarily of imported species (Table 6-3). This influence of the imported communities resulted in the Lake Littra and Lake Limbra post-flood egg-bank displaying greater similarity to the active community than the pre-flood egg-bank (Figure 6-2). The post-flood egg-bank was more diverse than the pre-flood egg-bank in both lakes due to the high diversity of imported and active communities (Table 6-3).

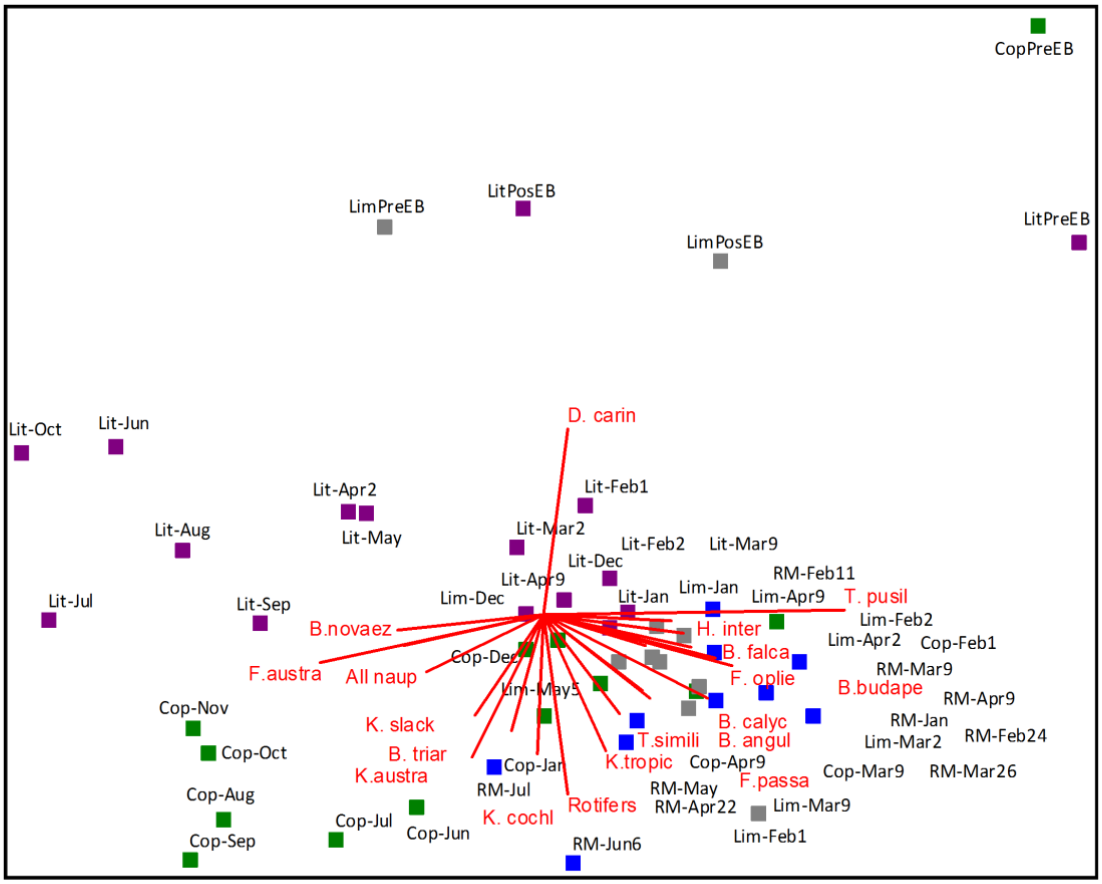
Table 6-3: The presence or absence of species within the active community at all sites and species that emerged from the pre-flood and post-flood egg-bank samples collected from each lake (excluding Coppermine Waterhole post-flood egg-bank). Imported = species imported to the floodplain via the floodwaters, Active = the active community, Pre-flood EB = pre-flood egg-bank, Post-flood EB = post-flood egg-bank and * = species present.

	River Murray	**Lake Littra**			**Lake Limbra**			**Coppermine Waterhole**	
	Imported	**Active**	**Pre-flood EB**	**Post-flood EB**	**Active**	**Pre-flood EB**	**Post-flood EB**	**Active**	**Pre-flood EB**
ROTIFERA									
Rotaria.neptunia	*	*			*			*	
Asplanchna priodonta	*	*		*	*			*	
Asplanchna sieboldi	*	*			*			*	
Asplanchna brightwelli	*	*						*	
Asplanchna asymmetrica		*			*			*	
***Anuraeopsis* species unidentified**	*	*			*			*	
Brachionus angularis	*	*	*		*	*		*	
Brachionus bidentatus testudinarius	*				*			*	
Brachionus budapestinensis	*	*			*		*	*	
Brachionus calyciflorus	*	*			*		*	*	
Brachionus calyciflorus amphiceros	*				*			*	
Brachionus calyciflorus complex	*	*						*	
Brachionus caudatus	*	*			*			*	
Brachionus diversicornis	*	*			*			*	
Brachionus dichotomus	*				*			*	
Brachionus falcatus	*	*			*			*	

Brachionus nilsoni	*	*			*			*	
Brachionus novaezealandia		*						*	
Brachionus quadridentatus	*	*			*		*	*	
Brachionus quadridentatus. quadridentatus	*				*			*	
Brachionus quadridentatus cluniorbicularis	*	*			*			*	
Brachionus lyratus	*	*			*			*	
***Brachionus* species unidentified**	*				*			*	
Brachionus urceolaris	*	*	*		*		*	*	
Keratella.australis	*	*						*	
Keratella cochlearis	*	*			*			*	
Keratella procurva	*	*			*			*	
Keratella slacki	*	*						*	
Keratella tropica	*	*			*		*	*	
Brachionus platyias patulus	*							*	
Platyias.quadricornis	*	*						*	
***Collotheca* species unidentified**	*								
Conochilus dossuarius	*	*			*			*	
***Dicranophoridae* species unidentified**	*	*			*			*	
Epiphanes brachionus* var. *spinosa	*								
Hexarthra intermedia	*	*	*	*	*	*	*	*	
Lecane closterocerca	*				*		*	*	
Lecane bulla	*				*			*	
Lecane flexilis					*			*	
Lecane papuana	*	*			*			*	
Lecane hamate	*				*			*	
Colurella.uncinata bicuspidate	*				*		*	*	
Lepadella patella					*			*	

Lepadella rhomboides	*	*			*				
Lepadella colurella	*				*			*	
Cephalodella **species unidentified**	*								
Cephalodella gibba	*	*			*			*	
Monommata **species unidentified**								*	
Polyarthra dolichoptera	*	*			*	*	*	*	
Synchaeta pectinata	*	*			*			*	
Synchaeta oblonga	*	*			*				
Synchaeta **species unidentified**	*	*			*			*	
Testudinella patina					*			*	
Trichotria.tetractis **var.** ***similis***		*						*	
Trichocerca pusilla	*	*	*	*	*		*	*	*
Trichocerca similis grandis	*	*			*			*	
Filinia australiensis	*	*			*			*	
Filinia grandis	*				*			*	
Filinia longiseta	*	*			*			*	
Filinia opoliensis	*	*			*			*	
Filinia passa	*	*			*			*	
Filinia pejleri	*	*			*			*	
Horaëlla. brehmi		*							
CLADOCERA									
Bosmina meridionalis	*	*		*	*			*	
Chydorus **sp.Unidentifed**	*	*		*	*	*	*	*	
Ceriodaphnia cornuta	*	*			*		*	*	
Ceriodaphnia **species unidentified**	*				*				
Daphnia lumholtzi		*			*			*	
Daphnia carinata		*		*		*	*		*

Daphnia projecta		*		*					*
Moina.micrura	*	*		*	*	*		*	
***Macrothrix* species unidentified**				*		*			
Diaphanosoma excisum		*						*	
Ilyocryptidae timmsii	*	*							
COPEPODA									
***Cyclopoid* species unidentified**	*	*			*			*	
Boeckella.fluvialis	*	*			*			*	
Boeckella. triarticulata					*	*		*	
Calamoecia lucasi	*	*		*	*			*	
All nauplii	*	*		*	*	*	*	*	
% of rotifer species	**86**	**79**	**100**	**30**	**83**	**38**	**71**	**85**	**33**
% of crustacean species	**14**	**21**	**0**	**70**	**17**	**63**	**29**	**15**	**67**
SPECIES TOTALS	**64**	**56**	**4**	**10**	**61**	**8**	**14**	**67**	**3**



[4]Figure 6-2: A Nonmetric Multidimensional Scaling (NMS) ordination of all zooplankton species within the active community across sites and dates and from the pre and post-flood egg-banks. Where RM = River Murray, Lim = Limbra, Lit = Lake Littra, Cop = Coppermine Waterhole, PreEB = pre-flood egg-bank and PosEB = post-flood egg-bank. The first three letters of the month sampled and the day within that month are next to site label.

There were nine species present within the pre-flood egg-bank within Lake Limbra including three rotifer, four cladocera and one calanoid copepod species (Table 6-3). Four of these species (*M. micrura*, *B. triarticulata*, *B. angularis*, and *P. Dolichoptera*), had lower abundances in the River Murray than within the active community during the first three months (Figure 6-3, Figure 6-4 and Figure 6-5), suggesting that the combination of higher reproduction rates and contributions from the egg-bank were increasing their abundance. There were 14 species present within the post-flood egg-bank of Lake Limbra

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which comprised of ten rotifer and three cladocera species as well as copepod nauplii (species unknown) (Table 6-3). This included species that peaked in Lake Limbra early in the study, before populations were reduced to very low numbers or disappeared completely and it is these species that most likely resulted in the post-flood egg-bank falling between the pre-flood egg-bank and the active community (Figure 6-2). These were *C. cornuta, B.meridionalis, M. micrura, B. calyciflorus* and *T. pusilla* (Figure 6-3, Figure 6-4 and Figure 6-5). There were also species that peaked in the months preceding desiccation in May, which was also observed for *Chydorus* species and *B. quadridentatus* (Figure 6-3 and Figure 6-4).

There were four rotifer species present within the pre-flood egg-bank within Lake Littra (Figure 6-4 and Figure 6-5). This included *B. urceolaris*, *B. angularis* and *H. intermedia* which had lower abundances in the River Murray than were present within the active community early during the study (Figure 6-4 and Figure 6-5) suggesting that the combination of higher reproduction rates and contributions from the egg-bank were increasing their abundance. There were 10 species within the post-flood egg-bank of Lake Littra including three rotifer, six cladocera and one copepod species (Table 6-3). This included species that peaked in Lake Littra early in the study, before populations were reduced to very low numbers or disappeared completely (eg. *B. meridionalis, M. micrura, and T. Pusilla*). It is these species that most likely resulted in the post-flood egg-bank falling closer to the active community (Figure 6-2).

There were twelve species present within the active community that were not detected within the imported community, including both cladocera and rotifera species (Figure 6-6). There was also one species that was present within the Lake Littra post-flood egg-bank and Lake Limbra pre-flood egg-bank that was not detected in the imported communities (Figure 6-6). The presence of these species could have been due to limitations associated with the sampling methods or disperal via means other than fluvial.

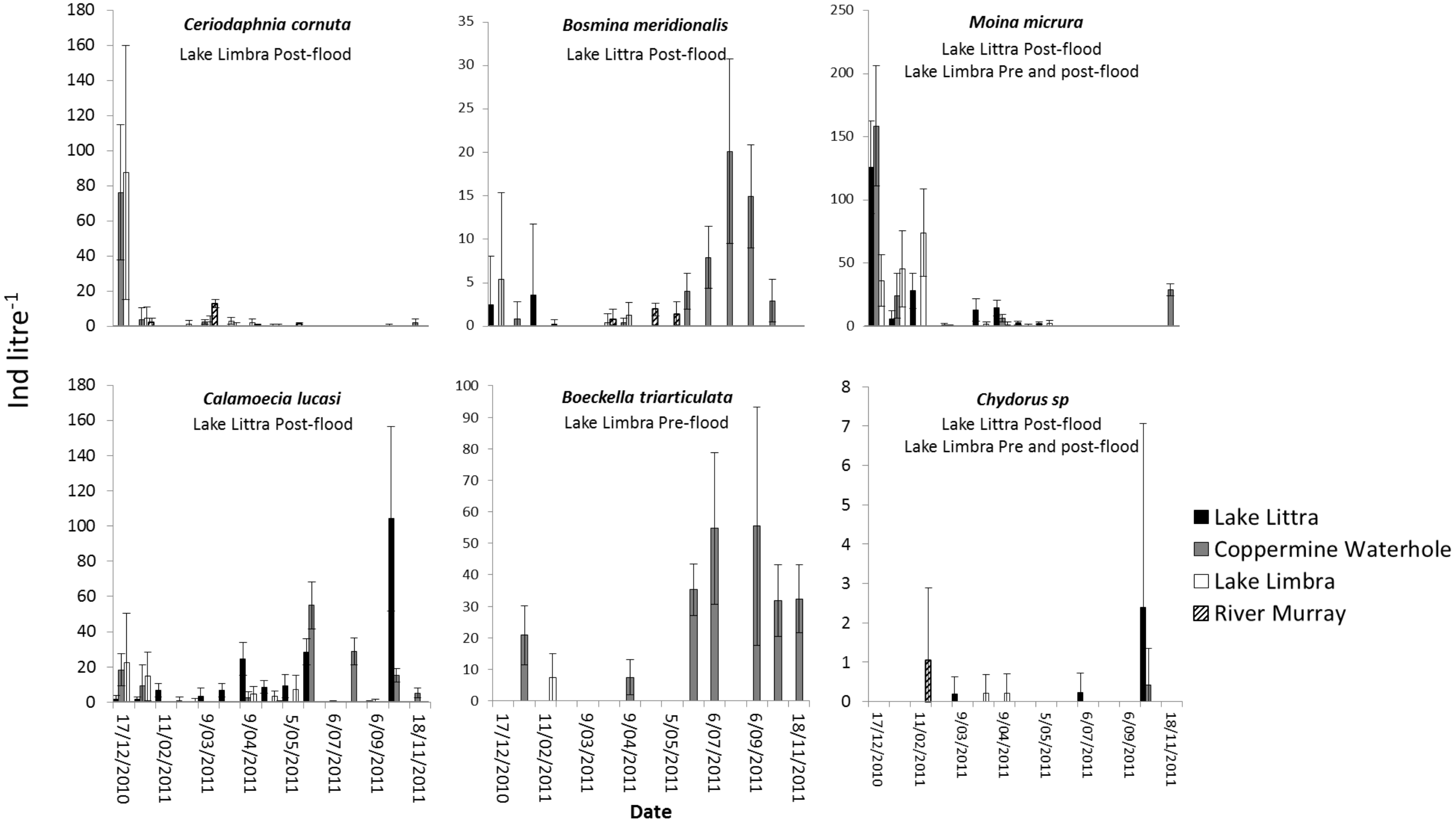

Figure 6-3:Temporal changes in the abundance (ind litre^{-1}) of cladocera and copepod species within the active community that were present within the Lake Littra, Lake Limbra or Coppermine Waterhole pre and/or post-flood egg-banks. The egg-bank and lake in which each species was present in indicated below the species name. Sites shown are Lake Littra, Coppermine Waterhole, Lake Limbra and the River Murray for each sampling date. Vertical bars represent ± 1 SD.

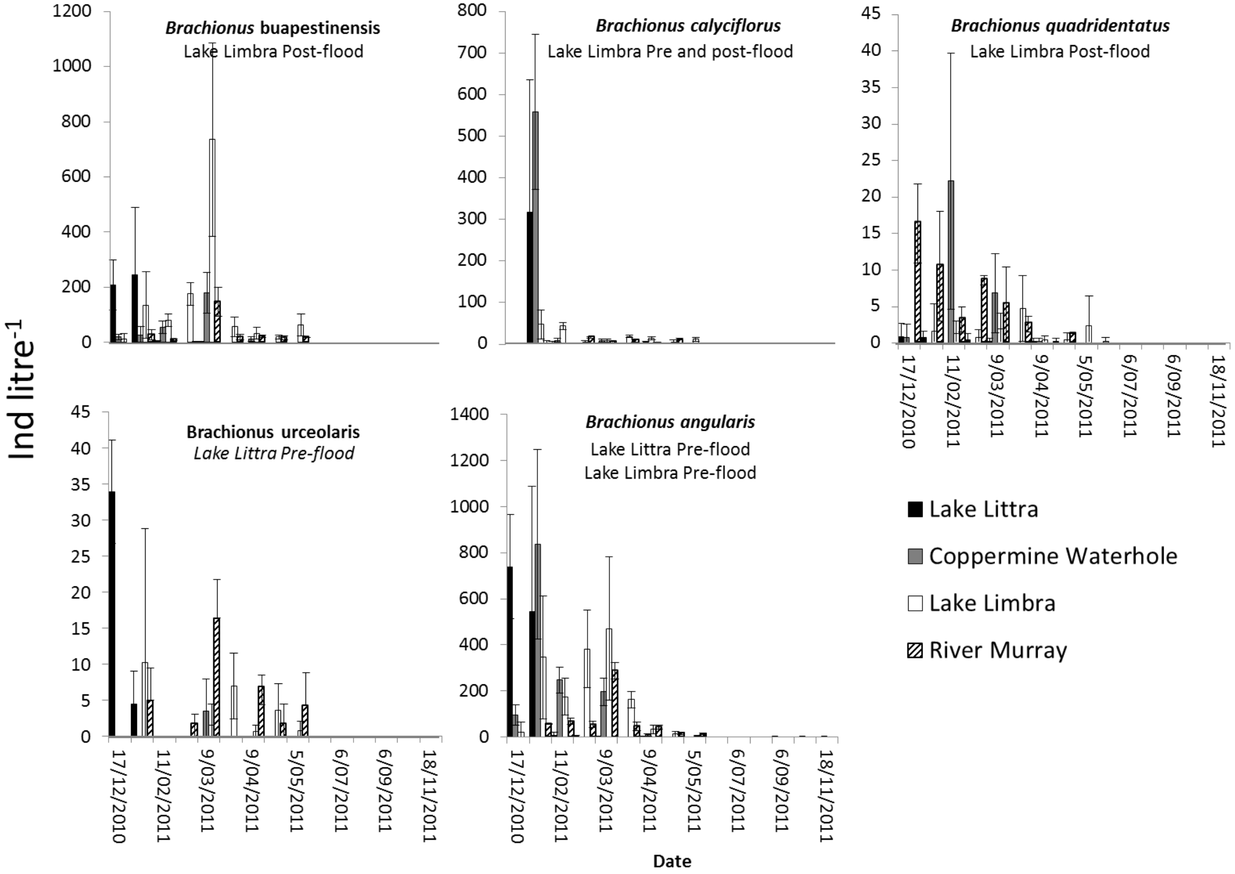

Figure 6-4: Temporal changes in the abundance (ind litre^{-1}) of *Brachionus* species present within the active community that were also present within the Lake Littra, Lake Limbra or Coppermine Waterhole pre and/or post-flood egg-banks. The egg-bank and lake in which each species was present in indicated below the species name. Sites shown are Lake Littra, Coppermine Waterhole, Lake Limbra and the River Murray for each sampling date. Vertical bars represent ± 1 SD.

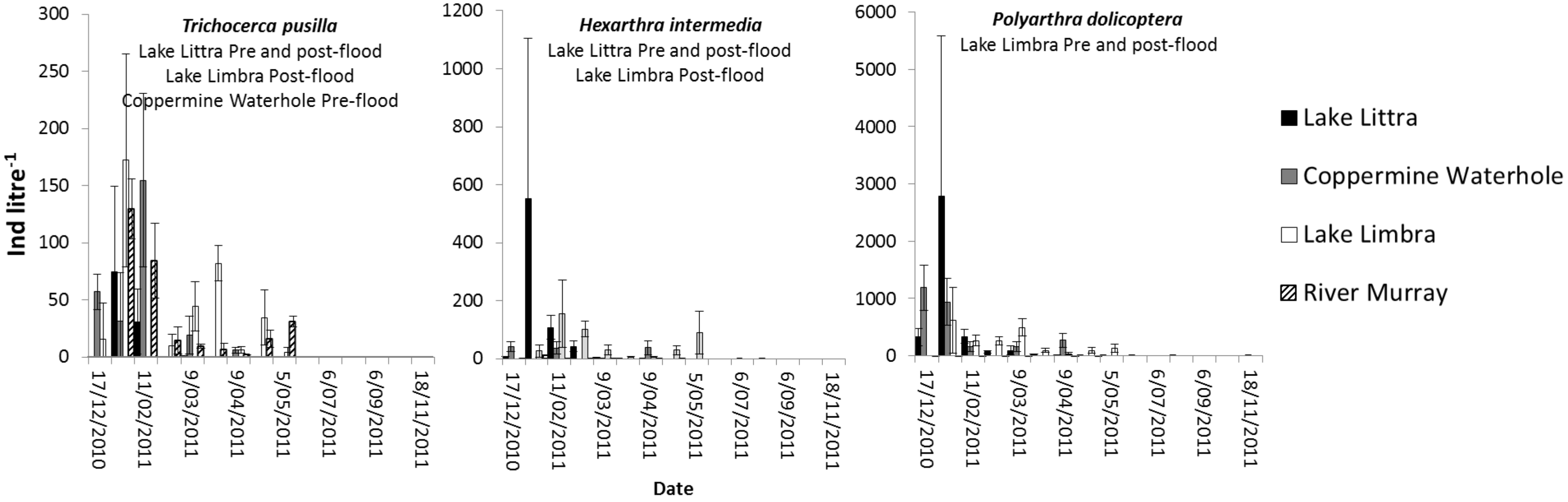

Figure 6-5: Temporal changes in the abundance (ind litre^{-1}) of rotifer species within the active community that were also present within the Lake Littra, Lake Limbra or Coppermine Waterhole pre and/or post-flood egg-banks. The egg-bank and lake in which each species was present in indicated below the species name. Sites shown are Lake Littra, Coppermine Waterhole, Lake Limbra and the River Murray for each sampling date. Vertical bars represent ± 1 SD.

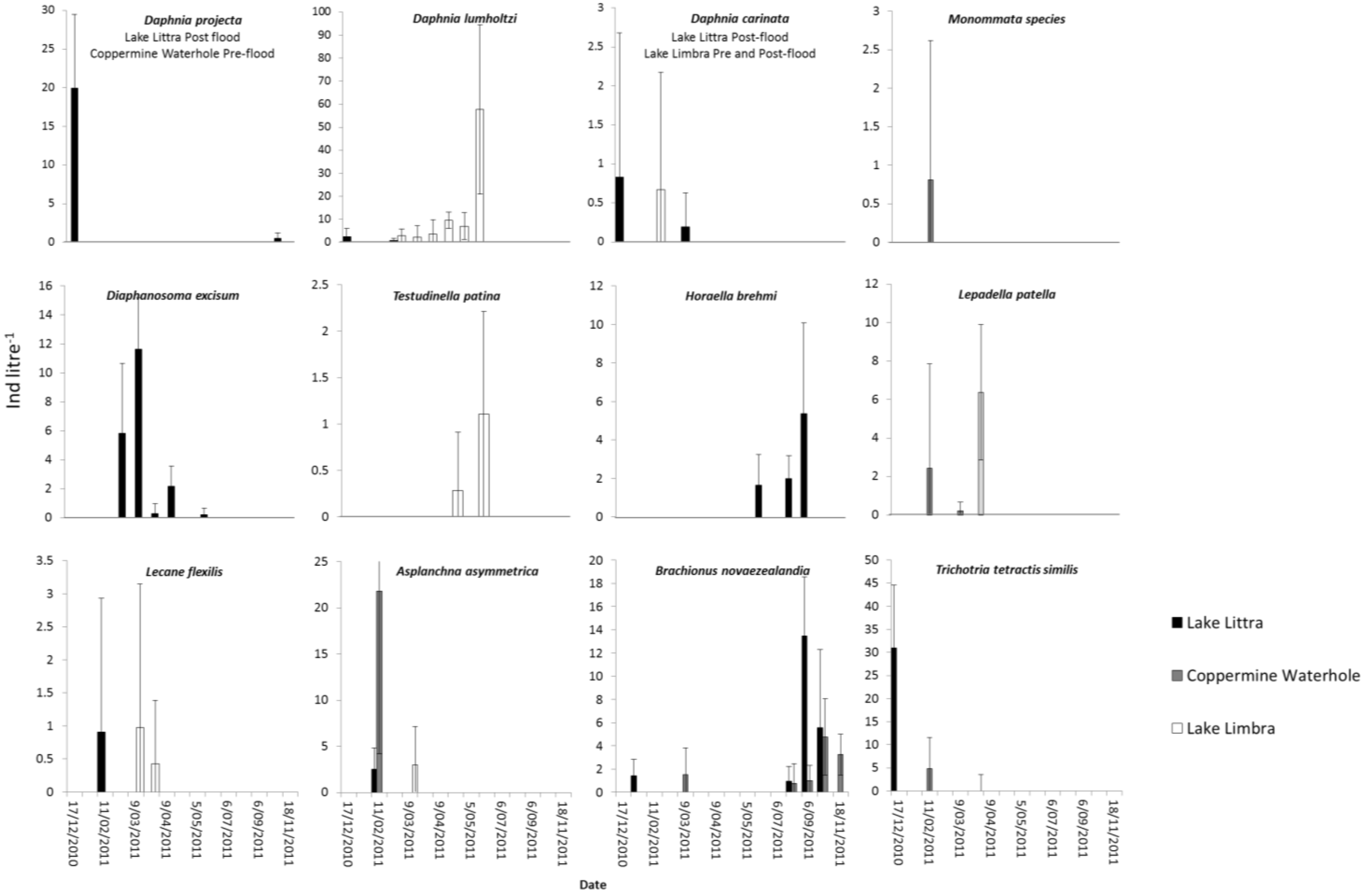

Figure 6-6: Temporal changes in the abundance (ind litre^{-1}) of species present within the active community but absent within the imported community. The egg-bank and lake in which each species was present in indicated below the species name. Sites shown are Lake Littra, Coppermine Waterhole and Lake Limbra for each sampling date. Vertical bars represent ± 1 SD.

6.4. **Discussion**

The active zooplankton community within all three floodplain lakes were comprised of species that were imported within the floodwaters and from the pre-flood egg-bank, as hypothesised, The active communities were comprised of between 56 and 67 species within a lake over the study period. This species diversity was primarily due to the diversity of imported communities, as there were only eight species within the pre-flood egg-banks and of these, all apart from two were also imported. Some species were found within the active community, but not in the imported or egg-bank communities. This may be due to egg dispersal via wind or by birds. It appears that due to the production of diapause eggs by some organisms within the active communities, the post-flood egg-bank within both Lake Littra and Lake Limbra were more diverse that the pre-flood egg-bank.

6.4.1. ***Pre-flood egg-bank***

The low diversity of the egg-bank prior to floodplain inundation could be due to artificial or natural causes. In this study the diversity of the pre-flood egg-bank was low in all three lakes (3-8 species) in comparison to that found in the upper River Murray (e.g. 19-38 species in Havel, Eisenbacher *et al.* 2000; 25 species in Nielsen, Smith *et al.* 2000) yet comparable to some (e.g. 8 species in Baird, Linton *et al.* 1987). Previous studies have demonstrated that reduced frequency of wetting and drying cycles, as well as permanent inundation, reduces emergence from sediments (Boulton and Lloyd 1992; Havel, Eisenbacher *et al.* 2000; MDBA 2012b). The lakes studied here were artificially flooded during the study period, largely for the purposes of improving the condition of long-lived vegetation stressed by an extended drought period. It is possible that it did not increase the number of taxa present within the egg-bank as other studies might suggest. This is because Lake Littra was the most frequently flooded lake (Table 6-1) and yet its egg-bank was the least diverse however this could be due to the different sampling approaches. If not due to the sampling approach it could be due to the failure of artificial flooding to replicate environmental cues associated with natural inundation. Additionally it does not achieve the concurrent connectivity to floodplain habitats upstream; which, then using the river channel as a conduit, seeds more diverse communities to downstream habitats. It has been suggested that this loss in hydrological variability may inhibit the conveyance of cues

(Green, Jenkins *et al.* 2008; Nielsen, Brock *et al.* 2003) or influence sediment disturbance and accumulation processes (BOM 2012; Shiel and Aldridge 2011). Other natural processes including wind-driven weathering or environmental factors on hatching success could also have played a role yet have rarely been investigated (e.g. exposure to salinity Bailey, Duggan *et al.* 2004). Whether due to artificial watering or due to natural causes the low species diversity within the egg-bank resulted in it having little effect on the species diversity within the active communities.

6.4.2. *The active community*

The majority of species within the active communities appeared to be imported from the river channel. Species diversity was high within the River Murray during this study (Chapter 5, page 103) compared to those found in the upper River Murray from 2006 until 2010 (Ning, Gawne *et al.* 2012), a period characterised by low flow. This diversity within the river could have been enhanced due to lateral connectivity and inputs from a range of habitats upstream as adjoining ephemeral communities can often be distinct to the river channel (Shiel, Green *et al.* 1998). Though due to the minimal species contributions from the Chowilla Floodplain egg-bank there was very little distinction between the active communities and the imported communities. The diversity of the active communities were similar or lower in comparison to other floodplain habitats (USA Havel, Eisenbacher *et al.* 2000; Australia Jenkins and Boulton 2003; Brazil Lansac-Tôha, Bonecker *et al.* 2009; Nigeria Okogwu 2010; India Sharma 2005). This highlights the importance of the river channel communities and upstream connectivity in structuring floodplain zooplankton communities within the lower reaches of the river.

6.4.3. *Relationship between the pre-flood egg bank and the active community*

Despite most species coming from the imported communities those that did appear to emerge from the egg-bank increased population abundance on the floodplain. Two cladocera species *D. carinata* and *D. projecta* unique to the floodplain emerged from the pre-flood egg-bank of Coppermine Waterhole. Both of these species were also present in the active community within Lake Littra. There were also a number of species within the active floodplain communities that were not imported or emergent species. The occurrence of these species could have been due to insufficient sampling of the egg bank or imported communities or via dispersal. In addition to via fluvial means the dispersal of diapause egg can also occur via wind or biota (see Geddes and Tanner 2007). Cladocerans are a preferred prey item of planktivorous fish and the ability to reproduce is inhibited within faster flowing water. Thus, their emergence from the floodplain egg-bank into the active community would provide an important food resource not commonly available within the lentic conditions of main channel habitats. Species including *M. micrura* and *P. dolichoptera* in Lake Limbra and *B. urceolaris*, *B. angularis* and *H, intermedia* in Lake Littra were in much higher abundance during the initial few months of inundation in the lakes than what was imported. This was probably in part due to reproduction, however, their presence within the pre-flood egg-bank provides evidence that emergence also contributed to the floodplain zooplankton community.

6.4.4. *The role of floods in maintaining floodplain egg-banks*

It appeared that the flood increased the diversity of zooplankton eggs present in the egg-bank of the Chowilla Floodplain. However, given the number of species within the active community, the increase was only marginal with the Lake Littra egg-bank increasing by six and the Lake Limbra egg bank by seven species. This suggests that eggs were lost due to factors such as displacement, mortality or predation or that a vast majority of the species present within the active community were not able to complete their life-cycle on the floodplain. This minor contribution to the egg-bank by the active community suggests that the conditions created by a flood were only suitable for some species to produce diapause eggs. Yet floods of different kinds may favour different species and therefore flood variability (not just flooding frequency) may be crucial in the development of a highly diverse egg-bank. Regardless, the post-flood egg-bank was still approximately twice as diverse and the pre-flood egg-bank having an important effect on future zooplankton communities.

6.4.5. *Conclusions*

Interactions between external sources of zooplankton and egg-bank populations that determine the composition of both the present and future communities are important for floodplain function. Whilst in this study the active community was largely determined by external sources, it was evident that internal sources also made a contribution.

Furthermore, it also appeared that that the reduced natural flooding frequency and the provision of environmental water via pumping potentially acted to reduce the diversity of the egg-bank and thus its contribution to the active community. The most severe threat to zooplankton communities within the River Murray is most likely the modification to the natural flow regime, which is also the case for other biota (see Bunn and Arthington 2002). The natural flow regime includes the frequency, extent, duration and timing of floodplain inundation and this and other studies have demonstrated that altering these characteristics can affect egg-bank replenishment, eliminate cues for the production and termination of diapause eggs and decrease biodiversity (e.g. Boulton and Lloyd 1992; Nielsen, Smith *et al.* 2000). Through the Murray-Darling Basin Plan (MDBA 2012a), water allocations that were previously used for irrigation are now being returned to the system for environmental purposes. To achieve optimal ecological outcomes it is important that the ecological responses to the different flow regime characteristics are not treated independently, but instead the interaction between the responses must be considered. For example, high flooding frequency of lakes may increase the abundance of diapause eggs however without extensive connectivity throughout the system at the time of delivery, diversity may be compromised. Environmental water should be delivered in a way that promotes the existence and development of floodplain egg-banks. This includes consideration that floodplains upstream provide resources to downstream habitats and regulators could perhaps be used in tandem to enhance environmental flows. Maintaining the health of these communities is important as they play a crucial role in the recovery of the system to disturbances such as drought.

Chapter 7. General conclusion

7.1. Conclusions

Dryland river floodplains have certainly been recognised as having the ability to produce a ‘boom’ in productivity following inundation (Balcombe, Arthington *et al.* 2006; Baldwin 1999; Baldwin and Mitchell 2000; Ballinger, Nally *et al.* 2005; Boulton and Lloyd 1992; Humphries, King *et al.* 1999; Kingsford, Curtin *et al.* 1999; Southwell 2000). Yet it has been suggested that we can increase our understanding of river-floodplain interactions by investigating the balance between processes driving biological transformations and the transportation of matter (Tockner, Malard *et al.* 2000; Walker, Sheldon *et al.* 1995). These processes are strongly linked to the expansion and contraction of the aquatic area on the floodplain, relative to the magnitude and duration of the flood pulse, and its role in creating a dynamic, heterogeneous landscape (Tockner, Malard *et al.* 2000). This thesis investigated some of the key functions, within river-floodplain systems during a large flood.

This study provided evidence that flood pulses drive a succession in physico-chemical factors across floodplain habitats that host unique and highly productive zooplankton communities. The physico-chemical attributes measured, reflect many biotic and abiotic processes such as the biological uptake of nutrients, respiration, photosynthesis and groundwater influences. This includes the influences exerted by the abundant and unique zooplankton communities across the floodplain. Spatio-temporal heterogeneity is crucial as it provides the template for ecological processes, drives fluxes in materials and energy between patches and satisfies a wider range of organisms and life history stages (e.g. Shiel and Tan 2013b). Consequently, spatio-temporal heterogeneity has been attributed to making floodplains one of the most species rich environments in the world (Ward, Tockner *et al.* 1999). This highlights the role that that large floods play in the possible maintenance of whole system biodiversity and the importance of managing these systems in a way maintains physico-chemical heterogeneity.

The inputs from upper reaches seeding the Chowilla Floodplain zooplankton communities has important implications for the utilisation of floodplain resources and future resistance and resilience. The rapid response of these communities to their altered environment facilitated the upsurge of energy. It is fair to assume that a proportion of this energy was transferred to higher order consumers having significant implications for their health, growth and survival (e.g. Shiel and Tan 2013a). The dominant pathway/s in which this energy is transferred throughout the food web is not known and further research into the key pathways between terrestrial organic material, phytoplankton, bacteria, zooplankton through to higher trophic organisms' warrants further research.

Additionally, those species imported from upstream areas played a crucial role in increasing the diversity of what were relatively depauperate egg banks in comparison to other River Murray floodplains (e.g. 31 taxa inNing and Nielsen 2011). The depauperate egg banks highlight the possibility that despite perhaps increasing the abundance of diapause eggs the reduced natural flooding frequency and the provision of environmental water via pumping potentially acted to reduce the diversity of the egg-bank. This is possibly due to a reduction in flow variability which is thought to be an important influence on aquatic biodiversity (Bunn and Arthington 2002). Some studies have highlighted the importance of flow variability, flow frequency and salinity in maintaining egg banks in Australia(e.g. Brock, Nielsen *et al.* 2005; Brock, Nielsen *et al.* 2003; Nielsen, Smith *et al.* 2000; Nielsen, Brock *et al.* 2003; Nielsen, Hillman *et al.* 2002) however still very little is known about the hydrological, climatic and environmental conditions required and further research is needed. This has important consequences for the resistance and resilience of these habitats. Resilience is improved as not all species hatch and germinate at the same time and resistance as the ability to withstand various levels of disturbance can be species specific (e.g. Brock, Nielsen *et al.* 2003). These results unexpectedly highlight the importance of such events in creating flow variability and triggering longitudinal dispersal in zooplankton and the key role that these organisms play in downstream areas.

This study also demonstrated that river-floodplain connectivity plays an important role in the functional role of the floodplain in the broader river landscape. The considerable quantities of nutrients, terrestrial organic material, phytoplankton and zooplankton exported from the floodplain are crucial energy inputs to the system. Nutrients and organic material are important fuels for heterotrophic microbial productivity and primary production, phytoplankton in supporting riverine food-webs (Balcombe, Bunn *et al.* 2005; Bunn, Davies *et al.* 2003; Fellows, Wos *et al.* 2007; Gawne, Merrick *et al.* 2007; Hadwen, Fellows *et al.* 2010; Medeiros and Arthington 2011; Oliver and Lorenz 2013; Oliver and Merrick 2006) and zooplankton as a food resource for higher trophic organisms. Overall, these findings demonstrate that despite the unpredictable nature in which flood pulses occur within dryland systems they exert a major driving force within the system. This highlights the importance of connectivity between river and floodplain habitats to whole system function.

7.2. Management implications

Management authorities around the world are now aiming to restore these floodplains that were once vibrant and resourceful habitats e.g. the Amazon (McGrath, Castro *et al.* 1993) and the Danube floodplains (Tockner, Pennetzdorfer *et al.* 1999). The delivery of flows for environmental purposes is now being implemented (MDBA 2010). In the past, management efforts have often lacked consideration of the natural dynamics of individual systems. However with a better understanding of how these systems function, environmental water can be being delivered with the aim of recovering some of the natural water regime to which the ecosystems are intrinsically linked.

During the drought, environmental water was delivered to floodplain habitats by pumping water from main channel habitats. This water was held within lakes using embankments and left to evaporate. However, to improve the delivery of environmental water, the planning of major environmental structures, including major regulators are now under construction (MDBA 2013). After the construction of these regulators a much broader range of management options will be possible for these areas. Numerous authors have highlighted the significance of hydrological connectivity in sustaining river health and the paucity of our understanding of the processes involved (e.g. Bunn and Arthington 2002; Ward, Tockner *et al.* 2002). Despite the likelihood of significant ecological outcomes for those species that respond to inundation different degrees of hydrological connectivity can be achieved with these regulators and therefore there is a need to understand the processes that rely on flow.

The findings discussed above enhance our broader and integrative understanding of the natural processes that occur within the system during large scale and magnitude floods within the lowland reaches. This understanding is an essential perquisite to viable ecosystem management. This study has highlighted a number of key factors that need to be considered when managing regulators. This includes:

(1) The inundation of a range of habitat types to promote physico-chemical diversity with the aim of satisfying a wider range of organisms and life history stages and therefore promoting high biodiversity.

(2) The generation of high lateral connectivity between the river and the floodplain promoting the exchange and mixing of resources between habitats fuelling both the riverine and floodplain food-webs.

(3) The use of regulators and environmental flows in tandem. This could include the use of multiple floodplains using the same environmental water to ensure that resources and propagules exiting upstream floodplains are delivered to downstream floodplains using the main river channel as a conduit. This is especially important following periods such as drought as egg banks degrade during these periods, decreasing the resistance and resilience of these environments.

Flows within these systems vary in scale both spatially and temporally. There are large flood such as that in this study which are low in frequency and cover large areas of floodplain (Leigh, Sheldon *et al.* 2010). This study and others have demonstrated that these floods play an important role in resetting the environment to earlier successional stages (Pettit, Froend *et al.* 2001; Stanley, Fisher *et al.* 1997), stimulating ecological processes (Fisher, Gray *et al.* 1982), connecting habitats (Chapter 3), transferring resources between floodplain and main channel environments (Chapter 4 and Chapter 5) and dispersing microfauna (Chapter 6). The smaller and more frequent floods however and are important for other biological and biogeochemical functions such as creating variability in the successional stages across floodplains (Robinson, Tockner *et al.* 2002). Other aspects such as the duration, timing and frequency of inundation also play a crucial role in floodplain production and community maintenance (Leigh, Sheldon *et al.* 2010), limiting or permitting the completion of breeding cycles (King, Humphries *et al.* 2003) and determining the magnitude of biological responses (Boulton and Lloyd 1992). To complicate thing further there aseasonal climatic factors such as the El Nin̄o Southern Oscillation which also need to be considered (Leigh, Sheldon *et al.* 2010). Possibly one of the biggest challenges when it comes to managing these systems is in understanding how these different flooding characteristics interact and then to use this knowledge to restore the ecological health of what are now and are likely to remain highly regulated systems.

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Sampling at Lake Littra. Photos taken by Todd Wallace.