SPATIAL HETEROGENEITY AND HYDROLOGICAL CONNECTIVITY IN A DRYLAND, ANABRANCHING FLOODPLAIN RIVER SYSTEM

A thesis submitted for the Doctorate of Philosophy in Applied Science degree of the University of Canberra.

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January 2007
‘Science is made up of so many things that appear obvious after they are explained.’

_Dune_, by Frank Herbert, 1965
ACKNOWLEDGEMENTS

Funding for this research was supported by a Land and Water Australia PhD Scholarship. Additional operational funding support was contributed by the Co-operative Research Centre for Freshwater Ecology. The Murray-Darling Freshwater Research Centre’s Northern Laboratory hosted the fieldwork component from Goondiwindi, and Jon Olley of CSIRO (Division of Land and Water) generously facilitated the stable isotope analyses. My employer, CSIRO Sustainable Ecosystems, allowed me flexibility in work hours and tasks to assist completion of the write-up.

My supervisor Martin Thoms - thankyou for introducing me to such interesting people; giving me opportunities to travel and put faces to names; encouraging scientific structure in my writing; and helping to organise funding and field and laboratory assistance.

Special thanks to Mark Southwell – for your time, expertise, and alternative perspectives. You have become a valued and respected colleague, and more importantly, a friend. Also, Fiona Dyer – for your advice, encouragement and patience, and together with Ben Dyer, for being there, backing and believing in me when I needed it the most – special thanks. And finally, Glenn Wilson – for your enduring support, your willingness to help, and your open-door policy at the lab in Goondiwindi, even at the most inconvenient of times, thankyou. And how could I forget Rhonda Wilson’s care for such dirty fieldworkers at short notice – I have fond memories of those caramel dumplings.

This project could not have been successful if it were not for the generosity of all the landowners. In particular, Betsy and David Turner of ‘Macintyre Downs’ truly showed me the meaning of the word ‘hospitality’. Allowing us to stay in beautiful ‘Camp David’ for weeks on end, providing us with assistance and information of any kind, big and small, whenever we asked, inviting us to share meals at their home, giving us free sheep liver (!), and inviting us to their Christmas party, are just a few examples of their exceptional kindness.
My invaluable field and laboratory assistants - Simon Foster, Anne Moore, Ben Broadhurst, Megan McCann, and Kattis Jonson – thankyou for all your help and for trusting and challenging me. Simon (our ex-chef), thankyou in particular for cooking such great meals, being so cheerful, and for supporting me through a particularly difficult and long field trip and its aftermath. Some members of staff of the University were also the saviours of my sanity on several occasions - Adam Scott, Ben Kropp, Mike Palmer-Allen, Frank Krikowa, and Glenn Fisher – your practical and technical expertise and generosity made a huge difference to my experience in running this project.

I appreciate the advice and time for productive scientific discussions given to me at various stages of the project by Fran Sheldon, Bill Maher, Jon Olley, Richard Norris, Ben Gawne, Cathy Francis, Dan Spooner, Darren Baldwin, Gavin Rees, Graeme Esselmont, Jim Thorp, Mike Delong, Rod Oliver, Stuart Bunn, and Terry Hillman. Past and present members of the University of Canberra River and Floodplain Group, with whom I have shared time in the office and the cafe – thanks for your companionship and for listening, especially Neil Sims, Vic Hughes, Craig Boys, Rob Cossart, Louisa Oswald, Melissa Parsons, John Foster, Evan Harrison, and Munique Webb.

For all their support and encouragement, as well as infinite patience, I am indebted to my colleagues, Deb O’Connell, Sonia Graham, Kate Harle, Trish Hill, Sarah Bruce, David Freudenberger, Sue Briggs and Paul Ryan. Their consideration and forbearance, with someone they hardly knew, under exceptional circumstances, are among the major reasons that I have been able to complete this marathon.

As for my long-suffering friends – I hope that soon I may have the energy and time to devote to you that you deserve. I am especially grateful to Alison, Louisa, Nerida, Jenni, Margot, Glenn, Cass, Nate, Rachel, Claire, Anne, Susanne, Jad, Cathy and Chris.

Finally, to my family, Elly, Peter, Mark, and David - thanks for believing that I would finish, and for loving me through everything.

Heather McGinness
ABSTRACT

Riverine landscapes are complex. More than just a single channel, they comprise a shifting mosaic of hydrogeomorphic patches with varying physical and biological characteristics. These patches are connected by water during flows of varying magnitude and frequency, at a range of spatial and temporal scales. Combined, landscape complexity and hydrological connectivity create biological diversity that in turn maintains the productivity, ecological function, and resilience of these systems. This thesis investigates the ecological importance of spatial heterogeneity and temporal hydrological connectivity in a dryland floodplain river landscape. It focuses on anabranch channels, and uses major carbon sources in these and adjacent landscape patches as indicators of ecological pattern and process.

A conceptual model was proposed, describing the potential effects upon the distribution and availability of major carbon sources of: a) a spatial mosaic of hydrogeomorphic patches in the landscape (e.g. anabanches, river channel, and wider floodplain); and b) four primary temporal phases of hydrological connection during flow pulses (disconnection, partial connection, complete connection, and draining). This was then tested by data collected over a three year period from a 16 km reach of the lower Macintyre River (NSW/QLD Australia). Results were examined at multiple spatial scales (patch scale – river channel vs. anabanches vs. floodplain; between individual anabanches; and within anabanches – entry, middle and exit sites).

The data indicate that spatial heterogeneity in the lower Macintyre River landscape significantly influences ecological pattern. Carbon quantity was greater in anabranch channels compared to adjacent river channel patches, but not compared to the floodplain; while carbon quality was greater in anabranch channels compared to both adjacent river channel and floodplain patches. Stable isotope analysis indicated that carbon sources that were predominantly found in anabranch channels supported both anabranch and river organisms during a winter disconnection phase. Other carbon sources found in the main
river channel and the wider floodplain appeared to play a comparatively minimal role in the food web.

Different phases of hydrological connection between anabranch channels and the main river channel were associated with differences in the availability of carbon sources. In the river channel, draining of water from anabranes (the draining phase) was associated with relatively high concentrations of dissolved organic carbon (DOC) and low concentrations of phytoplankton. Conversely, the disconnection phase was associated with relatively low concentrations of DOC and high concentrations of phytoplankton in the river channel. In anabranch channels and their waterbodies, the disconnection and draining phases were associated with high concentrations of both DOC and phytoplankton. Concentrations of these carbon sources were lowest in anabranes during the partial and complete connection phases.

Different hydrological connection phases were also associated with changes in trophic status in the aquatic components of the landscape. On the riverbanks, relatively low rates of benthic production and respiration during the complete connection phase were associated with heterotrophy. The remaining phases appeared to be autotrophic. Benthic production on riverbanks was greatest during the disconnection phase, and respiration was greatest during the partial connection phase. In the anabranch channels, rates of production and respiration were similar during the disconnection phase, and were associated with heterotrophy in the anabranch waterbodies. The remaining phases appeared to be autotrophic. Respiration was greatest in anabranes during the disconnection phase, and production was greatest during the draining phase. Both production and respiration were lowest during complete connection. These differences and changes varied according to the landscape patch examined.

At a landscape scale, anabranch channels act as both sinks and suppliers of carbon. High rates of sediment deposition facilitate their role as sinks for sediment-associated carbon and other particulate, refractory carbon sources. Simultaneously, anabranch channels supply aquatic carbon sources from their waterbodies, as well as via processes such as
inundation-stimulated release of DOC from surface sediments. Modelled data indicated that water resource development reduces the frequency and duration of connection between anabranch channels and the main river channel. This loss of landscape complexity via loss of connectivity with anabranches has the potential to reduce the total availability of carbon sources to the ecosystem, as demonstrated by a modelled 13% reduction in potential dissolved organic carbon release from anabranch sediments.

This thesis has demonstrated the importance of spatial heterogeneity in riverine landscapes, by documenting its association with variability in the distribution and quality of primary energy sources for the ecosystem. It has shown that this variability is augmented by different phases of hydrological connectivity over time. Spatial heterogeneity and hydrological connectivity interact to increase the diversity and availability of ecological energy sources across the riverine landscape, at multiple spatial and temporal scales. This has positive implications for the resilience and sustainability of the system. Anabranch channels are particularly important facilitators of these effects in this dryland floodplain river system. Anabranch channels are ‘intermediate’ in terms of spatial placement, temporal hydrological connection, and availability of carbon sources; of high value in terms of high-quality carbon sources; and relatively easy to target for management because of their defined commence-to-flow levels. Further research should be directed toward evaluating other ecological roles of anabranch channels in dryland rivers, thereby providing a more complete understanding of the importance of connectivity between these features and other patches. This knowledge would assist management of floodplain river landscapes at larger regional scales, including amelioration of the effects of water resource development.
CHAPTER SIX: HYDROLOGICAL CONNECTIVITY AND MAJOR CARBON SOURCES IN A DRYLAND, ANABRANCHING RIVER LANDSCAPE

6.1 INTRODUCTION

6.2 METHOD

6.2.1 Study design

6.2.2 Measurement of aquatic carbon sources

6.2.3 Sediment and carbon deposition

6.2.4 Laboratory flood-simulation experiment

6.2.5 Data analysis

6.3 RESULTS

6.3.1 Hydrological connection phases and aquatic carbon sources

6.3.2 Sediment and carbon deposition

6.3.3 Laboratory flood-simulation experiment

6.4 DISCUSSION

6.4.1 Anabranches, riverbanks and floodplain

6.4.2 Individual anabranches

6.4.3 Sites

6.5 Summary
6.4 DISCUSSION........................................................................................................234
6.4.1 Hydrological connection phases and the quantity, quality, production and respiration of carbon in the river channel..............................................................238
6.4.2 Hydrological connection phases and the quantity, quality, production and respiration of carbon in the anabranch channels......................................................242
6.4.3 Sediment and carbon deposition....................................................................246
6.4.4 Laboratory flood-simulation experiment.........................................................248
6.5 SUMMARY...........................................................................................................251

CHAPTER SEVEN: STABLE ISOTOPE ANALYSIS – LINKING CARBON SOURCES AND CONSUMERS.................................................................................................254

7.1 INTRODUCTION..................................................................................................254
7.1.1 The method....................................................................................................256
7.1.2 Advantages....................................................................................................257
7.1.3 Assumptions..................................................................................................259
7.1.4 Potential problems.........................................................................................259
7.1.5 Aquatic carbon isotope signatures................................................................262
Dissolved inorganic carbon....................................................................................262
Dissolved organic carbon.......................................................................................263
Suspended particulate organic matter....................................................................264
Algae......................................................................................................................265
Macrophytes..........................................................................................................266
7.1.6 Summary.......................................................................................................267
7.2 WHY USE STABLE CARBON ISOTOPE ANALYSIS FOR THIS STUDY?..............269
7.3 AIMS, HYPOTHESES AND RATIONALE............................................................269
7.4 METHODS........................................................................................................271
Carbon sources – sampling and preparation..........................................................271
Consumers – sampling and preparation.................................................................272
Laboratory procedure.............................................................................................272
7.5 RESULTS..........................................................................................................274
Carbon sources.......................................................................................................274
Consumers.............................................................................................................274
Linking potential food sources and consumers......................................................277
Signature ranges.....................................................................................................279
7.6 DISCUSSION....................................................................................................285
7.7 SUMMARY.......................................................................................................287

CHAPTER EIGHT: FRAGMENTATION BY WATER RESOURCE DEVELOPMENT.........................................................................................................................291

8.1 INTRODUCTION...............................................................................................291
8.2 METHOD..........................................................................................................297
8.2.1 Calculation of anabranch commence to flow discharges.............................297
8.2.2 Modelling flow change................................................................................299
8.2.3 Modelling changes in carbon availability......................................................299
Chapter One: Introduction

1.1 Context ................................................................................................................. 2
1.2 Hypothesis ............................................................................................................. 8
1.3 Approach ............................................................................................................... 8
1.4 Aims ...................................................................................................................... 12
1.5 Objectives ........................................................................................................... 12
1.6 Scope .................................................................................................................... 13
1 CHAPTER ONE: INTRODUCTION

1.1 CONTEXT

Riverine landscapes are complex. They are more than just a single channel – rather, they comprise a shifting mosaic of hydrogeomorphic patches with varying physical and biological characteristics (Pringle et al. 1988; Ward et al. 2002; Thorp et al. 2006). In the natural state, riverine landscapes are connected by water during flows of varying magnitude and frequency, at a range of spatial and temporal scales (Ward et al. 1999; Tockner et al. 2000; Sheldon et al. 2002; Wiens 2002). Combined, landscape complexity and hydrological connectivity create biological diversity, that in turn maintains the productivity, resilience, and ecological function of these systems (Ward and Tockner 2001; Amoros and Bornette 2002; Robinson et al. 2002; Thorp et al. 2006).

Humans rely on riverine ecosystems for fresh water and for food production. However humans have changed landscape complexity and hydrological connectivity in riverine landscapes. Hydrological connectivity between river channels and the remainder of the landscape is often reduced or eliminated by physical barriers such as levees and weirs, and by changes to the magnitude and frequency of flows by dams and abstractions (Thoms and Cullen 1998; Gurnell and Petts 2002; Thoms 2003; Thoms et al. 2005; Kingsford et al. 2006). These changes have implications for biodiversity, productivity, and resilience in riverine ecosystems (Uehlinger 2000; Amoros and Bornette 2002; Woodward and Hildrew 2002; Cardinale et al. 2004). Ultimately, the sustainability of these landscapes, upon which humans rely so heavily, may be at risk. Scientists, river managers, and the community alike have called for research to document the ecological importance of various components of the riverine landscape, and the role of hydrological connectivity between these components in supporting ecosystem function (Bunn et al. 1997; Finlayson et al. 1999; Robertson et al. 1999; Schiemer et al. 1999; Buijse et al. 2002; Gurnell and Petts 2002; Leuven and Poudevigne 2002; Thorp et al. 2006).
Many floodplain river landscapes in their natural state are characterised by the presence of multiple secondary channels (Nanson and Knighton 1996; Buijse et al. 2002; Gurnell and Petts 2002; Ward et al. 2002). Anabranch channels are one of the major types of these secondary channels, and can contribute much of the spatial configuration and complexity observed in a riverine landscape. Anabranches are individual channels that break out from a main or ‘parent’ river channel, flow across the floodplain, and rejoin the main or ‘parent’ channel at a distance downstream (Nanson and Knighton 1996). Their hydrological connection to the main river may range from permanent to intermittent, and they may also be isolated because of human activities (Thoms et al. 2005). Despite their contribution to landscape complexity, the ecological roles of anabranch channels in floodplain river systems have been largely ignored in the past (Gurnell and Petts 2002). This thesis focuses on anabranch channels as a primary spatial component of the floodplain river landscape, using them as an example to examine the importance of landscape heterogeneity and of maintaining the links between a variety of landscape patches via hydrological connectivity.

Anabranch channels are particularly common in low gradient, allogenic, semi-arid floodplain river systems. Until recently (Kingsford 2006), there has been limited scientific understanding of the ecology of these ‘dryland’ systems compared to those in wetter temperate, sub-tropical and tropical environments. Several factors have contributed to this limited understanding, including the large scale, size and complexity of dryland floodplain river systems (Davies et al. 1994; Walker et al. 1995; Puckridge et al. 1998; Puckridge et al. 2000; Thoms and Sheldon 2000; Ward et al. 2002), their hydrological and climatic variability and unpredictability (Davies et al. 1995), limited availability of flow-gauge data (A.S.L. 2000b; 2000a), and their frequent remoteness and associated field logistics issues. The development of landscape ecology as a discipline (Turner et al. 2001), together with new field and laboratory technology and new research and modelling techniques, has recently made the large-scale integrative research required in dryland floodplain river systems more practicable (Ward et al. 2002; Wiens 2002). Yet the study of complex processes in remote and variable floodplain river ecosystems remains a challenge.
Inundation of the floodplain via overbank flows does not occur as frequently in dryland rivers as in temperate streams (Walker et al. 1995). For dryland rivers, within-channel ‘flow pulses’ that occur at shorter time scales than overbank floods may be of particular ecological significance, sustaining populations, favouring primary production, and driving organic matter and nutrient exchanges between larger discharge events (Davies et al. 1994; Thoms and Sheldon 1997; Puckridge et al. 1998; Tockner et al. 2000; Amoros and Bornette 2002). Puckridge et al. (1998) argued that fluctuations in discharge within the main river channel are likely to be at least as significant for the ecology of large rivers as the ‘flood pulses’ which extend overbank. They defined such fluctuations or ‘flow pulses’ as ‘a rise and fall in discharge (or stage) at scales of space and time appropriate to the observer’s frame of reference’. Similarly, Tockner et al. (2000) suggested extending the Flood Pulse Concept (Junk et al. 1989) to take into account within channel flow pulses, because they determine the degree of hydrological connectivity and its ecological consequences.

Flow pulses are conceptually linked to the hydrological ‘expansion/contraction cycles’ described by other authors (Stanley et al. 1997; Tockner et al. 2000; Ward et al. 2002). Ward et al. (2002) stressed that hydrological expansion/contraction cycles over time are intimately related to heterogeneity and connectivity in river landscapes. For example, the Fiume Tagliamento, a Mediterranean river characterised by extensive island-braided reaches, was shown by Ward et al. (2002) to attain its highest landscape-level heterogeneity or physical habitat diversity at intermediate discharge. At higher discharges inundation has a homogenising effect, covering the entire floodplain – an effect that is probably repeated in most complex river systems. Flow pulses have been recognized by a growing number of researchers as having significant consequences for habitat heterogeneity and ecosystem processes (Tockner et al. 2000; Amoros and Bornette 2002; Ward et al. 2002), but few studies have explicitly studied them, particularly in semi-arid systems.
There have been several calls for freshwater ecologists to begin applying an explicit landscape-scale perspective to their work (Pringle et al. 1988; Ward 1998; Thoms and Parsons 2002; Tockner et al. 2002; Ward et al. 2002; Wiens 2002). Concepts derived from studies of terrestrial landscape ecology such as landscape heterogeneity, connectivity and fragmentation (Table 1.1) are particularly pertinent to the study of floodplain river ecosystems. This is because of their physical heterogeneity and the dominant roles of flow and flood pulses in connecting and disconnecting components of the landscape in floodplain river settings (Junk et al. 1989; Heiler et al. 1995; Tockner et al. 2000; Richards et al. 2002; Ward et al. 2002). The main river channel, anabranch or secondary side channels, and the surrounding floodplain may be viewed as ‘patches’ nested within the wider landscape or ‘matrix’ (Table 1.1). The ecological condition of these patches is dependent upon the hydrological connections that facilitate the interactions and exchanges that occur between them (Bayley 1991; Heiler et al. 1995; Tockner et al. 2000; Amoros and Bornette 2002; Hein et al. 2003). In effect, they form a single but complex ecosystem, with each component requiring the other for long-term productivity and survival.

Natural flow variability creates highly variable connections between patches in riverine systems, producing a naturally fragmented landscape over both space and time (Davies et al. 1994; Clausen and Biggs 1998; Puckridge et al. 1998; Harris et al. 2000; Thoms and Sheldon 2000). During flow and flood pulses, hydrological connection between the parent channel and floodplain features is thought to allow the exchange of water, sediment, nutrients and carbon sources (Dunne et al. 1998; Tockner et al. 1999; Amoros and Bornette 2002; Malmqvist 2002; Hein et al. 2003). Intervening dry periods allow production, decomposition and transformation processes to occur within each component, preparing material for exchange during the next connection event (Brinson et al. 1983; Janssen and Walker 1999; Baldwin and Mitchell 2000; Francis and Sheldon 2002). The spatial and temporal characteristics of these connection and fragmentation regimes may significantly affect the quantity and quality of resources available to organisms within the river, the anabranch channels and the floodplain. These characteristics have the potential to strongly influence habitat structure, the food web and ultimately ecosystem function.
Table 1.1 Definitions of terms used in Landscape Ecology (adapted from Turner et al. 2001).

<table>
<thead>
<tr>
<th>Term or concept</th>
<th>Definition</th>
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<tbody>
<tr>
<td>Landscape ecology</td>
<td>The interaction between spatial pattern and ecological process, i.e. the causes and consequences of spatial heterogeneity across a range of scales</td>
</tr>
<tr>
<td>Landscape</td>
<td>An area that is spatially heterogeneous in at least one factor of interest</td>
</tr>
<tr>
<td>Heterogeneity</td>
<td>Quality or state of consisting of dissimilar elements; opposite of homogeneity, in which elements are the same</td>
</tr>
<tr>
<td>Connectivity</td>
<td>Spatial continuity of a habitat, cover type, or movement medium across a landscape</td>
</tr>
<tr>
<td>Fragmentation</td>
<td>Breaking up of a habitat, cover type, or movement medium into smaller, disconnected parcels</td>
</tr>
<tr>
<td>Patch</td>
<td>A surface area that differs from its surroundings in nature or appearance</td>
</tr>
<tr>
<td>Corridor</td>
<td>A relatively narrow strip of a particular type that differs from the areas adjacent on both sides</td>
</tr>
<tr>
<td>Matrix</td>
<td>Background habitat, cover type or movement medium in a landscape, characterised by extensive area and high connectivity; not all landscapes have a definable matrix</td>
</tr>
<tr>
<td>Scale</td>
<td>Spatial or temporal dimension of an object or process, characterised by both grain and extent</td>
</tr>
</tbody>
</table>
Carbon is central to energy flow through the food web in aquatic ecosystems. An important structural component of cells, in conjunction with hydrogen, oxygen, nitrogen and phosphorus, it forms the basis of life (Chameides and Perdue 1997). The spatial distribution and movement of various carbon sources across a riverine landscape reflect the overall pattern of productivity observed in the system over both space and time (Robertson et al. 1999). Carbon sources derived from within aquatic landscape components such as the main river or other waterbodies include dissolved organic carbon, algae (benthic, epiphytic and pelagic), macrophytes, detritus and biofilms. These sources are thought to be generally readily available (labile) or highly palatable to consumers (Bunn and Boon 1993; Thorp and Delong 1994; Wotton 1994; Findlay and Sinsabaugh 1999). Terrestrial carbon sources associated with landscape components such as floodplains include sediment-bound carbon, terrestrial vegetation and associated leaf litter and detritus. These may be less available or palatable (more refractory). Hence the distribution of carbon, in terms of both quantity and quality, may be significantly affected by hydrogeomorphic complexity across the landscape. Together with the connection of various terrestrial and aquatic landscape patches by the movement of water during high flows, hydrogeomorphic heterogeneity has the potential to be a significant control on the availability of carbon as an energy source to the ecosystem. Consequently, carbon availability may be a useful indicator of a) the importance of specific landscape components; b) the effects of hydrological connectivity; and c) the potential effects of human interference. **This thesis investigates the ecological importance of spatial heterogeneity and temporal hydrological connectivity in a dryland floodplain river landscape, focusing on the role of anabranch channels, and using major carbon sources as indicators of ecological pattern and process.**
1.2 **HYPOTHESIS**

The central thesis of this study is that the spatial heterogeneity provided by anabranch channels in riverine landscapes, and the hydrological connectivity between anabranch channels and the parent river channel, play an important and linked role in maintaining the ecological patterns, processes and sustainability of semi-arid, anabranching floodplain river systems. In particular, the presence of anabranch channels, and the different phases of hydrological connection between anabranch channels and the main channel, affect the quality and quantity of major carbon resources available to the ecosystem. Therefore, spatial and temporal changes to hydrological connection phases following water resource development have the potential to change carbon quality and availability, and hence also alter ecosystem function.

1.3 **APPROACH**

A primary goal of science is to generate understanding. *Scientific understanding* implies knowledge of ‘certain patterns in nature, relationships among entities and processes, and causes of the patterns and their differences’ (Pickett *et al.* 1994). The size and complexity of large dryland floodplain river systems demand inter-disciplinary understanding at the interface between hydrology, geomorphology and ecology (Richards *et al.* 2002). However, research of this type has been relatively rare to date (Pickett *et al.* 1999; Thoms and Parsons 2002). The traditional falsification and reductionist approaches to science have also hindered research in these areas, primarily by restricting the ‘methods and modes of test that are legitimately available to scientists in diverse and divergent disciplines’ (Pickett *et al.* 1994). In contrast, contemporary scientific philosophy emphasises the role and potential of theory, and especially the interplay between its elemental conceptual approaches, models, and empirical content (Pickett *et al.* 1994).

This thesis is interdisciplinary, comprising geomorphological, hydrological and ecological methods and analyses. It applies the terrestrially-derived landscape ecology
concepts of connectivity and fragmentation, originally based on the population dynamics of higher organisms, to the spatial and temporal dynamics of a riverine landscape (Figure 1.1). The scientific approach taken in this thesis begins with a conceptual model, built from field observation and the literature, tests that conceptual model in the field, and then according to the results re-evaluates and adjusts the model. In doing so, it minimises reliance on reductionist statistical significance testing and instead searches for understanding of the system and how it functions. This approach may be viewed as a simple adaptation of the ‘information-theoretic’ paradigm advocated by Anderson et al. (2000), which avoids statistical hypothesis testing concepts and focuses on relationships of variables and on the estimation of effect size and measures of its precision.

Traditional reliance on null hypothesis or significance testing has proved inhibitive in ecological and interdisciplinary research (Pickett et al. 1994; Johnson 1999), and there are problems and limitations involved with the significance testing approach (Johnson 1999; Anderson et al. 2000). In particular, researchers often treat scientific hypotheses and statistical null hypotheses as the same thing, when they are not (Johnson 1999; Anderson et al. 2000). Yet in comparison to other disciplines, the ecological sciences have only recently recognised this fact (Anderson et al. 2000). In many cases this has hindered clarity in ecological understanding and stalled interdisciplinary research, with attendant implications for their usage in sustainable management. Modern ecological understanding is achieved through causal explanation, generalisation, and testing, and has two primary components: 1) observable phenomena and 2) conceptual constructs (Pickett et al. 1994).
Figure 1.1 Landscape ecology concepts and their uses in a riverine landscape context such as that employed in this thesis.
In this thesis, the first step toward answering the question of the importance of spatial heterogeneity and hydrological connectivity in a dryland floodplain river landscape was the development of the conceptual model describing how the system would be expected to function (Chapter 3). This model provides a framework within which to conduct the study, and is tested using four avenues of research:

1. Quantifying the distribution of carbon sources across major hydrogeomorphic patches of a semi-arid, anabranching floodplain river landscape (anabranch channels, the parent river channel and the surrounding floodplain)
2. Quantifying the influence of different phases of hydrological connection and fragmentation upon carbon pools in anabranch channels and the parent river channel (‘natural’ fragmentation)
3. Determining the potential value of anabranch carbon sources to consumers in anabranch billabongs and the main river channel (which sources are actually assimilated)
4. Modelling the potential influence of water resource development upon hydrological connection and fragmentation in the system (‘artificial’ fragmentation), and the potential effects of any changes upon carbon pools in anabranch channels and the parent river channel.

Information derived from each of these research avenues enables re-evaluation of the conceptual model to better fit reality. It demonstrates the importance of spatial heterogeneity and temporal hydrological connectivity in a dryland floodplain river landscape, as well as aspects of the potential implications of water resource development for human use, using a combination of field, laboratory and modelled data.
1.4 **AIMS**

This thesis has two broad aims:

1. To determine whether the presence of anabranch channels, and different phases of hydrological connection between anabranch channels and the main channel, affect the quality and quantity of major carbon sources available to a dryland floodplain river ecosystem.
2. To determine the influence of water resource development upon hydrological connectivity between anabranches and the main river channel, and the potential implications of any such influence for the availability of carbon to a dryland floodplain river ecosystem.

1.5 **OBJECTIVES**

Specifically, the objectives of this thesis are:

- To quantify the distribution of major carbon sources across major hydrogeomorphic patches of a semi-arid, anabranching floodplain river landscape (anabranch channels, the parent river channel and the surrounding floodplain).
- To quantify the influence of different phases of hydrological connection and fragmentation upon carbon pools in anabranch channels and the parent river channel (‘natural’ fragmentation).
- To determine which of the major available carbon sources the organisms are assimilating in anabranch waterbodies and the littoral zone of the Macintyre River.
- To model the potential influence of water resource development upon hydrological connectivity between anabranch channels and the main river channel (‘artificial’ fragmentation).
- To model the potential influences of artificial fragmentation upon carbon pools in anabranch channels and the parent river channel.
1.6 **SCOPE**

This thesis explores the influence of hydrogeomorphic heterogeneity and hydrological connectivity upon important landscape patterns (the distribution of sources of carbon) and processes (the potential transfers of carbon sources between patches in a fragmented landscape). The focus is not on ‘carbon’ *per se* – rather, the study is about the role of connectivity in the ecology of floodplain river landscapes, and the influence of water resource development on that role. The fundamental importance of carbon as an energy source for the ecosystem - together with the dependence of carbon dynamics in dryland rivers upon hydrological connectivity - makes carbon a good choice as a broad ‘indicator’ of the influences of hydrological connectivity and fragmentation upon ecological processes in these systems. It is assumed, to a certain extent, that all types of carbon sources are utilised eventually in the ecosystem, while acknowledging that sources actually vary in quality and assimilation. Thus, the study links hydrology, geomorphology and ecology by taking a systems approach rather than detailing specific ecological interactions.
CHAPTER TWO: SPATIAL HETEROGENEITY, HYDROLOGICAL CONNECTIVITY AND ANABRANCH CHANNELS IN SEMI-ARID FLOODPLAIN RIVER SYSTEMS: CONTEXT ................................................................. 15

2.1 RIVERINE LANDSCAPE ECOLOGY ................................................................. 15
2.1.1 Spatial configuration .............................................................................. 15
2.1.2 Hydrological connectivity and fragmentation ......................................... 17
Theoretical approaches to hydrological connectivity ...................................... 17
Effects of hydrological connectivity .............................................................. 22
Phases of hydrological connection ............................................................... 24
Hydrological fragmentation .......................................................................... 26
Knowledge gaps – hydrological connectivity and fragmentation .............. 28

2.2 SEMI-ARID FLOODPLAIN RIVER SYSTEMS .............................................. 30
Unique characteristics ................................................................................. 30
Morphology .................................................................................................. 31
Hydrology .................................................................................................... 32
Ecology ........................................................................................................ 33
Human use ................................................................................................... 34
Knowledge gaps – semi-arid floodplain river systems .................................. 36

2.3 ANABRANCH CHANNELS ........................................................................... 37
Development ................................................................................................ 37
Distribution .................................................................................................. 38
Ecological benefits and characteristics ....................................................... 39
Water resource development ..................................................................... 41
Knowledge gaps – anabranch channels ....................................................... 44

2.4 CARBON IN SEMI-ARID ANABRANCHING FLOODPLAIN RIVER SYSTEMS ........ 46
Carbon sources in semi-arid environments .................................................. 49
Water resource development – ecological impacts ................................... 53

2.5 CONCLUSIONS ....................................................................................... 55
2 CHAPTER TWO: SPATIAL HETEROGENEITY, HYDROLOGICAL CONNECTIVITY AND ANABRANCH CHANNELS IN SEMI-ARID FLOODPLAIN RIVER SYSTEMS: CONTEXT

What are the key aspects of spatial heterogeneity and hydrological connectivity in floodplain river landscapes, and how have they been approached in freshwater ecological theory? How do semi-arid, dryland floodplain river landscapes provide unique context for application of these concepts? What are the characteristics of anabranch channels and carbon sources that may be used to investigate these concepts in riverine landscapes? Does adequate knowledge exist for researchers and managers to understand, model and ameliorate the potential influences of rapid water resource development? This chapter reviews the literature with regard to these issues, highlighting gaps in knowledge and areas addressed by this thesis.

2.1 RIVERINE LANDSCAPE ECOLOGY

2.1.1 Spatial configuration

A riverine landscape consists of a mosaic of spatial patterns and ecological processes (Pringle et al. 1988; Ward et al. 2002). Water drives and connects these patterns and processes, making the mosaic dynamic over both space and time (Wiens 2002). The explicit composition, form and arrangement of the mosaic affects the functioning of the system in ways that would be different if the mosaic were different (Turner et al. 2001). Consequently, obtaining a predictive knowledge of the role of a particular part of the riverine landscape, such as an anabranch channel, requires consideration of its size and position in the broader mosaic.

The spatial configuration of a riverine landscape mosaic is controlled by interactions between climate, geology, geomorphology, hydrology and biology (Poff and Ward 1990; Tockner et al. 2000; Poole 2002; Ward et al. 2002). These are in turn influenced by
human activity (Sheldon et al. 2000; Thoms 2003; Kingsford et al. 2006b). Primary elements forming a hierarchical template for the mosaic are geomorphic features such as the primary river channel and its in-channel features (bars, islands, benches), secondary channels (e.g. anabranche features, side-arms, oxbows), the wider floodplain, ridges, swales, levees, fans, and deltas (Ward et al. 2002). These geomorphic features are overlaid by surface waters (including various waterbodies grading from lentic to lotic, and permanent to ephemeral), and vegetation communities (e.g. riparian forest, wetland, grassland), and underlaid by the ‘fluvial stygoscape’ (alluvial aquifers; Ward et al. 2002).

Elements of a landscape mosaic that differ from their surroundings in nature or appearance are termed ‘patches’ (Turner et al. 2001). Hence all the physical, hydrological, and vegetative features described above may be regarded as patches in a riverine landscape. Their spatial continuity across the landscape defines their spatial ‘connectivity’ (Table 1.1, Chapter 1). Temporal connectivity is also provided by the fluctuating movement of water in riverine landscapes, which promotes the movement and dispersal of sediment, carbon, nutrients, and aquatic plants and animals (Pringle et al. 1988; Bornette et al. 1998; Tockner et al. 1999a; Sheldon et al. 2002; Hein et al. 2003; Hooke 2003). Fragmentation occurs when this spatial continuity or the temporal connectivity provided by water are disrupted. The surrounding terrestrial environment, with air as its medium, may be viewed as the ‘matrix’ or background against which these patches and their connections are highlighted.

The portion of a patch near its perimeter, within which environmental conditions may differ from the interior, is termed the ‘edge’ or the ‘boundary’, and its characteristics can have important effects on ecosystem processes (Turner et al. 2001). For example, for a given area, a circular shape (e.g. a round floodplain waterbody) will have the least edge habitat, whereas a very long narrow shape (e.g. a channel) will have much more, and perhaps only, edge habitat, depending on the width. Because some organisms specialise on edges while others require interior habitats, patch shape has important implications for biotic patterns and processes (Forman and Godron 1981; Bowers and Dooley 1999; Amoros and Bornette 2002). The nature of the matrix and the size, shape, and
arrangement of physical patches across the riverine landscape become particularly important when: a) patches are fragmented over space or time; b) patches are under threat of change; c) edge effects are important components of the process being studied; or d) movement between patches is naturally limited (Turner et al. 2001). All of these situations are common in floodplain river landscapes, and are multiplied by the additional dynamic role of water as a medium for connectivity.

2.1.2 Hydrological connectivity and fragmentation

Theoretical approaches to hydrological connectivity

The spatial and temporal characteristics of the connections between different habitat patches – their ‘connectivity’ – heavily influence patterns of productivity across the landscape (Turner 1989). Connectivity across the landscape in traditional landscape ecology has air as its primary medium, whereas in riverine landscapes water is the primary medium for connectivity. This difference can be more significant than the structural configuration of the landscape itself (Wiens 2002). Hydrological connectivity occurs over four dimensions of riverine systems - longitudinal (upstream-downstream), lateral (river channel-floodplain), vertical (surface-subsurface) and temporal (Ward 1989). Connections in these four dimensions produce a dynamic connectivity regime in both space and time, which in turn influences ecosystem functioning in many complex ways. Consequently hydrological connectivity is a primary determinant of the integrity and sustainability of river-floodplain systems (Heiler et al. 1995; Ward et al. 2002).

Several major models of freshwater ecological function emphasise the importance of connectivity in freshwater ecosystems, although different authors focus on different scales and directions of interaction. The River Continuum Concept (RCC) of Vannote et al. (1980) emphasises the large-scale, longitudinal connections within a river system, from its headwaters to its mouth. The concept proposes that the continuous gradient of physical (geomorphic and hydrologic) variables and conditions within a river system results in consistent patterns of loading, transport, utilisation and storage of organic carbon (food energy) along the length of a river (Vannote et al. 1980). The emphasis on
longitudinal connectivity in the RCC has been controversial, because of the limited recognition given to the role of floodplains as sources of organic carbon (Barmuta and Lake 1982; Lake et al. 1985; Junk et al. 1989). A review of the RCC suggested that the concept was of limited value for predicting large river ecosystem function (Sedell et al. 1989).

The Flood Pulse Concept (FPC) of Junk et al. (1989) stresses the importance of large-scale lateral connectivity and the hydrological exchange of carbon and nutrients between the floodplain and its parent river. The ‘flood pulse’, determined by the frequency, duration, magnitude, rate of rise and fall, and predictability of floods, is recognised as the major link between the river and its floodplain. The FPC suggests that the transport of organic carbon from upstream catchment areas into floodplain areas is of relatively little importance to the overall productivity of river-floodplain systems, and that allochthonous floodplain inputs are essential for productivity of the parent river (Junk et al. 1989).

The FPC has been criticized for its focus upon long, predictable, overbank flood events in large tropical floodplain river systems, and an extension of the concept was proposed by Tockner et al. (2000) in which rivers in temperate zones were examined. These authors highlighted the role of temperature in floodplain river ecology, and emphasised the expanding and contracting nature of temperate floodplain river ecosystems in terms of flow pulses, landscape heterogeneity, ecosystem processes and biodiversity. A ‘flow pulse’ is a rise and fall in discharge, that may or may not be overbank (Puckridge et al. 1998). The ongoing need for empirical data addressing the potentially important role of flow pulses below bankfull has been stressed by Tockner et al. (2000) and other authors (Davies et al. 1994; Thoms and Sheldon 1997; Puckridge et al. 1998; Sheldon et al. 2000; Tockner et al. 2000), together with the suggestion that landscape approaches are the most appropriate for elucidation of related ecological processes and patterns in floodplain river systems (Tockner et al. 2000).

The Riverine Productivity Model (RPM) of Thorp and Delong (1994) was proposed in an attempt to achieve some balance between the views of the RCC and the FPC, and to
account for carbon supply in large rivers without floodplains. The RPM emphasises the importance of lateral connectivity between the river channel and the adjacent riparian zone (especially the supply of organic carbon through litterfall), and the role of autochthonous or in-situ production (Thorp and Delong 1994). Although the RPM was originally restricted to rivers with constricted channels and minimal or no floodplain interactions, a revised version of the RPM (Thorp and Delong 2002) suggested that even in floodplain river systems, autochthonous autotrophic production may be the primary annual energy source, entering food webs via algal-grazer and decomposer pathways.

Most of the above concepts of river functioning were created to describe form and function in relatively ‘natural’ systems. However, many riverine systems have been influenced by flow regulation (Petts 1984), which interrupts connections between patches. The Serial Discontinuity Concept (SDC) of Ward and Stanford (1983) utilised longitudinal gradients (sensu the RCC of Vannote et al., 1980) as a ‘baseline’, from which to make predictions of the effects of impoundments upon biotic and abiotic connectivity, patterns and processes in river systems (Ward and Stanford 1983). The SDC has since been extended to explain floodplain river functioning (Ward and Stanford 1995b). In this model, the importance of lateral connectivity between rivers and their floodplains is stressed, particularly emphasising that interruption to this connectivity (e.g. fragmentation by flow regulation) can have important ramifications for river system functioning (Ward and Stanford 1995b; Ward and Stanford 1995a).

A limitation of all of these concepts is the paucity of conceptual frameworks and data from or regarding river floodplain ecological functioning in arid and semi-arid (dryland) systems. Dryland floodplain river systems are highly variable and unpredictable, with hydrology and ecology fundamentally different to those in other biomes (Davies et al. 1994). The original FPC is based upon tropical systems; while its extension, the RCC, the SDC, and the RPM are based upon relatively humid temperate systems (although they do occasionally mention work from arid areas; c.f. Thorp and Delong, 2002). Researchers in arid and semi-arid systems have discussed these concepts to some extent (Walker et al. 1995; Puckridge et al. 1998; Bunn and Davis 1999; Puckridge et al. 2000;
Sheldon *et al.* 2002; Bunn *et al.* 2003), but questions still remain about their applicability outside of tropical and humid temperate zones.

The Riverine Ecosystem Synthesis (RES) collated by Thorp *et al.* (2006) attempts to contribute to ‘conceptual cohesiveness’ for river ecosystems from all climate zones, by bringing together a selection of earlier perspectives and frameworks, and proposing a series of 14 ‘model tenets’ as hypotheses to guide future research. In particular, it draws on a terrestrial hierarchical patch dynamics model (Wu and Levin 1994; Wu and Loucks 1995; Wu 1999), and some aspects of ecogeomorphology (Thoms and Parsons 2002). The RES views rivers as ‘downstream arrays of large hydrogeomorphic patches formed by catchment geomorphology and flow characteristics’ (Thorp *et al.* 2006, p.126).

Examples of hydrogeomorphic patches quoted include areas with constricted channels, compared to areas with many anabranch channels or slackwater areas, and areas with broad floodplains. Different types of hydrogeomorphic patches differ in physical and chemical conditions, and the RES suggests that they should also differ in productivity, metabolism, carbon dynamics, nutrient spiralling and community composition.

Understanding of these differences begins with identification of the proportional importance and distribution of individual features (such as anabranch channels), within each broad hydrogeomorphic setting. However the authors note that a paucity of research on structurally complex floodplain rivers has resulted in an oversimplification of perceptions of pattern and process in these systems (Thorp *et al.* 2006).

The model tenets proposed by the RES that are potentially most relevant to this thesis state that:

- The most important feature of the environment regulating community composition is a hierarchical habitat template, as determined primarily by interactions between geomorphic habitat features and both short- and long-term flow characteristics
- On an annual basis, authochthonous autotrophy provides, through an algal-grazer food web pathway, the trophic basis for most metazoan productivity for the river network as a whole, but allochthonous organic matter may be more important for some species and seasons and in shallow, heavily canopied headwaters; however, a
collateral and weakly linked decomposer food pathway (the microbial-viral loop) is primarily responsible (with algal respiration in some cases) for a river’s heterotrophic state (P/R <1)

- Algal production is the primary source of organic energy fuelling aquatic metazoan food webs in the floodplains of most riverine landscapes during supra-bankfull floods, especially in rivers with seasonal, warm-weather floods
- Average current velocity and nutrient spiral length are positively correlated with river discharge, but both decrease in functional process zones with extensive lateral components
- Naturally dynamic hydrological patterns are necessary to maintain the evolved biocomplexity in river networks
- Biocomplexity generally peaks at intermediate levels of connectivity between the main channel and lateral aquatic habitats of the riverine landscape, but the relationship varies substantially among types of connectivity, evolutionary adaptation of taxa to flowing water, and functional processes examined

The RES uses the terms ‘riverscape’ and ‘river landscape’ to represent different entities (Thorp et al. 2006). In the RES context, the ‘riverscape’ consists of the main channel and slackwaters (e.g. shorelines, bays, secondary channels, wetlands and backwaters). The ‘riverine landscape’ contains a) the riverscape; b) sub-bankfull inundation areas; and c) supra-bankfull inundation areas. The distinction, if any, between slackwater areas and sub-bankfull inundation areas is not clear, except that slackwater areas are ‘nearly continuously wetted’, whereas sub-bankfull inundation areas are more like the aquatic-terrestrial transition zones of Junk et al. (1989). These concepts were introduced earlier by Tockner et al. (2000), who used the term ‘riverscape’ to refer only to the aquatic components of the landscape. They defined the riverine landscape more broadly as ‘the surface area composed of intersecting terrestrial and aquatic units that are directly influenced by the river’ (Tockner et al. 2000). Wiens (2002) used the term ‘riverscape’ to mean a ‘riverine landscape’, representing the spatial heterogeneity that exists within a river or stream system – although he did not give a specific definition. In this sense, the riverscape may include the wider floodplain and its lakes, ponds or waterholes, secondary
channels such as anabranches and side-arms, the primary river channel, and in-channel features such as benches. This thesis is concerned with the ‘riverine landscape’ as a whole, *sensu* Tockner *et al.* (2000), focusing on the main river channel, intermittently connected anabranch channels and their ephemeral waterbodies, and the adjacent floodplain as major patches.

**Effects of hydrological connectivity**

Water is the key process driver in floodplain river ecosystems. Its presence, absence, origin and physical and chemical characteristics in every dimension determine ecological function and sustainability. The movement of water between rivers, their riparian and hyporheic zones and their floodplains (and associated geomorphic features) is known to directly or indirectly affect many ecologically important patterns and processes (Table 2.1). However the explicit relationships between hydrological connection *per se* and the variables of interest are not generally elaborated – rather, hydrology is vaguely and implicitly assumed to be a major influence. This is partly because the precise effects of hydrological connection are not simple to elucidate, due to major interactions between many processes operating at different spatial and temporal scales. In a paper discussing connectivity and biocomplexity in waterbodies of riverine landscapes, Amoros and Bornette (2002) proposed that the major functions of water are 1) hydrological connection responsible for exchanges between landscape patches; and 2) kinetic energy responsible for fluvial dynamics. They suggest that three kinds of hydrological connection may be distinguished according to the water origin: 1) River water; 2) Groundwater from river infiltration; and 3) Groundwater from hillslope aquifers (Amoros and Bornette 2002).

Various temporal scales in hydrological connectivity dynamics have been described. The Flood Pulse Concept (FPC; Junk *et al.* 1989) drew attention to the frequency, duration, size, timing and rate of rise and fall of ‘flood pulses’ or overbank discharges. Distinctions have been made between the ‘flood pulse’ of the FPC and the concept of a ‘flow pulse’ (a rise and fall in discharge, that may or may not be overbank), ‘flow history’ (the sequence
of flow pulses before any point in time) and the ‘flow regime’ (a long-term, statistical
generalization of the hydrograph) (Walker et al. 1995; Puckridge et al. 1998). Tockner et
al. (2000) emphasised the ecological importance of spatial expansion and contraction of
water across floodplain river systems, especially in terms of below-bankfull changes,
which they also termed ‘flow pulses’.

Table 2.1 Ecological patterns and processes influenced by hydrology

<table>
<thead>
<tr>
<th>Patterns and processes</th>
<th>References</th>
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<tbody>
<tr>
<td>Water chemistry, temperature, depth, and clarity/turbidity</td>
<td>(Tockner et al. 1999b; Amoros and Bornette 2002)</td>
</tr>
<tr>
<td>The sediment and water nutrient status of and exchange between floodplain features and waterbodies</td>
<td>(Brunet and Astin 1997; Tockner et al. 1999a; Amoros and Bornette 2002);</td>
</tr>
<tr>
<td>Organic carbon flow including: allochthonous and autochthonous sources of particulate organic matter; dissolved organic matter concentrations and sources; benthic organic matter production and distribution; and large wood distribution</td>
<td>(Mulholland 1981; Rounick and Winterbourn 1986; Mulholland 1997b; 1997a; Findlay and Sinsabaugh 1999; Tockner et al. 1999a; Gurnell et al. 2002; Wanner et al. 2002; Hein et al. 2003)</td>
</tr>
<tr>
<td>Primary production; including riparian vegetation and planktonic productivity</td>
<td>(Hein et al. 1999; Tockner et al. 1999b; Tabacchi et al. 2000)</td>
</tr>
<tr>
<td>Fauna; including fish reproduction and aquatic invertebrates</td>
<td>(Amoros and Bornette 2002; Malmqvist 2002; Robinson et al. 2002)</td>
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<tr>
<td>Food web links</td>
<td>(Power et al. 1995; Woodward and Hildrew 2002)</td>
</tr>
<tr>
<td>Species diversity</td>
<td>(Tockner et al. 1999b)</td>
</tr>
<tr>
<td>Biocomplexity</td>
<td>(Amoros and Bornette 2002)</td>
</tr>
<tr>
<td>Landscape diversity</td>
<td>(Ward et al. 2002)</td>
</tr>
<tr>
<td>Influences of dams and water diversions on floodplain wetlands</td>
<td>(Kingsford 2000)</td>
</tr>
<tr>
<td>Riverine landscape ecology as a whole</td>
<td>(Wiens 2002)</td>
</tr>
</tbody>
</table>

Amoros and Bornette (2002) identified two primary temporal flow scales: ‘within years’, and ‘decades to centuries’. These temporal frameworks do not explore ‘within flow pulse’ connectivity dynamics and potential effects. Can different phases of connection within a single flow pulse be distinguished? What ecological influence might such phases exert on the river and its floodplain features?
Phases of hydrological connection

Recent work on the Danube River has described three phases of hydrological connection between floodplain waterbodies and the main river channel (Hein et al. 1999; Tockner et al. 1999a; Tockner et al. 1999b; Hein et al. 2003): (I) Disconnection, (II) seepage inflow, and (III) upstream surface connection. The work was conducted in a 10 km reach and focused on a former river channel (the ‘floodplain side channel’) that was cut off artificially from the main river channel at its upstream end over 100 years prior to the study. This side channel was subdivided by weirs into seven semi-isolated water bodies and thus was highly modified. A total of three sampling sites were used, located in the main river, the downstream end of the side channel and in the upper section of the side channel. During disconnection (Phase I), the floodplain side channel was described as ‘stagnant’ with low nutrient levels and low primary productivity. Biotic interactions and processes such as sedimentation of autochthonous material, nutrient uptake and grazing dominated. During seepage inflow, Phase (II), water levels began to rise, there was a subsurface connection to the main channel at the upstream end of the floodplain side channel, and the side channel was fed by nutrient-rich groundwater. These conditions favour phytoplankton development, and during this phase the side channel began to contribute algal biomass and dissolved organic carbon to the main river channel. Primary production was the dominant identifying process during this phase. Periodic overbank flows produced Phase III, upstream surface connection between the main channel and the floodplain side channel. This phase lasted an average of three days and was responsible for the majority of the annual transport of organic matter. The floodplain side channel shifted from autotrophy during Phase II to heterotrophy during and after Phase III. During Phase III, dissolved organic carbon (DOC) concentrations were higher in the floodplain side channel relative to both previous phases and the main river channel. This was explained by the mobilisation of soluble organic matter that accumulated on the floodplain during low water conditions. Similarly, Amoros and Bornette (2002) described short-term phases of hydrological connection between floodplain waterbodies.
in relation to river stages, with emphasis on subsurface connections. These phases were
described in relation to productivity in floodplain waterbodies:

- Phase A - disconnection - low or medium production
- Phase B - high water stage - partial connection - high planktonic production (high
  water transparency and relatively long residence times)
- Phase C - flood - complete connection - scouring and transport

Amoros and Bornette (2002) suggested that ‘pulsing connectivity’ is important not only
for the exchange of nutrients and organic matter, and therefore ecosystem processes at the
landscape scale, but also for the exchange of living organisms between the diverse
patches of the riverine landscape.

Thus, changes in water chemistry and biotic communities can be directly linked to
within-pulse changes in hydrological connection. These changes have been termed
‘phases’ of connection. But what effect do flow pulses have upon floodplain features and
waterbodies that are ephemeral, and have little or no hyporheic connection to the river?
For example, anabranch channels in Australian semi-arid systems are predominantly
disconnected and frequently dry, with little or no hyporheic influence. They contain
relatively small, shallow, disconnected waterbodies (‘billabongs’) that may persist for
only part of the year. Anabranches are geomorphologically different to other floodplain
channels (Nanson and Knighton 1996), in terms of both their origin and present
characteristics. Anabranch channels in many areas of Australia are also relatively
unmodified by human influence compared to the other secondary channels described by
the aforementioned authors. Does surface connection during flow pulses in these systems
produce the same effects in these waterbodies and the adjacent river channel? Can the
potential influences of water resource development upon connectivity and exchanges
between these features be quantified?
Hydrological fragmentation

Fragmentation is usually defined as the ‘breaking up of a habitat, cover type, or movement medium into smaller, disconnected parcels’ (Turner et al. 2001). For the purposes of this thesis, fragmentation is defined as the reduction or elimination of connectivity between habitats or patches within a landscape. The concept of fragmentation is important in landscape and conservation ecology, however in use it can be ambiguous (Haila 2002). Fragmentation often involves a concomitant loss and isolation of landscape patches (Collinge 1996), but it can also serve to increase patchiness and heterogeneity in more uniform landscapes. It has been described as the root cause of many conservation problems (Debinski and Holt 2000), but can also be actively managed in some environments for positive outcomes (Turner et al. 2001). The influences of fragmentation can vary with scale, across organisms, habitat types, and geographic regions (Bowers and Dooley 1999; Haila 2002), and the magnitude and extent of these influences are influenced by the size, connectivity, shape, context, internal heterogeneity and spatial arrangement of remaining patches (Collinge 1996). Fragmentation can prevent dispersal of nutrients and populations across the landscape, often resulting in declines in productivity, population size and community diversity (Robinson et al. 2002; Woodward and Hildrew 2002). More specific changes include loss of native plant and animal species, invasion of exotic species, increased soil erosion and decreased water quality. Fragmentation associated with anthropogenic developments has been said to constitute the most serious threat to the Earth’s biological diversity (Collinge 1996).

Floodplain rivers are ecologically ‘sensitive’ landscape systems (Miles et al. 2001) because of their dependency upon hydrological connection. Yet in unaltered semi-arid floodplain river systems some habitat fragmentation is natural. Fragmentation of floodplain river systems is facilitated by the natural flow regime, with flow and flood pulses and associated wet-dry cycles dictating the frequency and duration of connection and disconnection between various landscape patches or features. Depending upon the frequency and duration of flow pulses, and the extent of inundation, sediments and decomposing litter in floodplain river systems may experience conditions ranging from complete submergence to complete exposure to the atmosphere (Brinson et al. 1981).
These conditions control detrital decomposition and nutrient cycling, and alternate wetting and drying of soils results in well-known pulses of carbon, nutrients, respiration and microbial density during rewetting (Brinson et al. 1981; Briggs and Maher 1985; Patrick et al. 1985; Willet 1989; Briggs et al. 1993; Qui and McComb 1995; 1996). These pulses strongly influence productivity in both the floodplain and the main river channel, and can determine the quantity and quality of exchanges within them.

‘Natural’ fragmentation in floodplain rivers is influenced by the hydrological regime at a range of spatial and temporal scales. For example, the timing and magnitude of flow pulses in Australian rivers are highly variable (Thoms and Sheldon 2000b). This is a result of unstable rainfall conditions influenced by aseasonal factors such as the El Nino-Southern Oscillation (ENSO) (Walker et al. 1995; Puckridge et al. 2000), as well as significant water losses due to evaporation, evapotranspiration and groundwater recharge (Davies et al. 1994). A common measure of flow variability is the coefficient of variation (CV), for which values of between 1.59 and 3 have been reported for major Australian rivers (Thoms and Sheldon 2000a). In comparison, CV values for mean annual flows of humid regions centre around 0.3 (North America) and 0.2 (Europe), illustrating the variable nature of flow in Australian river systems (Davies et al. 1994). This variability means that hydrological connectivity between patches in Australian floodplain river landscapes is exceptionally fragmented under natural conditions.

Artificial or human-induced habitat fragmentation of floodplain river systems in its basic sense negates all the benefits of connection, as well as many of the benefits of ‘natural’ fragmentation. It alters both the lateral connectivity between the river and the floodplain and the temporal and spatial variance in connectivity in the main stem of the river (Wiens 2002). Water resource development and the regulation of rivers can alter flood pulse characteristics such as flood frequency, magnitude and duration, thereby altering the wetting-drying regime, and disrupting nutrient cycles and patterns of exchange between the parent river and its floodplain. Seasonal ‘pulsing’ of hydrological connection and fragmentation can be especially important for the reproduction and recruitment of riverine organisms such as fish, which are adversely affected by changes in the seasonal
timing of flow pulses and hence connection with floodplain breeding habitat (Ward and Stanford 1989; Schlosser 1991). Through flow regulation, levee building and other activities, water resource development also prevents dispersal of carbon, nutrients and plant and animal populations across the landscape, often resulting in declines in productivity, population size and community diversity. Consequently, water resource development and associated agricultural activities have had a profound influence upon riverine food webs at the landscape scale (Woodward and Hildrew 2002). Thus artificial fragmentation has serious implications for the ecological functioning of floodplain river systems, and hence also for their value as resources.

Knowledge gaps – hydrological connectivity and fragmentation

The potential value of landscape ecology to the study of floodplain river systems has been recognised, and was highlighted in Chapter 1 of this thesis (Palmer et al. 2000; Jackson et al. 2001; Amoros and Bornette 2002; Poole 2002; Ward et al. 2002; Wiens 2002). The study of connectivity and fragmentation in floodplain river landscapes is a rapidly expanding field (Poole 2002). Despite the work documented to-date regarding hydrological connectivity dynamics and ecological responses, such as that conducted in the Danube system (Tockner et al. 1999a; Tockner et al. 1999b; Tockner et al. 2002; Hein et al. 2003), significant knowledge gaps remain.

Expansion and contraction of channel networks without overbank flooding is a common phenomenon in river corridors, but requires further detailed study (Tockner et al., 2000; Ward et al., 2002). These within-channel flow pulses provide unique spatial and temporal patterns of hydrological connectivity, and for rivers with little or no development, understanding their ecological importance may provide a basis upon which to assess and minimise future impacts (Puckridge et al. 1998; Kingsford 2000). Different phases of connection that influence ecological parameters have been distinguished in heavily modified floodplain waterbodies of temperate systems (Hein et al., 1999; Tockner et al., 1999a; Hein et al., 2003) – however whether such phases exist or function similarly in relatively unmodified arid and semi-arid systems is not known. The relative
influences and roles of ‘natural’ versus ‘artificial’ (human induced) fragmentation have also received limited attention in terms of riverine landscape ecology. The differences and interactions between these at different spatial and temporal scales could prove to be a productive field of theoretical research that is also informative for river system managers. The concept of ‘natural’ fragmentation is particularly apt, though not necessarily unique to riverine landscapes (Wiens 2002).

Finally, there is a need for better understanding of the highly variable and unpredictable dryland river landscapes that dominate areas of Australia, Africa and North America. What might the role of connectivity be in a floodplain river system that over time is dominated by the disconnection phase rather than connection? Analysis of connectivity is required in diverse systems, and should yield better understanding of landscape level functional processes that sustain floodplain rivers (Robinson et al. 2002; Ward et al. 2002). This information would then assist in the future management, restoration and rehabilitation of riverine landscapes (Robinson et al. 2002).
2.2  **SEMI-ARID FLOODPLAIN RIVER SYSTEMS**

Semi-arid zones occur where mean annual precipitation (MAP) is between 200 and 500 mm a year, while arid and hyper-arid zones occur where MAP is 25-200 mm and <25 mm yr\(^{-1}\) respectively. They may exist in both hot and cold climates, and occupy over half of the world’s land area (Kingsford and Thompson 2006). Rivers in these zones (termed ‘dryland’ rivers) provide vital water resources for most of the world’s people (Wishart 2006). Well over half of the continent of Australia is dominated by dryland areas of low relief (Bowler 1986) and is drained by rivers and streams with temporary or intermittent flow (Boulton and Lake 1988). Despite being the focus of many pivotal scientific and management issues in Australia (A.S.L. 2000), until recently these systems have received little of the research attention they deserve (Kingsford 2006b).

**Unique characteristics**

Floodplain river systems in semi-arid areas have many unique attributes (Walker *et al.* 1995; Knighton and Nanson 1997; Kingsford 2006b). They have extremely high evaporation rates (Dahm *et al.* 2002; Young and Kingsford 2006), their soils and sediments are often relatively low in nutrients and organic matter, making flooding important for fertility (Roberts 1993; Balba 1995; Ogden and Thoms 2002). Discharge is often extremely variable and unpredictable (Knighton and Nanson 1994; 2001; Young and Kingsford 2006), which together with high sediment loads (Davies *et al.* 1994), causes complexity, variability and unpredictability in sedimentation, channel change and channel character (Rust 1981; Graf 1983; Nanson *et al.* 1986; Graf 1988; Nanson *et al.* 1988; Schumann 1989; Pickup 1991; Thoms and Walker 1992; Tooth and Nanson 1999; Tooth 2000a; Thoms *et al.* 2006).

Spatial and temporal landscape patterns can be distinctive in semi-arid riverine landscapes (Pickup 1991; Belsky 1995; Thoms *et al.* 2006), with physical and ecological associations that are complex and variable over both space and time (Friedel *et al.* 1993;
Fanning 1999; Davis and Thoms 2002). Flow pulses in dryland river systems have been related to ‘boom’ and ‘bust’ periods for waterbird, fish and tree populations (Roberts 1993; Kingsford and Porter 1999), and refugia such as in-channel waterholes and terminal wetlands are known to be important for sustainability of biological diversity (Morton et al. 1995; Timms and Boulton 2001; Sheldon et al. 2002). Variable connectivity has also been shown to influence aquatic invertebrate communities (Morton et al. 1995; Timms and Boulton 2001; Sheldon et al. 2002). Native plants and animals are either highly mobile or tolerant of the extremes of these environments, and often rely on cues from flooding and flow pulses for reproduction (Boulton et al. 2006; Brock et al. 2006; Kingsford et al. 2006a). Semi-arid river floodplain landscapes are fragile systems, susceptible to anthropogenic influences because they are typically ancient and finely tuned to the availability of water (Robertson and Rowling 2000; Sheldon et al. 2000; Thoms and Sheldon 2000b; Kingsford 2006a). These and other characteristics make understanding their ecology, conservation and management a challenge (Davies et al. 1994; Kingsford 2006b).

**Geomorphology**

The geomorphology of semi-arid floodplain rivers is typically highly complex and variable over both space and time (Thoms et al. 2006). Controlling factors include discharge, sediment load, physiographic setting (geology and slope) and history. These produce a variety of river landscape patterns and create a large degree of spatial and temporal habitat heterogeneity. Highly variable water and sediment regimes (Young and Kingsford 2006), together with changes in slope, are largely responsible for this complexity, both temporal and physical, and create the multitude of geomorphic features found particularly in the floodplain. Geomorphic variability in dryland rivers has also been attributed to flow transmission losses and a lack of tributary inflows beyond the headwaters (Tooth 2000a).

Rivers are capable of adjusting their channel slope by adopting different sinuosities and channel widths (Kellerhals and Church, 1989) especially where the riparian vegetation is
scarce, as is often the case in dryland areas (Tooth 2000b; Brock et al. 2006). Work on the Okavango fan, Botswana, has emphasised the potential sensitivity of large floodplain river systems to small changes in elevation or gradient, ‘whether induced by tectonics, by endogenous agencies such as sedimentation, or by anthropogenic interference’ (McCarthy et al. 1997). In extremely low gradient systems such as those that dominate Australia, this sensitivity is magnified and is a major influence on channel geomorphology. The geomorphic sensitivity of these systems, combined with their bank stability, makes them prone to channel change by avulsion, frequently resulting in anabranching channel patterns (Nanson and Knighton 1996).

**Hydrology**

The habitat complexity and variability caused by the geomorphology of dryland rivers over space and time is augmented by the hydrological variability that they experience (Puckridge et al. 1998). Globally, dryland rivers display extreme hydrological variability when compared to rivers in other climates (Kingsford and Thompson 2006; Young and Kingsford 2006), and it has been suggested that large Australian dryland rivers in particular may be ‘the most variable in the world’ (Puckridge et al., 1998). The reasons for this overarching hydrological variability include unpredictable and variable rainfall, low runoff, a non linear response of runoff to rainfall and basin size, high evaporation rates, and highly variable seasonal flow characteristics (Thoms and Sheldon 2000a). This variability and unpredictability drives ecological functioning in these rivers (Kingsford, 2000).

The hydrographs of dryland rivers are strongly influenced by aseasonal factors, and the effect of the irregular atmospheric circulation phenomenon known as the El Nino-Southern Oscillation (ENSO) is apparent in discharge patterns of semi-arid rivers worldwide (Puckridge et al. 2000; Young and Kingsford 2006). For example, in the Cooper Creek system of inland Australia, floods tend to occur in clusters associated with La Nina episodes (Puckridge et al., 2000). This “hydrological persistence” or partial auto-correlation between floods in successive years can significantly influence the
ecology (e.g. fish recruitment) of dryland rivers (Puckridge et al., 2000). In Australia, the remoteness of dryland rivers and the unpredictability and infrequent nature of flow events means that there are generally few measured flow, sediment or nutrient load data (Tooth 2000b). In addition, relatively few flows in Australian dryland rivers occur due to local rainfall – many are allogenic, sourced from well-watered headwater areas. Hence, the scientific study, understanding and management of these systems require innovation, long-term commitment and effort.

Ecology

Until recently, literature addressing semi-arid and arid river-floodplain ecology has been relatively depauperate compared to that for other climatic zones (Hughes 1990; Kingsford 2006a). Hydrological variation in dryland rivers is ecologically important at all temporal scales, including both within and between years. When linked with temperature variation, it is a powerful determinant of ecosystem integrity (Harris et al. 2000). Plant communities, invertebrates, and vertebrates in dryland river systems are adapted to the wet-dry cycles and temperature extremes that they must experience (Boulton et al. 2006; Brock et al. 2006; Bunn et al. 2006; Kingsford et al. 2006a). For example, flow variability parameters influence the length of fish breeding seasons, spawning periodicity, length of life cycles, age at maturity, colonization ability, species richness and major variations in assemblage structure (Gehrke 1991; Puckridge et al. 1998). Floodplains act as ‘seedbanks’ for many organisms, the rapid emergence and growth of which following flooding is thought to be an important resource for waterbirds and juvenile and post-larval fish (Boulton and Lloyd 1992). Invertebrate adaptations to flow variability in dryland rivers have been classified as ‘behavioural avoidance’ and ‘physiological tolerance’ (Boulton and Lake, 1988). Invertebrates can avoid desiccation by taking refuge in billabongs, pools, the hyporheic zone, stones, leaf litter, algae and large woody debris, and by burrowing down to the water table. Particular life-stages of some aquatic invertebrates can survive without water for months; others produce special substances to reduce water loss; and still others lay either terrestrial eggs or eggs containing nymphs that are almost fully developed. Dryland aquatic macroinvertebrates also frequently have
efficient dispersal mechanisms, allowing them to rapidly recolonise rivers when conditions are more favourable (Boulton et al. 2006).

Floodplain river ecosystems in dryland areas often depend on minimum flooding frequencies and durations (Hughes, 1990). Changes to hydrological connectivity between floodplains and the main river channel, or even physical disturbance of the sediments and vegetation, may dramatically alter overall productivity of the food web and the ecosystem (Boulton and Lloyd, 1992). Important variables include the amount of time since the last flood, the duration of past and present floods, flood timing and seasonality, and the source of the floodwater. In floodplain forests, the duration of flooding is important not only for the provision of water, but also because it determines the success of waterbird breeding, restricts invading plants, breaks the life cycle of some leaf-eating insects, and defers the onset of drought (Bren 1987; Bren et al. 1987).

**Human use**

Dryland rivers have been relied upon heavily by human societies from time immemorial. Ancient civilisations of Egypt, India, Asia and Africa were, and still are, based upon the supply of water from these systems, and the productivity of their floodplains. In modern times, growing populations and demand for particular crops have resulted in ever-increasing pressure for the exploitation of these systems. This is despite recognition, at least in the scientific community, of the fact that dryland rivers possess extremely limited amounts of water and are particularly sensitive to change. The historical solution to balancing the variability and paucity of the water supply with high demand in these systems has been to install dams and impose regulation of the hydrological regime (i.e. the introduction of ‘water resource development’). Yet both scientific and management understanding of ecological patterns and processes in these systems is lacking.

Water resource development has had a major influence upon the hydrology of large dryland rivers, with critical ecological implications (Davies et al. 1994; Dynesius and Nilsson 1994; Maheshwari et al. 1995; Thoms and Sheldon 2000b; McGinness and
Thoms 2002; Kingsford et al. 2006b). In many of these systems, serious conflicts arise between irrigation, social/government and environmental demands for water (Kingsford 1999; Wishart 2006). Yet due to the uniqueness, complexity and long-term variability of dryland systems, the exact nature of the ecological response to change has not been well understood in the past. Hughes (1990) commented on the concern for reduced flooding in semi-arid and arid floodplain ecological literature, while Davies et al. (1994) stated that where linkages between river and floodplain are broken, perhaps by regulation or by inter-basin transfers, both river and floodplain environments will be changed. They gave examples of this dual change in several large semi-arid floodplain rivers, including the Pongolo, Zambezi and Colorado Rivers.

Significant hydrological change has also occurred in Australian dryland river systems (Rutherfurd 1994; Thoms and Sheldon 2000b), despite a relatively low population density and brief duration of European settlement (1788AD) with associated changes to ecological condition (Williams 1993). In particular, the Murray River (Thoms and Walker 1989; Rutherfurd 1990; Thoms and Walker 1992; 1993; Rutherfurd 1994; Maheshwari et al. 1995) and Barwon-Darling River (Riley 1988; Thomson 1992; Thoms and Sheldon 1997; 2000b) have been centres of change. Williams (1993, p.3) points out that:
‘...the major rivers have been dammed or diverted, deep freshwater impoundments occur where none occurred before, wetlands have been drained, running waters bear heavy loads of pollutants, extensive areas of catchment basins have been salinised, floodplains have been alienated, blue-green algal blooms are a common occurrence, and introduced aquatic animals and plants are dominant or important elements of the biota’ (Williams 1993).

The effects of water resource development in Australia have been described as ‘far reaching, comprehensive, largely irreversible and usually deleterious so far as the natural character of inland bodies of water is concerned’ (Williams 1993, p.1).

More recently, the significance of water resource development for the ecological condition of areas at the ends of dryland rivers has been recognised, including terminal
wetlands, deltas, estuaries and groundwater recharge areas (Kingsford et al. 2006b). Changes to flow destroy ecosystem processes, reduce biodiversity, and cause the contraction or collapse of flow-dependent communities in these areas – however lag times for these effects can be very long (Kingsford 2000). Ecological impacts are especially severe in dryland environments, because the nature of regulation is directly contradictory to the boom-and-bust ecology of these systems (Walker et al. 1997; Kingsford et al. 1999). Indeed, dryland rivers respond differently, both physically and biologically, to hydrological change in comparison with temperate rivers. This response may differ across a range of spatial and temporal scales (Thoms and Walker 1993; Walker et al. 1995; Thoms and Sheldon 2000b; 2000a).

Knowledge gaps – semi-arid floodplain river systems

Semi-arid river systems have received little of the ecological attention they deserve until recently (Kingsford 2006b). Understanding their ecology, conservation and management is a challenge because of their age, fragility, remoteness and complexity (Davies et al., 1994). Consequently, both scientific and management understanding of ecological patterns and processes in these systems is insufficient. This is particularly the case in Australia. Ecosystem functioning within floodplain rivers of semi-arid Australia is thought to be primarily driven by flood and flow pulses (Walker et al. 1995; Puckridge et al. 2000; Sheldon et al. 2002). However, these rivers have not been well represented by most models of riverine processing (Walker et al., 1995; Puckridge et al., 2000), until the compilation of the recent Riverine Ecosystem Synthesis (Thorp et al. 2006). Within-channel flow pulses may be of particular ecological significance, especially in terms of maintaining production (Puckridge et al., 1998; Amoros and Bornette, 2002), but few studies have explicitly addressed this issue. If these systems are to be developed, maintained, rehabilitated or restored sustainably, significantly more information is required, particularly regarding the ecological role of hydrological connectivity during within-channel flow pulses. The significance of semi-arid floodplain river systems in both ecological and economic terms demands thorough scientific and management
understanding of how they function, as well as exactly how they are changed by water resource development.

2.3 **ANABRANCH CHANNELS**

The term ‘anabranching’ is used to describe multi-channel river systems in a wide range of environments, within which individual ‘secondary’ channels may meander, braid or be relatively straight. Nanson and Knighton (1996, p.218) define an anabranching river as ‘*a system of multiple channels characterised by vegetated or otherwise stable alluvial islands that divide flows at discharges up to nearly bankfull.*’

Anabranching rivers form a channel pattern that can resemble braiding, but in which the vegetated, semi-permanent islands are stable and wide relative to the width of the river channel at average discharges. The width of the islands is generally more than three times that of the primary river channel, while their height is similar to that of the surrounding floodplain (Knighton and Nanson 1993; Knighton and Nanson 1994; Nanson and Knighton 1996; Tooth 2000b). Islands separating anabranches usually persist for decades or centuries (Kellerhals and Church 1989; Nanson and Knighton 1996). Some studies of anabranching and braided rivers have focused more on the islands separating the channels than the channels themselves (Gurnell and Petts 2002; Gurnell *et al.* 2002). Anabranch islands have been described as buffer zones that influence fluxes of sediment, nutrients, and biota, and that should be restored and conserved (Girel and Pautou 1997; Gurnell and Petts 2002).

**Development**

River planforms respond to complex sets of interacting variables. Partly because of this complexity, the causes and function of anabranch development were not well understood until relatively recently (Bowler 1986; Huang and Nanson 2000; Tooth 2000b). It is now thought that the fundamental advantage of an anabranching river is that, by constructing a semi-permanent system of multiple channels, it can concentrate stream
flow and maximise bed-sediment transport (work per unit area of the bed) under conditions where there is little or no opportunity to increase gradient (Nanson and Knighton 1996).

Individual anabranch channels are often formed by avulsion (a sudden shift in channel location; Tooth and Nanson 1999). Channel avulsion is the major mode of long-term channel change of many of the world’s largest rivers including the Mississippi, lower Rhine-Meuse, and Brahmaputra, and many Australian rivers including the Murray, Darling, Murrumbidgee and Lachlan rivers and the Cooper Creek system (Bowler, 1986). Typically, anabranching occurs in river systems that have low gradients, a flood-dominated flow regime, stable banks that are resistant to erosion, and mechanisms that block or constrict channels and trigger avulsion (Nanson and Knighton, 1996). Avulsion and anabranch development are usually initiated by the breaching or crevassing of levees together with floodplain scour (Knighton 1999). Thus the islands between anabranch channels are effectively cut out of the existing floodplain. Anabranching is also related to the influence of tributaries - some large rivers change from single-thread/channel to anabranching along their length in response to tributary inputs of water and sediment (Tooth and Nanson 1999). Thus anabranching is frequently not spatially or temporally persistent along the length of the entire river or catchment (Nanson and Knighton 1996; Tooth 2000a).

**Distribution**

Anabranching rivers are found worldwide. It has been suggested that anabranching planforms once dominated the landscapes of large floodplain and lowland rivers in Europe and North America (Schumann 1989; Golladay et al. 2000; Brown 2002; Gurnell and Petts 2002). In the Amazon River Floodplain, small floodplain channels have been observed with a wide range of widths and depths, which diverge from and rejoin the main channel after excursions of a few kilometres to more than 100 km across the floodplain (Dunne et al. 1998). Most lowland floodplain rivers of inland Australia display the anabranching pattern for at least some of their length, notable examples including the
Cooper Creek, Paroo River, Lachlan River, Wimmera River; Murrumbidgee River, Murray River and the Macintyre/Barwon/Darling River (Nanson et al. 1988; Western et al. 1997; Gibling et al. 1998; Timms and Boulton 2001).

At present, active secondary channels such as anabranches are generally missing along large European rivers, primarily because of anthropogenic change. Several projects have been initiated in Europe to restore river-floodplain interactions by re-opening or artificially creating secondary channels, because secondary channels are thought to play major roles (e.g. as flow refugia) for sustaining endangered lotic communities (Muhar 1996; Tockner and Schiemer 1997; Hein et al. 1999; Tockner et al. 1999a; Tockner et al. 1999b; Buijse et al. 2002; Hein et al. 2003). It is hoped that these measures will help to re-establish a flow gradient across the river-floodplain system - from the main channel to shallow side arms, to permanent and ephemeral floodplain lakes and ponds. Restoration pilot projects have found that these systems require multiple connections between the main and side channels as well as strong lateral connections to riparian wetlands (Muhar 1996). Some of the proponents of restoration of secondary channels in these environments believe that ‘from an ecological point of view, permanently flowing conditions are preferable in secondary channels’ (Buijse et al. 2002, p.898). This may or may not be the case in temperate environments, but is unlikely to be the ideal situation in dryland floodplain river systems that are naturally hydrologically fragmented.

**Ecological benefits and characteristics**

There are many ecological benefits associated with anabranching river systems. Anabranch channels generally become inundated at flow levels below bankfull (during flow pulses) and thus provide connection between the river and other landscape patches at relatively low river discharges. The presence of multiple channels and their islands in anabranching rivers increases habitat heterogeneity and availability relative to single-channel systems with the same discharge (Ward and Stanford 1995a; Brown 2002; Ward et al. 2002). Under low flow conditions, river reaches with islands and secondary channels have been shown to have higher aquatic area per unit channel length, higher
aquatic-terrestrial ecotone length per unit length of channel, and higher diversity of
habitats compared to reaches dominated by other channel patterns (Amoros and Bornette,
2002). The diversity of biotically important habitat conditions in floodplain secondary
channels and waterbodies is primarily a function of: 1) the distance from the patch to the
river; 2) the existence of permanent versus temporary connections to the river; and 3) the
size and shape of the waterbody (patch), which can be described by its length, width,
depth and sinuosity (Amoros and Bornette, 2002).

Anabranch, secondary, or floodplain channels in temperate or anthropogenically
developed areas are frequently described and studied simply as floodplain waterbodies,
since they are often permanently or semi-permanently connected to the river channel, or
retain water for most of the year (Tockner et al. 1999a; Hein et al. 2003). However many
of the physical and ecological observations made in these waterbodies are relevant to the
characteristics of dryland anabranch channels and their ephemeral waterbodies. For
example, relationships have been described between the grain-size and composition of
the substratum and 1) waterbody connectivity; 2) distance from the river; and 3)
deposition conditions (Amoros and Bornette, 2002). The ecological character of
floodplain waterbodies such as those found in anabranch channels is influenced by many
interacting factors, including water temperature, turbidity, nutrient concentrations and
sediment character, all of which are affected by the geomorphology and water origin of
the anabranch and the waterbody (Amoros and Bornette, 2002). These, in turn, are
determined by hydrological connectivity at various spatial and temporal scales.
In Australian semi-arid floodplain river systems, anabranch channels vary in the ‘sill
height’ or level at which they commence to flow, depending on local morphology. As a
result, some anabranches require only minimal flows in the parent channel in order to
start flowing, while others require nearly bankfull flows for water to break out into the
anabranch channel (Thoms et al. 2005). Inundation of the floodplain via overbank flows
in Australian dryland rivers does not occur as regularly as in temperate rivers (Walker et
al., 1995). For these rivers, within channel ‘flow pulses’ that occur at shorter time scales
than overbank floods may be of great ecological significance, sustaining populations and
maintaining nutrient input between larger discharge events (Davies et al. 1994; Thoms
and Sheldon 1997; Puckridge et al. 1998; Tockner et al. 2000). Inundation of anabranche channels during flow pulses may therefore be crucial for ecological sustainability in these systems.

Inundation pattern can differ between anabranches. Floodwaters moving down a river system may enter an anabranche at its upstream end and exit at the downstream end; alternatively, anabranches may be inundated from their downstream ends during the rising limb of the flood hydrograph, and drain back through the same breakout point as the flood recedes (Southwell 2002). Such differences in inundation pattern would be expected to result in differences in sedimentation patterns and processes, in water residence times, and in the duration of lotic connection within each anabranche. The duration of inundation affects decomposition processes, nutrient fluxes and the biomass and productivity of plants and animals (Hein et al. 1999; Tockner et al. 1999a; Tockner et al. 2000; Amoros and Bornette 2002). Thus these differences have implications for carbon dynamics within each anabranche, as well as for carbon transfers between the anabranche and its parent river.

Anabranches and other secondary channels have been hypothesized (and in a few cases, shown) to influence several ecological variables (Table 2.2). Thorp and Delong (1994) suggested that primary production may be maximised in rivers with complex cross-profiles having elements that are inundated and desiccated at a range of water levels. Yet the detailed nature of these characteristics and the ways in which anabranche channels might influence such ecological variables have received little if any empirical study (Kellerhals and Church, 1989; Buijse et al., 2002; Gurnell and Petts, 2002; Ward et al., 2002).

**Water resource development**

It has been suggested that nineteenth century engineers believed that no channel needed more that one bed (Brown 2002). One of the most significant influences of this approach, associated with water resource development, has been the isolation of river channels from
their floodplains and associated features, including secondary channels. This isolation may be deliberate, via levees and weirs, or indirect, via changes to flows. For example, in the Peace River (British Columbia), predictions indicated that following regulation the river would become narrower and shallower. In fact, it was found that the most important change was abandonment of secondary channels (a reduction in total length of 56%), which originally carried significant portions of high flow. The Peace River was found to be undergoing a change from being irregularly sinuous and frequently split toward being a single thread channel with perhaps more of a meandering tendency (Kellerhals and Church, 1989). Habitat value was degraded because of this loss of shallow secondary channel area, as well as changes to the river edge environment associated with a new pattern of sedimentation and vegetation succession (Kellerhals and Church, 1989).

Floodplain wetland areas such as anabranch billabongs have suffered some of the greatest changes from water resource development, ranging from permanent drying, to dramatic alteration of their hydrological connectivity regimes, to permanent flooding, as well as clearing of vegetation, tillage and grazing and feral weed and animal invasion (Kingsford 2000). Significant changes in waterbodies due to water resource development have been suggested for: aquatic plant diversity and community structure (Neilsen and Chick 1997; Bornette et al. 1998; Ogden 2000), macroinvertebrate assemblages (Boulton and Lloyd 1991), nitrogen and suspended matter concentrations (Brunet et al. 1994), leaf litter breakdown rates and nutrient dynamics (Glazebrook and Robertson 1999), suspended POM concentration and transport (Golladay et al. 2000), large woody debris (Gurnell et al. 2002), trophic structure (Maridet et al. 1998; Woodward and Hildrew 2002), wetting and drying cycles (Kingsford 2000) and sources, sinks and transformations of organic carbon (Robertson et al. 1999; McGinness et al. 2002). Hence the integrity, function, and biocomplexity of waterbodies in anabranch and other secondary channels can be fundamentally changed by water resource development (Ward and Stanford 1995b; Ward and Stanford 1995a; Ward 1998a; 1998b). Consequently changes to connectivity with secondary or anabranch channels have led to the loss and decline of a diverse range of wetlands as well as the degradation of the ecological integrity of entire river systems (Kingsford 2000; Buijse et al. 2002).
Table 2.2 Ecological variables thought to be influenced by anabranches and other secondary channels.

<table>
<thead>
<tr>
<th>Ecological variables</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Habitat condition and diversity, including secondary aquatic habitats and exposed sediment habitats</td>
<td>(Kellerhals and Church 1989; Sedell <em>et al.</em> 1989; Ward and Stanford 1995a; Gurnell and Petts 2002; Ward <em>et al.</em> 2002).</td>
</tr>
<tr>
<td>Habitat presence/absence for life stages of fish, molluscs, beetles, grasshoppers and plants</td>
<td>(Muhar 1996; Tockner <em>et al.</em> 2000; Gurnell and Petts 2002)</td>
</tr>
<tr>
<td>Ecotone presence, extent and character</td>
<td>(Petts 1990; Thorp <em>et al.</em> 2006)</td>
</tr>
<tr>
<td>Invertebrate density, diversity and production</td>
<td>(Boulton and Lloyd 1991; Timms and Boulton 2001; Malmqvist 2002)</td>
</tr>
<tr>
<td>Current velocity</td>
<td>(Kellerhals and Church 1989)</td>
</tr>
<tr>
<td>Waterhole or waterbody formation and processes</td>
<td>(Ward and Stanford 1995a; Knighton and Nanson 2000)</td>
</tr>
<tr>
<td>Sediment transport</td>
<td>(Kellerhals and Church 1989)</td>
</tr>
<tr>
<td>Organism and community metabolism</td>
<td>(Kellerhals and Church 1989)</td>
</tr>
<tr>
<td>Hydraulic refuge during flow pulses and floods</td>
<td>(Muhar 1996)</td>
</tr>
<tr>
<td>Primary production</td>
<td>(Thorp and Delong 1994; Hein <em>et al.</em> 1999; Tockner <em>et al.</em> 1999a; Tockner <em>et al.</em> 2000; Amoros and Bornette 2002)</td>
</tr>
<tr>
<td>Vegetative enhancement of cross-profile complexity</td>
<td>(Gurnell and Petts 2002)</td>
</tr>
<tr>
<td>Large wood distribution and associated fluvial processes</td>
<td>(Gurnell <em>et al.</em> 2002)</td>
</tr>
<tr>
<td>Food web structure</td>
<td>(Woodward and Hildrew 2002)</td>
</tr>
</tbody>
</table>

Anabranch channels are affected by hydrological change over both the short and the long term. Such changes have the potential to alter not only their ecological and hydrological roles, but also their physical structure. Water resource development and European-style land use throughout the drylands of Australia have accelerated geomorphic processes.
such as erosion, and many channels, including anabranches, are currently subject to substantial enlargement and knickpoint retreat (Fanning 1999). Geomorphic factors influenced by water resource development include avulsion, the movement of sediment, channel morphology, bank stability, tributary base levels, floodplain meander migration and cut-offs, floodplain sedimentation and stability, and salinity gradients (Arthington and Zalucki 1998). Flow regulation also affects in-channel habitat by reducing the complexity of channel morphology. For example, Thoms and Sheldon (1997) in their study of in-channel benches in an unregulated river stretch, found 5 distinct groups of benches that corresponded to flow bands in the hydrograph. They also surveyed a regulated stretch and found that benches were present at high bank levels but absent at lower levels, resulting in a more uniform channel bed. Thus, the more variable the flow regime, the greater the number of benches present (Thoms and Sheldon 1997). This result may also apply to other geomorphic features such as anabranch channels, if their formation is reliant on flow variability.

**Knowledge gaps – anabranch channels**

In large floodplain river landscapes, secondary or anabranch channels are thought to be key elements of spatial heterogeneity (Ward and Stanford 1995a; Gurnell and Petts 2002). Despite the importance and prevalence of anabranch channels (especially in semi-arid systems), little is known about their specific ecological role (Buijse et al., 2002; Gurnell and Petts, 2002; Ward et al., 2002). Kellerhals and Church (1989) saw the need to call for ‘far more attention’ to be paid to secondary channels, side channels, deltaic distributary channels and floodplain lakes, in terms of physical habitat description in rivers. Ecological research on river systems has been dominated by studies of rivers with single-thread channels from headwaters to the sea, and until recently the role of secondary channels has been almost totally ignored by ecologists (Ward and Stanford, 1995a; Buijse et al., 2002; Gurnell and Petts, 2002). In particular, questions remain regarding their potential roles when they are hydrologically connected to the primary river channel, especially with regard to carbon (energy) storage and supply to the ecosystem as a whole, over various spatial and temporal scales. Conceptual advances in
riverine ecology require expanded understanding of the crucial roles of hydrological connectivity, spatial complexity and fluvial dynamics in natural river ecosystems (Ward and Stanford, 1995a; Gurnell and Petts, 2002; Ward et al., 2002; Wiens, 2002).

Water resource development has placed many restrictions on the functioning of floodplain rivers. The reliance on lateral connectivity provided by flow pulses in these systems for ecosystem functioning emphasises the importance of floodplain features such as anabranch channels, that become inundated under bankfull level. Land and water development has the potential to reduce the already fragmented connectivity experienced in these systems, affecting the exchange of resources between the river, anabranches and floodplain. However the exact nature of these changes with regard to anabranch channels is not well understood. Filling this knowledge gap would enable better understanding and management of anabranch channels, especially in terms of their value as ecological resources.
2.4 **Carbon in Semi-Arid Anabranching Floodplain River Systems**

A primary goal of ecology is to understand patterns of energy flow and material cycling, and how food webs in populations, communities and ecosystems are structured (Rounick and Winterbourn 1986). The biogeochemical cycle of carbon is central to our understanding of energy flow in aquatic ecosystems. Inorganic carbon is metabolised by aquatic macrophytes and algae during photosynthesis, while organic carbon forms the basis of the trophic cascade for most other aquatic organisms.

**Sources of carbon**

Organic carbon in rivers is derived from two main sources:

- Autochthonous carbon, from primary production within the river system (e.g. phytoplankton), and
- Allochthonous carbon, being of terrestrial origin or external to the river system (e.g. floodplain leaf litter).

There has been debate regarding whether production in lowland floodplain-river systems is predominantly reliant upon allochthonous or autochthonous material (Thorp and Delong 2002). It has also been suggested that lowland floodplain river systems fluctuate between heterotrophy (dependence upon external/allochthonous carbon) and autotrophy (dependence upon internal/autochthonous carbon), depending on factors such as hydrology, turbidity and temperature (Thorp and Delong 2002). Indeed, oscillation between heterotrophy and autotrophy has been suggested as a general phenomenon in river systems at different temporal scales (Boulton and Lake, 1988; Tockner *et al.*, 1999a; Tockner *et al.*, 1999b), but it is not well understood. Hydrological connectivity may play an important role influencing these factors and the availability of each carbon source. If seasonal switches between heterotrophy and autotrophy occur (Thorp and Delong 2002), then it is theoretically possible for switches to occur on much shorter time scales, such as at the within-flow pulse scale, during which various connection phases may occur. Switching at this scale was observed in a side channel of the temperate Danube River (Tockner *et al.*, 1999a), yet the mechanisms behind this pattern are complex. The relative
importance of allochthonous versus autochthonous carbon sources within and among
rivers and at different times remains a major question for freshwater ecologists (Thorp et
al. 2006).

Autochthonous carbon sources include dissolved organic carbon, algae (benthic,
epiphytic and pelagic), macrophytes, detritus and biofilms. The carbon produced by
riverine algae and macrophytes is generally readily available to consumers (Bunn and
Boon 1993; Thorp and Delong 1994; Findlay and Sinsabaugh 1999). Allochthonous
carbon sources include sediment-bound carbon, terrestrial vegetation and associated leaf
litter and detritus. Dissolved organic carbon can also come from allochthonous sources
such as rainfall, leaf-litter leaching, stem flow and canopy throughfall, release from
floodplain sediments during inundation, and movement of soil water (Findlay and
Sinsabaugh 1999).

The value of dissolved organic carbon

Organic carbon is conventionally classified into three size categories or fractions; coarse
particulate organic carbon (CPOC; >1 mm), fine particulate organic carbon (FPOC; <1
mm but >0.45 µm) and dissolved organic carbon (DOC; <0.45 µm) (Wotton 1994). All
of these fractions are important for riverine ecosystem functioning, yet the total organic
carbon pool in many freshwater systems is dominated by dissolved organic carbon (DOC;
(Degens et al. 1991). Between 50 and 80% of the total organic matter transported by
rivers is dissolved organic carbon (Spitzy and Leenheer 1991). DOC may comprise
compounds in aqueous solution, small particles, colloids, the smallest bacteria and
viruses (Wotton 1994). Concentrations in natural fresh waters range from about 1 to 60
mg C l⁻¹ but are commonly 1 to 10 mg C l⁻¹ (Degens et al. 1991; Spitzy and Leenheer
1991). Dissolved organic carbon in aquatic ecosystems represents a large pool of energy
for organisms adapted to the uptake of its compounds, and is highly important to stream
productivity (Sepers 1977; Fiebig et al. 1990; Nelson et al. 1991). It is important for
nutrient mineralisation and transport, as well as heavy metal transport (Richey et al.
The uptake of dissolved organic carbon in natural waters is primarily a bacterial process (Sepers 1977; Wotton 1994). Bacteria, as a food source, make available to higher trophic levels the dissolved organic carbon that dominates the aquatic carbon pool and which is otherwise unavailable to other organisms (the ‘microbial loop’; Robertson et al. 1999). However, of the DOC found in natural fresh waters, it is thought that only about 20% is compounds easily assimilated by bacteria (Spitzy and Leenheer 1991). DOC may become available to particle feeders after flocculation, and a specialised fauna of suspension-feeders (particularly larvae) capture a fraction of the dissolved material transported by rivers (Wotton 1994; Malmqvist 2002). Although the percentage of 'usable' DOC might be low, total concentrations in river water and water that drains from floodplains are generally high (Robertson et al. 1999), making it one of the most important sources of carbon in these systems.

The importance of carbon quality

The quality of carbon sources in floodplain river systems is of fundamental importance to ecological functioning. High quality carbon sources are easily and quickly utilised by consumers, influencing overall productivity over short time scales of minutes, days and months (Boulton and Brock 1999; Malmqvist 2002). However their availability can be sporadic and variable. Lower quality carbon sources are degraded and utilised over longer time scales of months, years and decades, and supply is probably steadier over time (Elwood et al. 1983; Boulton and Brock 1999). Sustainable and healthy river systems require the supply of carbon sources over both short and long time scales.

In the context of carbon sources, the term ‘quality’ can be somewhat subjective. Usually it is used with implicit reference to the availability or ease of utilisation of a particular carbon source for a specific consumer or group of consumers (Malmqvist 2002). Some carbon sources (such as leaves) are easily consumed or broken down by some organisms, and are therefore of high quality for those organisms. However other organisms may find another carbon source (such as algae) more palatable, and therefore of higher quality.
Another perspective may be to label a source ‘high quality’ when it is utilised readily by a relatively great number of consumers, and vice versa.

The quality of carbon sources is, however, usually defined by the composition of the carbon itself, and technically depends on whether or not it is decomposable by high-intensity ultraviolet radiation in the laboratory (Moss 1998). In general:

**Refractory** carbon sources are those that are:
- Comprised of high molecular weight compounds such as humic and fulvic acids, which come from the decomposition of lignin.
- Utilised by relatively few organisms
- Resistant to degradation and are utilised or broken down relatively slowly.
Examples include aged leaf litter and bark, and a large component of the dissolved organic carbon pool derived from terrestrial sources.

**Labile** carbon sources are those that are:
- Dominated by low molecular weight compounds such as simple sugars, and are ‘turned over’ within minutes to hours to days.
- Utilised by many organisms
- Readily utilised or broken down relatively quickly
Examples include algae, and dissolved organic carbon sources such as leachate from leaves and carcases, and exudates from algae and macrophytes.
Thus in simple terms refractory carbon is generally of low quality, while labile carbon is of high quality.

**Carbon sources in semi-arid environments**

In semi-arid zone floodplain river systems, the limiting effects of extreme temperatures, high evaporation rates, and low rainfall result in relatively low primary production and hence also reduced quantity and quality of carbon sources. The ephemerality and unpredictability of water supply, and hence also hydrological connectivity, results in
characteristic opportunism and ‘boom and bust’ cycles of flora and fauna production. Consequently the availability and utilisation of carbon sources over both short and long time scales is of great importance for the sustainability of these systems.

Surface and subsurface water availability and movement is the primary determinant of the quantity and quality of carbon sources in arid and semi-arid areas (Klopatek et al. 1998), with temperature also an important factor. Interactions between temperature and moisture levels determine the nature, extent, and rates of ecological processes such as carbon production, sequestering, degradation and release (Klopatek et al. 1998). Processing of carbon in semi-arid rivers is dominated by leaching, microbial respiration and physical breakdown, rather than invertebrate consumption (Davies et al., 1994). Because of this, the rate of processing in these environments is closely related to temperature, which influences microbial and chemical processes, as well as to flow characteristics (Davies et al., 1994). The ‘terrestrial’ aging of organic matter during dry phases in dryland floodplain river systems influences the quantity and quality of dissolved organic matter and nutrients available when inundation occurs (Baldwin, 1996; Baldwin, 1999; Baldwin and Mitchell, 2000; O'Connell et al., 2000).

The distribution of carbon in dryland floodplain river systems is patchy over a range of scales (McGinness, 1999). Both floodplain and in-channel geomorphology have been shown to significantly influence carbon distribution in Australian floodplain river systems (Thoms and Sheldon 1997; McGinness 1999). Carbon sources may be concentrated in a billabong patch within a floodplain landscape, while within that billabong patches of carbon will exist in different forms and concentrations, for example algae, macrophyte stands and leaf litter. This patchiness exists and varies at both spatial and temporal scales, because of such differences as vegetation composition and water level, which change over the seasons.

Sediments in the floodplain and riparian zone are important sources of dissolved organic carbon, but have received comparatively little attention in ecological literature (Fiebig et al., 1990; Nelson et al., 1991; Wainright et al., 1992). Storage and release of organic
carbon from floodplain sediments is thought to be particularly important in semi-arid river-floodplain systems, where both terrestrial and aquatic primary production occurs on a much smaller scale to that in temperate or sub-tropical zones (Oades and Ladd, 1977; Robertson et al., 1999). Carbon in sediments may be supplied to the river from the floodplain in two main ways: flushing of organic material upon flooding, where non-adsorbed carbon is physically lifted out of the sediments into the water column; and oxidation of carbon adsorbed to sediment particles, where chemical reactions allow release to the water column in different forms. Organic carbon oxidation on the inundated floodplain may occur via electron acceptors such as dissolved oxygen, carbon dioxide and other organic molecules, while under anaerobic conditions potential electron acceptors include nitrate, sulfate and ferric iron (Mulholland, 1981). Temperature is probably the single most important variable in rates of carbon exchange and decomposition, where moisture and oxygen availability are not limiting (Brinson et al., 1981).

Sediment particle size can determine the proportions of carbon stored and released from floodplain sediments. Clay particles (<2μm diameter) adsorb carbon and other nutrients readily due to their generally large specific surface areas, and because their composite minerals are more reactive than those in the larger size fractions (Burford and Bremner, 1975; Oades and Ladd, 1977; Nelson et al., 1991). The higher the clay content of the soil, the greater the retention of carbon. Thus, the clay content and the presence, velocity, and flow path of water are important factors in predicting the distribution of soil carbon, its water solubility, and stream DOC concentrations (Nelson et al., 1991). This influence is apparent within secondary channels. For example, Amoros and Bornette (2002, p. 764) observed that:

'in floodplain waterbodies connected at both upstream and downstream ends, the substratum usually ranges from medium to coarse-grain mineral sediment (i.e. sand, gravel or pebble), depending on the frequency of connection and scouring flow velocity. Waterbodies connected only downstream are characterised by fine mineral sediment (clay, silt) with moderate organic content, resulting mainly from backflow inputs and
deposits combined with the in situ production and deposition of organic matter. The sediment of disconnected waterbodies consists of deposits of autogenic organic matter.'

Particle size is known to vary between other, different river and floodplain geomorphic features, and because of this, quantitative comparative studies on carbon retention and release in different geomorphic units are important for understanding pattern and process in the context of the whole riverine landscape.

Compared to temperate, tropical and sub-tropical zones, little is known about aquatic food webs in arid river systems (Bunn et al. 2006). However recent studies have produced interesting results regarding sources of carbon (Klopatek et al., 1998; Bunn and Davis, 1999; Bunn et al., 2003). It has been suggested that dryland rivers may experience seasonal ‘switches’ between autochthonous and allochthonous energy sources, with ‘an abundance of scrapers or grazers using autotrophic energy sources in early summer to a predominance of shredders feeding on the large amounts of coarse detritus present in late summer’ (Boulton and Lake, 1988). The spatially and temporally fragmented and highly turbid nature of many semi-arid floodplain river systems would suggest that terrestrial or allochthonous carbon should be the primary energy source for aquatic production. However recent studies have suggested that this is not always the case, and that the situation may in fact be quite the reverse. For example, production in waterholes of the major Cooper Creek system in central Australia is dependent upon a filamentous band of algae lining the littoral zone, despite the availability of large quantities of allochthonous carbon sources (Bunn et al., 2003).

The sources, sinks and transformations of organic carbon in Australian floodplain rivers (which are primarily semi-arid/dryland) were reviewed by Robertson et al. (1999). They concluded by hypothesizing that ‘for those rivers where floodplains have been alienated from their river channels by altered flow regimes, and for which there have been changes to the quality of in-channel organic matter, there has been a shift in the balance such that longitudinal fluxes of organic matter and in-channel algal production dominate carbon pools' (Robertson et al. 1999, p.825). This is because allochthonous inputs from
floodplains and riparian habitats have been greatly reduced. This hypothesis is of course debatable, but difficult to argue either way since there is so little information regarding primary carbon sources and trophic status pre-European colonisation. Tockner et al. (1999) have suggested that (at least for the Danube) reducing hydrological connectivity limits flushing of carbon sources to extreme flow events, when retention capacity is lowest, and that therefore carbon sources are less available to riverine organisms. If this is the case, then connection with anabranch channels is all the more important for carbon dynamics in rivers where overbank flooding no longer or rarely occurs. Despite recent progress, the role of hydrological connectivity in terms of carbon dynamics in floodplain rivers is only beginning to be understood, and requires significantly greater research effort, especially in Australia (Robertson et al., 1999).

**Water resource development – ecological impacts**

The alterations to natural connectivity that occur as a result of water resource development (Ward, 1998a) have the potential to affect ecosystem energy fluxes and the internal dynamics of the food web, since these processes are intricately coupled to each other as well as to hydrological connectivity in floodplain river systems (Woodward and Hildrew, 2002). Hydrology and geomorphology together influence carbon concentrations and transport in rivers (Golladay et al., 2000) – hence changes to these parameters will also change carbon dynamics. Yet investigation of the effects of water resource development upon floodplain-river carbon dynamics is rare, particularly in semi-arid systems (McGinness and Thoms 2002; McGinness et al. 2002; Thoms et al. 2005).

There has been growing recognition that temperature is a significant driver of biological processes in floodplain rivers (Humphries et al., 1999; Tockner et al., 2000). Changed seasonality of flows in floodplain rivers changes many processes that rely on temperature. The alteration in timing of floods in many systems has affected the decomposition of organic material (Tockner et al., 2000), where cold winter floods may decrease decomposition rates while summer floods may accelerate decomposition rates. More frequent and prolonged summer and autumn floods in the Murray River (Australia)
induced by water resource development are thought to have decreased standing stocks and increased C:N:P ratios of leaf litter in low lying areas of the floodplain such as secondary channels (Glazebrook and Robertson, 1999). As a consequence, nutrients may be less available to support primary production in this system (which is greatest during late winter and spring floods in floodplain channels), and the remainder of the food web will also be affected (Glazebrook and Robertson, 1999). Since even a single change (e.g. seasonality) to the natural flow regime can result in such significant changes to the carbon dynamics of a system, the cumulative effect upon carbon dynamics of all the changes to hydrological connectivity that occur due to water resource development must be substantial. However these changes have not been traced, explored or integrated as a whole.

Three major ways in which water resource development influence the ecology of river systems at a landscape scale are: Loss of habitat and cues for organisms adapted to natural discharge and water level regimes; loss of both lateral and longitudinal connectivity (reducing the availability of ‘corridors’); and impairment of the ecological roles of the river channel, floodplain and riparian zone (such as the role of the floodplain/riparian zone as a buffer or filter (Dynesius and Nilsson, 1994). Water resource development decreases the spatial heterogeneity and connectivity of physical habitats, shifts functional interactions between terrestrial and aquatic landscape elements and between trophic levels, increases the instability of the physical-chemical environment, and reduces the availability of refugia from harsh physical-chemical conditions (Schlosser, 1991). Fragmentation via alienation of floodplains and changes to flood recurrence frequency deplete floodplain river system productivity, by reducing the exchange of carbon and nutrients, and the emergence and growth of vegetation and invertebrates, and hence reducing the resource base for the remainder of the food web (Boulton and Lake, 1992; Glazebrook and Robertson, 1999). Water resource development has resulted in changed distributions of flora and fauna (Walker, 1985; Bren et al., 1987); changed biodiversity patterns and natural disturbance regimes (Bren and Gibbs, 1986; Ward, 1998a); reduced habitat diversity, species richness and productivity (Petts, 1996); changes in composition, health or vigour of floodplain vegetation.
Restoration and maintenance of natural hydro-geomorphological dynamics is now understood to be the first step toward holistic ecosystem management (Tockner et al., 1999b; Amoros and Bornette, 2002). For the Danube River, Tockner et al. (1999) suggested that restoring hydrological connectivity should maintain higher overall productivity, since a balance between the retention and export of nutrients and organic matter is established, fostering the export of non-refractory organic matter from the floodplain into the river system. However the use of these measures remains limited worldwide, and in many countries, rivers continue to be deliberately isolated from their floodplains and associated carbon pools. Restoration and management of carbon dynamics in floodplain river systems changed by water resource development has in the past has been largely overlooked in favour of ‘iconic’ components of the ecosystem such as major trees, fish and waterbirds. Yet sustainability of the ecosystem as a whole depends upon the maintenance of the correct and natural balance of carbon sources.

2.5 CONCLUSIONS

The ecological roles of physical heterogeneity and hydrological connectivity in highly variable and unpredictable semi-arid ecosystems are not well understood. Different phases of connectivity that influence ecological parameters have been distinguished in heavily modified floodplain waterbodies of temperate systems (Hein et al., 1999; Tockner et al., 1999a; Hein et al., 2003) – but do such phases exist or function similarly in relatively unmodified arid and semi-arid systems? Does surface connection during flow pulses in these systems occur in similar phases and produce similar effects to those found in other systems? Detailed analysis of connectivity is required in diverse landscapes, and should yield better understanding of landscape level functional processes that sustain floodplain rivers (Robinson et al., 2002; Ward et al., 2002). This thesis
investigates phases of hydrological connectivity in a dryland landscape, which over time is dominated by the *disconnection* phase rather than connection.

The concept of ‘natural’ fragmentation over both space and time is significant in terms of both scientific conceptual understanding of ecosystem function and river system management. The function of within-channel flow pulses as drivers of natural hydrological connectivity and fragmentation requires research in order to provide a basis on which to assess and minimise the influences of water resource development (Kingsford, 2000). Flow pulses may be of particular ecological significance in semi-arid systems, especially in terms of maintaining production (Puckridge *et al.*, 1998; Amoros and Bornette, 2002), but few studies have explicitly addressed this issue. As a result, both scientific and management understanding of ecological patterns and processes in these systems is insufficient. This is particularly the case in Australia, where ecosystem functioning within floodplain rivers of semi-arid Australia is thought to be driven by flow pulses (Walker *et al.*, 1995; Puckridge *et al.*, 2000; Sheldon *et al.*, 2002). If these systems are to be developed, maintained, rehabilitated or restored sustainably, significantly more information is required, particularly regarding the ecological role of hydrological connectivity during within-channel flow pulses. In this context, anabranch channels provide ideal subjects for research focus in this thesis, because they are connected to the main river channel by within-channel flow pulses that do not connect the wider floodplain.

Besides being ideal for investigation of the nature of hydrological connections via flow pulses, anabranch channels themselves are of scientific interest. Scientific progress and more effective resource management require better understanding of the complex interactions between landscape components and biotic properties, and their role in sustaining semi-arid floodplain river systems (Malmqvist, 2002; Robinson *et al.*, 2002). How might anabranch channels play a special role in increasing or maintaining spatial heterogeneity and hydrological connectivity in dryland river landscapes? How does artificial fragmentation influence hydrological connectivity with specific floodplain features such as anabranch channels? Can the potential influences of water resource
development upon connectivity between anabranch channels and the river channel be quantified? What effects might such influences have upon the ecological functioning of the system? Answering some of these questions would enable better understanding and management of anabranch channels, especially in terms of their value as ecological resources.

Fundamental information about carbon in Australian floodplain rivers is limited, and Robertson et al. (1999) indicated a need for more data sets over a greater variety of spatial scales. Spatial patterns of carbon distribution in a dryland riverine landscape, and their changes over time during hydrological connection phases, are initially explored in the conceptual model described in Chapter 3 of this thesis. Chapter 4 describes the spatial heterogeneity forming the physical template or background for these patterns. Quantification of the spatial distribution of carbon sources across a riverine landscape forms a basis from which to evaluate the importance of spatial heterogeneity and of hydrological connectivity, and the potential influences of water resource development. Such research will help to clarify the potential ecological role of anabranch channels when they are hydrologically connected to the primary river channel, with regard to carbon storage and supply to the ecosystem as a whole, over various spatial and temporal scales. Variation in carbon quantity and quality across the riverine landscape, between and within patches (e.g. within anabranch channels), may be related to hydrological connectivity in these systems, and has implications for understanding ecological function, as well as important management ramifications (e.g. environmental flow volumes and durations). Chapter 5 of this thesis details a landscape-scale assessment of the distribution of major carbon sources among and within geomorphic patches in a semi-arid, anabranching floodplain river landscape (anabranch channels, the parent river channel and the surrounding floodplain). In addition, Chapter 6 investigates associations between different phases of hydrological connectivity and fragmentation and the quantity and quality of carbon sources in anabranch channels and the parent river channel. Chapter 7 then investigates the uptake of carbon sources into the food web, focusing on the question of whether anabranch channels act as sources for carbon in terms of utilisation as well as in terms of abundance.
Carbon pools in floodplains and their associated geomorphic features (e.g. anabranch channels) need to be managed, like the ‘seedbanks’ of resting stages of vegetation and fauna in dry floodplain sediments (Boulton and Lloyd, 1992). However limited understanding of the ‘natural’ status of carbon pools in these environments is compounded by a dearth of basic information regarding specific influences of water resource development on these pools at a landscape scale. Flow regulation in semi-arid floodplain river systems has reduced the frequency, magnitude and duration of ‘flow pulses’ (Thoms and Sheldon, 2000a). Thus, the roles that hydrological connectivity and anabranch channels play in carbon dynamics and sustaining ecosystem functioning have potentially been altered - yet how these roles have changed is unknown. Chapter 8 of this thesis explores the question of how hydrological connectivity and carbon pools might change in these systems as a result of artificial fragmentation from water resource development.

In summary, spatial heterogeneity and hydrological connectivity are fundamentally and implicitly important in floodplain river landscapes. However the details of the ecological roles of hydrological connectivity and fragmentation are not fully understood worldwide. Moreover, current levels of ecological research and awareness in this area do not reflect the importance of hydrological connections in semi-arid riverine landscapes, although efforts are increasing (Kingsford 2006b). Anabranch channels, one of the most prevalent features of these systems, have been virtually ignored in terms of their potentially significant ecological role. Carbon distribution and exchange is also poorly understood in these systems, even though it forms the fundamental basis of their long-term sustainability. Evaluation of the potential influences of water resource development in these systems is also required, especially in terms of hydrological connectivity and carbon dynamics. These issues form the focus of this dissertation.
CHAPTER THREE: CONCEPTUAL MODEL .............................................................. 60

3.1 INTRODUCTION ........................................................................................................... 60

3.2 CONNECTIVITY AND CARBON EXCHANGE BETWEEN ANABRANCH CHANNELS AND
THE RIVER CHANNEL .............................................................................................. 62

3.2.1 Overview of model ......................................................................................... 63
Spatial component ..................................................................................................... 63
Temporal component ................................................................................................ 66
Phase designation ........................................................................................................ 67

3.2.2 The Disconnection Phase ............................................................................... 71

3.2.3 The Partial Connection Phase ........................................................................ 73

3.2.4 The Complete Connection Phase ................................................................. 75

3.2.5 The Draining Phase ......................................................................................... 77

3.2.6 Differences between this model and others ................................................... 79
3 CHAPTER THREE: CONCEPTUAL MODEL

3.1 INTRODUCTION

Contemporary scientific philosophy emphasises the role and potential of theory, and especially the interplay between its elemental conceptual approaches, models, and empirical content (Pickett et al. 1994; Johnson 1999; Holling and Allen 2002). A model is an abstract representation of a system or process (Turner et al. 2001). It is a simplification of reality (Heemskerk et al. 2003), and may be a verbal or pictorial description, a set of rules, a physical object, or a set of mathematical expressions. Models help define questions and concepts more precisely, generate hypotheses, assist in testing these hypotheses, and generate predictions (Turner et al. 2001). All research has an underlying model of the phenomena it investigates, be it tacitly assumed or explicit (Järvelin and Wilson 2003).

A conceptual model is a qualitative model of a domain consisting of the main concepts and their relationships (Turner et al. 2001). It presents information logically and plainly, and is sometimes referred to as a ‘conceptual framework’ or ‘mental map’, although these are different entities. It shows a set of relationships between factors that are believed to impact or lead to a target condition, and is often presented as a diagram that defines theoretical entities, objects, or conditions of a system and the relationships between them (Heemskerk et al. 2003; Järvelin and Wilson 2003). A conceptual model should be simple, accurate and broad in scope, rather than technical or elaborate, and include the following (Järvelin and Wilson 2003):

- essential objects or components of the system to be studied
- the relationships of the objects that are recognised
- what kinds of changes in the objects or their relationships affect the functioning of the system (and in what ways)
A conceptual model provides a working strategy or scheme (Järvelin and Wilson 2003) requiring few resources and little prior modelling experience (Heemskerk et al. 2003). It is a useful tool for formulating hypotheses and theories, orienting research toward specific sets of research questions, clarifying system boundaries, identifying gaps in existing data and knowledge, revealing assumptions, and improving interdisciplinary communication (Turner et al. 2001; Heemskerk et al. 2003; Järvelin and Wilson 2003).

The approach taken in this thesis conforms with the contemporary scientific view in that it begins with a conceptual model, built from field observation and the literature, tests that conceptual model in the field, and then according to the results re-evaluates and adjusts the model. This procedure minimises reductionist statistical significance testing (Johnson 1999) and instead searches for understanding of the system and how it functions. This approach may be viewed as a simple adaptation or application of the ‘information-theoretic’ paradigm advocated by Anderson et al. (2000), which avoids statistical hypothesis testing concepts and focuses on relationships of variables and on the estimation of effect size and measures of its precision.

The development of the conceptual model used in this thesis provides a framework within which to conduct four major avenues of research:

1. Quantifying the distribution of carbon sources across a semi-arid, anabranching floodplain river landscape (anabranach channels, the parent river channel and the surrounding floodplain - Chapter 5)
2. Quantifying the influence of different phases of hydrological connection and fragmentation upon carbon pools in anabranch channels and the parent river channel (‘natural’ fragmentation – Chapter 6)
3. Determining which of the major available carbon sources the organisms in anabranch billabongs (waterbodies) and the littoral zone of the Macintyre River are assimilating (Chapter 7)
4. Modelling the potential impact of water resource development upon hydrological connection and fragmentation in the system (‘artificial’ fragmentation), and the
potential effects of changes upon carbon pools in anabranch channels and the parent river channel (Chapter 8)

Information derived from each of these research avenues enables reshaping of the conceptual model to better fit reality. It yields a description of the influence of spatial heterogeneity and hydrological connectivity in this landscape, using a combination of field, laboratory and modelled data.

3.2 CONNECTIVITY AND CARBON EXCHANGE BETWEEN ANABRANCH CHANNELS AND THE RIVER CHANNEL

The conceptual model developed for this thesis was created following observation of flow events and their effects in the anabranches of the dryland lower Macintyre River, Australia, and extensive review of relevant literature regarding connectivity, anabranch channels, and carbon sources in semi-arid floodplain river systems (Chapter 2). The basic premise of the conceptual model is that the spatial patchiness of a naturally anabranching floodplain-river landscape (described in Chapter 4) creates variability in carbon quantity and quality (addressed in Chapter 5). This spatial patchiness is augmented through its interaction with temporal variability in hydrological connectivity (Chapter 6). Hydrological connection between riverine landscape patches is important because it can increase the availability of a variety of carbon sources to consumers (Chapter 7). Yet the nature of hydrological connectivity may be changed by water resource development, with implications for carbon availability to the ecosystem (Chapter 8). The result of this layering of multiple sources of variability is multi-scalar complexity in carbon dynamics, in terms of both pattern and process.
3.2.1 Overview of model

Spatial component

At any moment in time, a floodplain river landscape may be viewed as a spatial mosaic of patches (Chapter 2). This mosaic comprises:

a) Complex geomorphic/physical features, primary examples of which include the river channel, its secondary channels or anabranches, and the surrounding floodplain (Figure 3.1). These features are complex at multiple scales – for example, a river channel may contain several in-channel benches; an anabranch channel may contain multiple scours or depressions, and a floodplain may contain a mixture of levees, low-lying areas, splays, or floodways.

b) Hydrological patches across the landscape (e.g. stationary billabongs or waterbodies, flowing river water, or slow-moving floodplain water)

The above interact with and influence each other, creating:

c) Patchiness in carbon distribution, in terms of both quality and quantity (Figure 3.2). This patchiness subsequently influences carbon availability and dynamics, and ultimately determines the state of the ecosystem in both the short- and long-term.
Figure 3.1 Planform view of primary spatial patches in a dryland floodplain river landscape.
CARBON SOURCES

Anabranch

Local autochthonous C sources:
- Benthic primary production (e.g., benthic algae)
- Pelagic primary production (e.g., phytoplankton)

Local allochthonous C sources:
- Leaf litter
- Woody debris
- Vegetation
- Sediment

Downstream transport:
- Sediment
- DOC and POC
- Leaf litter and woody debris

River

Floodplain

C sources:
- Leaf litter
- Woody debris
- Vegetation
- Sediment

Figure 3.2 Major carbon (C) sources of the main river channel and anabranch channels in a semi-arid floodplain river system. Arrows denote symbols used in subsequent diagrams within this chapter.
Overlaying this spatial landscape mosaic is a temporal component. The spatial heterogeneity of the physical and hydrological patches, with their variable carbon quantity and quality, is further complicated by variable hydrological connection and disconnection over time. Water acts as a medium via which carbon sources are moved, altered, and made accessible to consumers over multiple and ever-changing spatial and temporal scales, resulting in a dynamic landscape mosaic with complex patterns, processes and interactions.

**Temporal component**

This model proposes that anabranch channels in dryland riverine landscapes experience four main phases of hydrological connection and disconnection:

1) **Disconnection**
2) **Partial connection**
3) **Complete connection**
4) **Draining**

These phases are caused by fluctuations in stage height within the main river channel (Figure 3.3). During a flow pulse, the connection phases generally occur in sequence, although complete connection is not always achieved (Figure 3.4). Phases can occur in different anabranches within the same reach at different times. Also, parts of an individual anabranch channel may undergo partial connection at the same time that other parts are disconnected. Each of these phases has the potential to create changes or differences in the pools of carbon in both the parent river and anabranch channels (Figures 3.6 – 3.9). Such differences in turn may cause changes in production and respiration within the parent river channel, with possible switching between autotrophy and heterotrophy (Hein et al. 1999; Tockner et al. 1999; Hein et al. 2003). The frequency and duration of each phase will influence the quantity and quality of carbon made available. Changes to the frequency and duration of the phases (e.g. due to water resource development) will therefore impact upon the quantity and quality of carbon available, and hence also upon the functioning of the system.
**Phase designation**

The anabranch channels in this study were each divided into three sites: ‘Entry’, ‘Middle’ and ‘Exit’. This division was necessary for analysis and interpretation of results in terms of the effects of connection phases and different flow paths or directions. The ‘entry’ corresponds to the ‘upstream’ end of the anabranch, while the ‘exit’ corresponds to the downstream end, with respect to the river, regardless of flow direction within the anabranch (Figure 3.5). The ‘middle’ is located approximately halfway between the ‘entry’ and the ‘exit’ points, usually at the planform apex of the anabranch channel. For the purposes of analysis, a site is deemed ‘Partially connected’ as long as complete connection throughout the anabranch does not exist, even if that particular site is fully inundated. A site is only deemed ‘Completely connected’ when the entire anabranch is inundated. For the purposes of analysis, a river site is allocated the phase appropriate to the anabranch site that it is closest to – if the anabranch site is partially connected, then the river site will be affected by that and is also deemed ‘partially connected’.
A) Relative water level changes in anabranch and river channels during each of the four connection phases.

B) Corresponding stage of flow pulse hydrograph

1. Disconnection
2. Partial connection
3. Complete connection
4. Draining

Figure 3.3 Schematic of connection phases and stage height changes in anabranch and river channels during a flow pulse.
Figure 3.4 Spatial and temporal sequence of phases of connection between anabranch channels and the parent river channel. Partial connection is usually followed by complete connection; however it may also be followed immediately by the draining phase, depending upon the geomorphology of the anabranch channel and the character of the flow hydrograph.
Figure 3.5 Schematic representation of the spatial context used for phase designation, showing locations of patch types (river, anabranch, floodplain) and sites for a single individual anabranch-river-floodplain set. E = Anabranch entry; M = Anabranch middle site (apex); X = Anabranch exit (rejoining river). RAE = River above entry; RBE = River below entry; RAX = River above exit; RBX = River below exit. EF = Floodplain adjacent to anabranch entry; MF = Floodplain adjacent to anabranch middle; XF = Floodplain adjacent to anabranch exit.
3.2.2 The Disconnection Phase

The disconnection phase exists during low river flow periods, when stage heights in the main river channel are lower than the ‘commence to flow’ thresholds defined by the morphology of the entries and exits of the anabranch channels. Cycling of carbon is restricted to local sources within each patch or channel type (Figure 3.6). During this phase, the river channel ecosystem functions independently of the anabanches and the surrounding floodplain. Primary and secondary production in the river is dominated and driven by autochthonous sources such as phytoplankton and benthic algae. Hence chlorophyll a concentrations will be at their highest in the river during this phase, as will benthic primary production (GPP) and respiration (R24). Dissolved organic carbon concentrations will be at their lowest in the river channel during the disconnection phase relative to other phases, as other phases are expected to inject the river with extra dissolved organic carbon.

Anabranch channels may be completely dry during disconnection, or may contain a single billabong (waterbody), or a chain of billabongs of varying duration. These billabongs function as ecologically discrete units, and are not connected by surface or groundwater. Carbon source concentrations would be expected to be high in anabranch billabongs during this ‘storage’ phase compared to those in the river channel and those present during other phases. Dry sections of anabranch channel are dominated by bare sediment with associated carbon pools, store leaf litter from fringing trees, and are sparsely vegetated by grasses and pioneer mud-colonising herbs. Anabranch billabongs contain relatively large pools of dissolved organic carbon, algae and phytoplankton. Benthic production, respiration, and production to respiration ratios (P/R ratios) are consequently at their highest in billabongs during this phase, but are dependent upon season and the hydrogeomorphic character of individual billabongs.
1. DISCONNECTION PHASE

Anabranch

- Semi-lentic: dry channel and isolated ephemeral billabongs
- Leaf litter and woody debris accumulation and storage
- Incorporation of carbon into sediments
- High DOC, algae and phytoplankton concentrations
- High billabong production and respiration
- P/R ratios: Billabong and seasonally dependent

River

- Lotic, low-flow conditions
- Low turbidity/sediment transport
- Minimal leaf litter and woody debris
- Low DOC concentrations
- High phytoplankton concentrations
- High littoral production and respiration
- P/R ratio: > 1

Figure 3.6 Schematic representation of relative water levels, available carbon sources, and trophic status in anabranch channels and the main river channel of a semi-arid floodplain river system, during the disconnection phase.
3.2.3 The Partial Connection Phase

The partial connection phase begins with river water flow over the entry or exit point of an anabranch channel, during the rising limb of a flow pulse hydrograph. This phase may be followed by complete connection; alternatively it may be followed by the draining phase, depending upon the geomorphology of the anabranch channel and the character of the flow hydrograph (Figure 3.4). Since billabongs are frequently located immediately inside the entry and exit points of anabranch channels (due to scouring), the partial connection phase immediately results in the re-filling of billabongs and dilution of their existing carbon pools (Figure 3.7). Hence dissolved organic carbon concentrations in the anabranches would be at their lowest at this point, and phytoplankton (chlorophyll a) concentrations much reduced. This initial connection may temporarily inject the river channel with dissolved organic carbon and phytoplankton in the areas immediately adjacent to the anabranch entry and exit points, increasing concentrations in the river slightly, however the dilution effect would be expected to override this increase in local river concentrations reasonably quickly. In addition, labile carbon from the anabranch billabongs is likely to be utilized rapidly upon entering the river, further reducing recorded concentrations.

In other areas of the anabranch channels, the re-wetting of dry sediment and surface leaf litter instigates the release of dissolved organic carbon. However as the dominant direction of water flow during this phase is from the river to the anabranch, minimal or no impact on the river would be expected in terms of dissolved organic carbon from this release. Rather, the effect of this release on both river and anabranch carbon pools would become apparent in subsequent phases. During this phase, primary and secondary production in the river is still dominated and driven by autochthonous sources such as phytoplankton, because the direction of water (and hence carbon) flow is still away from the river and toward the anabranch. Benthic GPP and R24 on the riverbanks and in the anabranches may be slightly depressed by the arrival of turbid, colder water in the flow pulse, but the P/R ratio would still be larger than one (indicating benthic autotrophy), and relatively high compared to subsequent connection phases.
2. PARTIAL CONNECTION PHASE

Anabranch

- Lotic, rising-water conditions
- Increasing turbidity/sediment transport
- Increasing DOC concentrations (release from bank sediments and downstream transport)
- Decreasing phytoplankton concentrations
- Brief injection of DOC and phyto-plankton from anabranch?
- P/R ratio: > 1

Semi-lotic: dry channel and gradual connection of billabongs
- Increasing turbidity
- Leaf litter transport within anabranch
- Diluting DOC and phytoplankton concentrations in billabongs
- DOC release from wetting of dry sediments and litter breakdown
- Billabong P/R ratio: > 1

River

- Lotic, rising-water conditions
- Increasing turbidity/sediment transport
- Increasing DOC concentrations
- Release from bank sediments and downstream transport
- Decreasing phytoplankton concentrations
- Brief injection of DOC and phyto-plankton from anabranch?
- P/R ratio: > 1

Figure 3.7 Schematic representation of relative water levels, available carbon sources, and trophic status in anabranch channels and the main river channel of a semi-arid floodplain river system, during the partial connection phase.
3.2.4  The Complete Connection Phase

The complete connection phase occurs when river discharge is sufficient to cause water to flow throughout an anabranch (Figure 3.8). During this phase, individual anabranch billabongs become successively connected. Water that has flowed into the anabranch flows back into the river channel, carrying with it dissolved organic carbon from billabongs and sediment release, particulate carbon, billabong phytoplankton, and surface leaf litter, increasing the availability of a mix of labile and refractory carbon sources in the river channel ecosystem.

The much greater area of dry sediment and associated surface leaf litter inundated during this phase (compared to partial connection) results in significant releases of dissolved organic carbon into the water column. Concentrations of dissolved organic carbon in the water column of both channel types would be expected to increase significantly during this phase. When flow is strong, carbon is pushed to the point within an anabranch where it empties into the river channel, creating a concentration gradient of all carbon fractions observable both during and after the flow event. The relatively high water velocities and turbulence during this phase, together with high turbidity, would result in phytoplankton (chlorophyll a) concentrations in both the river and anabranch channels lower than any other phase. For the same reasons, benthic GPP and R24 are expected to be at their lowest during this phase. Although in realistic terms metabolic activity during this phase would be minimal, that which remains may begin to switch to heterotrophy (P/R ratio of less than one), because of the new availability of mixed carbon sources from anabranch channels.
3. COMPLETE CONNECTION PHASE

Anabranche

- Lotic: billabongs all connected; continuous flow
- High turbidity and sediment transport
- Leaf litter and woody debris transport
- Diluted DOC and phytoplankton concentrations
- Extensive DOC release from wetting of dry sediments
- Depressed production and respiration: P/R ratio: ? < 1

River

- Lotic, high water conditions
- High turbidity/sediment transport
- High DOC concentrations
- Low phytoplankton concentrations
- Injection of DOC, POC, phytoplankton, leaf litter from anabranche
- Depressed production and respiration
- P/R ratio: ? < 1

Figure 3.8 Schematic representation of relative water levels, available carbon sources, and trophic status in anabranche channels and the main river channel of a semi-arid floodplain river system, during the complete connection phase.
3.2.5 The Draining Phase

The draining phase begins when complete connection ceases, usually during the receding limb of a flood hydrograph. Water drains out one or both ends of the anabranch, carrying various dissolved and suspended carbon sources (Figure 3.9). Some of these sources enter the river; others are deposited within the anabranch. Billabongs begin to re-form as separate waterbodies, and the anabranch is gradually disconnected from the river, usually one end at a time. Sediment is deposited within the anabranch and on the riverbanks, covering the previous surface and any remaining leaf litter.

Concentrations of dissolved organic carbon would be expected to continue to increase in the anabranch channels and in the river channel downstream of the drainage points during this phase. Continued leaching of leaf litter and surface sediments, combined with reduced volumes of water as the anabranches drain, billabongs separate, and the falling limb of the flow pulse hydrograph passes, facilitate concentration of both dissolved organic carbon (DOC) and phytoplankton.

During this phase, both anabranch and river phytoplankton concentrations would begin to increase again as hydraulic conditions stabilize and suspended sediment settles out, allowing greater light penetration. As the draining phase progresses, a benthic and pelagic primary production boom would occur in the anabranches and to a lesser degree in the river channel. This may cause a switch back to autotrophy in the water column, especially in the anabranches. However since benthic R24 would also be at its highest due to the abundant carbon resources made available by connection, P/R ratios would be at their lowest, with benthic metabolism dominated by heterotrophy in the river channel, and potentially also in the anabranches. Benthic metabolism in the river channel during this phase would be expected to be generally elevated due to the increased availability of a) highly-labile anabranch billabong carbon sources, such as phytoplankton and algae; and b) mixed-quality allochthonous carbon from anabranches such as leaf litter and dissolved organic carbon released from sediments.
4. DRAINING PHASE

Lotic, falling water conditions
Increasing DOC concentrations (draining from anabranch, release from sediments and downstream transport)
Increasing phytoplankton concentrations
Sediment deposition

P/R ratio: < 1

Figure 3.9 Schematic representation of relative water levels, available carbon sources, and trophic status in anabranch channels and the main river channel of a semi-arid floodplain river system, during the draining phase.
3.2.6 Differences between this model and others

The conceptual model proposed in this thesis is based on a reach of the lower Macintyre River, Queensland, Australia. It differs from those previously described in the literature (Hein et al. 1999; Tockner et al. 1999; Amoros and Bornette 2002; Hein et al. 2003) in several respects. It describes the ecological functioning of a floodplain river landscape in a southern hemisphere, Australian context, and focuses on semi-arid zone floodplain rivers rather than temperate-zone, tropical or sub-tropical rivers. The model considers anabranch channels rather than oxbows or cutoffs, and humans have not significantly modified the channels described – they are in a near-natural state in terms of geomorphology, sediment and vegetation. In addition, the anabranch waterbodies examined are ephemeral, rather than permanent or semi-permanent. The Draining Phase is distinguished as a period during which distinct processes occur and particular effects take place, while the Partial Connection Phase is characterised by surface water connection, rather than subsurface seepage. Importantly, the hydrological connection phases described are not complicated by groundwater exchange, since the water table in the study area is deeper than the maximum depth of the anabranch channels. Finally, a broader landscape scale view is employed, with fewer detailed analyses.

Subsequent chapters in this thesis will use this conceptual model as a background against which to investigate the distribution of carbon, the influence of hydrological connectivity, and the impact of water resource development in a semi-arid, anabranching floodplain river landscape.
CHAPTER FOUR: STUDY AREA .................................................... 81

4.1 THE MACINTYRE RIVER CATCHMENT......................................................... 81
  4.1.1 Climate ...................................................................................................... 81
  4.1.2 Geomorphology ........................................................................................ 84
  4.1.3 Anabranch channels ................................................................................ 85
  4.1.4 Soils and sediments .................................................................................. 90
  4.1.5 Hydrology and flooding ............................................................................ 90
  4.1.6 Vegetation and fauna ................................................................................. 94
  4.1.7 Water quality ............................................................................................. 96
  4.1.8 Land and water use ................................................................................... 98

4.2 SITE SELECTION ............................................................................................. 100

4.3 THE STUDY REACH ...................................................................................... 101
  4.3.1 Overview ................................................................................................. 101
  4.3.2 Anabranch 1 ............................................................................................ 108
  4.3.3 Anabranch 2 ............................................................................................ 112
  4.3.4 Anabranch 3 ............................................................................................ 112
  4.3.5 Anabranch 4 ............................................................................................ 113
  4.3.6 Anabranch 5 ............................................................................................ 113
  4.3.7 Anabranch 6 ............................................................................................ 113

4.4 SUMMARY ....................................................................................................... 120
4 CHAPTER FOUR: STUDY AREA

4.1 THE MACINTYRE RIVER CATCHMENT

The Macintyre River Catchment forms a major portion of the northern Murray-Darling River Basin in eastern Australia. It extends in a general east-west direction from the Great Dividing Range, at elevations of up to 1350 m ASL, to the western plains, at elevations of below 150 m ASL (Figure 4.1). The Macintyre River forms the border between the states of Queensland (QLD) and New South Wales (NSW), and it is renamed the Barwon River near Mungindi. For this reason, the catchment is also often called the ‘Border Rivers’ catchment, basin, or region. The total catchment area of the Macintyre-Barwon River, excluding the Moonie, from the Moonie-Barwon junction (45 km downstream of Mungindi) is 49,500 km$^2$, of which 25,600 km$^2$ is in NSW.

4.1.1 Climate

The Macintyre River is located between the summer-rainfall dominated systems of northern Australia and the winter-rainfall systems of southern Australia. As a result, it is variably influenced by weather cycles and events originating from both. The climate is dominantly semi-arid, with associated unpredictability and variability in rainfall and discharge. Average temperatures increase from east to west across the catchment (Table 4.1). The western or lower Macintyre River experiences hot summers with associated high evaporation rates, and mild winters. Evaporation exceeds precipitation in the catchment, ranging from 1200 mm per annum in the east to 2000 mm in the west.

<table>
<thead>
<tr>
<th>Temperature</th>
<th>Summer</th>
<th>Winter</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Max.</td>
<td>Min.</td>
</tr>
<tr>
<td>East Catchment</td>
<td>27°C</td>
<td>14°C</td>
</tr>
<tr>
<td>West Catchment</td>
<td>35°C</td>
<td>20°C</td>
</tr>
</tbody>
</table>

Table 4.1 Seasonal temperature statistics for the Macintyre River Catchment.
Figure 4.1 The Macintyre River Catchment, showing the location of the Study Reach (red box).
Average annual rainfall decreases from over 900 mm at Tenterfield in the east of the catchment, to less than 500 mm at Mungindi in the west (Table 4.2). Monthly rainfall is highest during summer, from December through to February. Intense rainstorms are generated by depressions, which originate in the northern tropics over the oceans and intensify as they move southwards and over the continent. These storms can deposit 50% of the total annual rainfall of an area in a matter of days, with daily totals of over 200 mm causing floods. Rain during winter results from low-pressure systems and associated cold fronts that normally affect the southern areas of the continent. Long-term rainfall patterns are extremely variable. For example, at Mungindi in the west of the catchment, maximum and minimum mean monthly rainfalls range from 547% to 0.2% of the mean. Frequent spells of near total drought are interspersed with periods where rain falls consistently for a few months. These factors together with extreme evaporation rates make the western lowland parts of the Macintyre River catchment effectively ‘dryland’ and heavily dependent upon flows from upstream.

Table 4.2 Annual climate statistics for the Macintyre River Catchment.

<p>| Source: Queensland Dept. Natural Resources and Mines Patched Point Dataset/Datadrill |
|---------------------------------------------------------------|-----------------|-----------------|-----------------|</p>
<table>
<thead>
<tr>
<th>Station</th>
<th>Tenterfield</th>
<th>Goondiwindi</th>
<th>Mungindi</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Rainfall (mm)</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Annual mean (1956-2005)</td>
<td>907</td>
<td>633</td>
<td>495</td>
</tr>
<tr>
<td>Annual mean (2001-2005 study period)</td>
<td>750</td>
<td>587</td>
<td>440</td>
</tr>
<tr>
<td><strong>Temperature (°C)</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean annual daily maximum</td>
<td>21.4</td>
<td>26.7</td>
<td>27.3</td>
</tr>
<tr>
<td>Mean annual daily minimum</td>
<td>8.1</td>
<td>13.0</td>
<td>12.6</td>
</tr>
</tbody>
</table>
4.1.2 **Geomorphology**

The Macintyre River Catchment can be divided into three zones: the Upland, Billabong and Plains Zones (McCosker 1996). The following description will focus upon the western Plains Zone that extends from about 20km west of Goondiwindi to the end of the catchment near Mungindi. The Plains Zone is the larger hydrogeomorphic template within which the study area of this project is set, and is characterized by an extensive alluvial flood plain. Anabranches are common, and major flooding can produce an extensive, shallow body of water covering the majority of the valley floor. Because of the low slope and poor drainage, flooding may persist for several weeks.

Five general reach types have also been identified within the Macintyre River catchment: Pool, Constrained, Armoured, Mobile and Anabranching (Thoms *et al.*, 1997). According to this classification scheme, the Macintyre River in the Plains Zone is dominated by ‘lowland anabranching’ or ‘lowland meandering’ reaches. These reaches are generally narrower and deeper than those upstream, are characterized by high sinuosity, and are low energy, with attenuated flow peaks compared to those upstream. Pools are the dominant habitat type, followed by runs, and individual logs and root cover provide most instream fish habitat. More specifically, the Macintyre River downstream of Goondiwindi (Lat. 28°32’30” Long. 150°18’27””) is an anabranching, cohesive sediment system, with relatively uniform and narrow width, low gradient (<1°) and stable banks. It is highly sinuous (Table 4.3), exhibits very little lateral migration, and appears to relocate by avulsion. Stream power is relatively low, and the channels are often canal-like in cross-section. These characteristics place it as a ‘Type 1’ anabranching river system, according to the classification scheme described by Nanson and Knighton (1996).

<table>
<thead>
<tr>
<th>River reach</th>
<th>Channel length (km)</th>
<th>Sinuosity</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dumaresq R. to Callandoon Ck.</td>
<td>35.4</td>
<td>1.39</td>
</tr>
<tr>
<td>Callandoon Ck. To Terrewah Gauge</td>
<td>83.6</td>
<td>2.18</td>
</tr>
<tr>
<td>Terrewah gauge to Coomonga Ck.</td>
<td>53.3</td>
<td>2.57</td>
</tr>
</tbody>
</table>
Upstream of Goondiwindi, high flows usually remain within the banks of the main river channel. Downstream of Goondiwindi channel capacity is markedly reduced (Table 4.4), and high flows are dispersed through anabranch channels.

### Table 4.4 Channel capacity of the Macintyre River channel at selected locations in megalitres per day (Connell-Wagner, 1991).

<table>
<thead>
<tr>
<th>Gauging station</th>
<th>Bankfull capacity (ML day$^{-1}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Goondiwindi</td>
<td>&gt; 100 000</td>
</tr>
<tr>
<td>Terrewah</td>
<td>&gt; 9 000</td>
</tr>
<tr>
<td>Boomi Weir</td>
<td>3 260</td>
</tr>
</tbody>
</table>

#### 4.1.3 Anabranch channels

Anabranch channels are a significant patch type in the lower Macintyre River landscape. In the 150 km reach of the lower Macintyre River from Goondiwindi to Boomi, a total of 69 anabranch channels were identified using aerial photos, topographic maps and field truthing (Thoms et al. 2005). Combined, anabranch channels comprise 62% of the total channel length in this reach, with a total length of more than 236 km, compared to 143 km of river channel. The median length of individual anabranch channels is approximately 0.9 km, but they range in length from 0.32 km to 113 km (Thoms et al. 2005). Despite this dominance of anabranches in terms of channel length, the river channel has a slightly greater total surface area in the reach (658 ha) compared to anabranch channels (586 ha), because the mean wetted perimeter of the river channel (46.00 ± 10.65 m) is nearly twice that of the mean for anabranches (24.81 ±11.81 m).

The largest of the anabranches in this area are Whalan Creek, the Boomi River and Callandoon Creek (or Branch). Flows through these and other large anabranch channels (including Dingo Creek and Coomonga Creek) are regulated for irrigation purposes by various structures such as weirs. Others of various sizes have been converted to on-farm water storages by damming or weirs, at one or both ends. However there are many types of anabranch channels in this area, the most common being relatively small in cross-
sectional dimension and length (median 0.9 km). The character and roles of these more common smaller anabranches are poorly understood.

Four major geomorphic types of anabranch channel are distinguishable in the Goondiwindi to Boomi reach (Thoms et al. 2005; Figure 4.2):

1. Single channel anabranches that have single, well-defined entry and exit points to and from the main channel.

2. Anabranch channels with a single connection to the main river channel at one end only (usually the exit or downstream end). These typically feature a distinct channel including large billabongs. These channels often meander out into the floodplain and curve back toward the main channel only to terminate within 100m of the main channel.

3. Single anabranches that have one outlet to the main channel and the other outlet emptying into a separate anabranch or cutoff channel. Channel dimensions of the Type 3 channel are distinctly different to those of the anabranch channel with which it connects.

4. Complex anabranches. These have multiple entry or exit points joining the main river channel.

Type 1 anabranches are the most common (52% of the Goondiwindi – Boomi reach), followed by types 2, 3, and 4. They are also the dominant type in terms of both length and surface area (Table 4.5). The anabranches sampled as part of this study include examples of each of the four types (Section 4.3).
Figure 4.2 Anabranch planform types of the lower Macintyre River, in order of increasing channel complexity. Source: (Southwell 2002). Used with permission.
Table 4.5  Summary statistics for anabranch channel planform types, Goondiwindi to Boomi.

<table>
<thead>
<tr>
<th>Anabranch planform type</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total number of channels</td>
<td>36</td>
<td>15</td>
<td>13</td>
<td>5</td>
</tr>
<tr>
<td>Total length (km)</td>
<td>147</td>
<td>24</td>
<td>52</td>
<td>13</td>
</tr>
<tr>
<td>Total area (ha)</td>
<td>364</td>
<td>60</td>
<td>129</td>
<td>33</td>
</tr>
</tbody>
</table>

The distribution of anabranch channels also varies along the length of the lower Macintyre River. They are most abundant approximately halfway between Goondwindi and Boomi (Figure 4.3), and increases in their abundance appear to coincide with transitions to lower river gradients (Southwell 2002). This is consistent with the concept that rivers construct multi-channel systems in order to concentrate stream flow and maximise bed sediment transport through areas of low gradient (Nanson and Knighton 1996). The study area for this thesis is located where anabranch abundance is at its highest.
Figure 4.3 Anabranch channel distribution and river elevations between Goondiwindi and Boomi. Adapted from Southwell (2002).
4.1.4 **Soils and sediments**

The surface of the Plains Zone is composed of recent (Quarternary, Pleistocene) alluvia (McCosker 1996). These sediments are deposits of sandy and silty material with minor amounts of gravel on which brown to grey to black clay soils have formed. Black earths intermingle with grey and brown soils of heavy texture, the latter dominant in alluvial situations. The clay content of these soils is between 50 – 80 %, and they develop wide, deep cracks and high strength when dry. When wet, they become plastic, sticky and weak. The volume expansion of these clays from dry to wet can exceed 50%, giving them extremely high initial infiltration rates, which decline rapidly with long duration storms or with flooding. Under cultivation the floodplain soils of the Plains Zone are highly fertile, but are vulnerable to flood erosion, even at very low slopes. They cannot be worked for quite some time after they have become saturated, and as a road medium, are extremely poor and remain untrafficable for long periods during and after rainfall or inundation (McCosker 1996). This makes the logistics of fieldwork difficult.

4.1.5 **Hydrology and flooding**

Daily discharges for the lower Macintyre River are recorded at Goondiwindi (at the town and also at the weir); at Terrewah, a property directly opposite the sites chosen for this study; and at Boomi Weir, downstream of the study area (see Table 4.6 for annual statistics). Flows are variable, with recorded annual flows at Goondiwindi (1949-2003; Figure 4.4) ranging from 61,000 ML day$^{-1}$ (1994/95) to 4,488,000 ML day$^{-1}$ (1955/56).

The flow duration curve derived from the Goondiwindi gauge (Figure 4.5) is typical of the influence of regulation on the hydrology of a river system – elevated and consistent low flows predominate; while the occurrence of medium sized and large flows is reduced, with the high flows not as heavily affected as medium flows. Flow magnitudes decrease with distance downstream, reflecting a change in channel dimensions and the influence of anabranch channels (Table 4.6).
Table 4.6 Annual hydrology statistics for selected gauging stations of the lower Macintyre River (1917 – 2003).

<table>
<thead>
<tr>
<th>Gauging station</th>
<th>Median (ML/year)</th>
<th>Maximum (ML/year)</th>
<th>Minimum (ML/year)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Goondiwindi</td>
<td>585, 704</td>
<td>4,488,000 (1955/56)</td>
<td>61,000 (1994/95)</td>
</tr>
<tr>
<td>Terrewah</td>
<td>376,000</td>
<td>1,274,000 (1997/98)</td>
<td>70,000 (1993/94)</td>
</tr>
<tr>
<td>Boomi Weir</td>
<td>166,000</td>
<td>390,000 (1995/96)</td>
<td>20,000 (1993/94)</td>
</tr>
</tbody>
</table>

The flood season is summer-autumn in the Macintyre River. Flooding occurs throughout the entire length of the catchment, and can be derived from either local or upper catchment rainfall, or both. Flow distribution across the floodplain can vary considerably from one event to the next depending on the source of flooding and the timing of the peaks. Intense but localized summer thunderstorm activity can produce local flooding events. In addition, long-duration cyclonic storms can produce almost as much precipitation on the plains as in the hills, resulting in major floods. Thus, the western plains zone can be in effect flooded twice. These major floods can spread over an immense area, with complete isolation of landholders in rural areas, which can persist for long periods. The largest recorded floods in the Goondiwindi area occurred in March 1890 and February 1976 (although this was in some areas exceeded by the 1956 flood), with peak stage heights at Goondiwindi of 10.21m and 10.48m respectively. The average recurrence intervals of floods of various sizes are presented in Table 4.7.

There is an aquifer system in the area between Goondiwindi and Mungindi, with two layers, the average combined thickness of which is about 25 m. These water bearing layers are not very productive as aquifers. The relationship between the surface water features and the groundwater system in this area is not well understood, however in the vicinity of the sites used for this study the depth of the water table (14 - 16 m; QLD Dept. Natural Resources and Mines) is such that there is minimal or no interaction between the water table and the anabranch channels.
Figure 4.4 Historical hydrograph of Macintyre River discharge at Goondiwindi (1949 – 2004).

Data courtesy of NSW DIPNR.
Figure 4.5 Flow duration curve (log scale) for the Macintyre River at Goondiwindi (1949 – 2003).
### Table 4.7 Annual flood frequencies for the Macintyre River at Goondiwindi.

<table>
<thead>
<tr>
<th>Annual Exceedence Probability</th>
<th>Natural Discharge (ML day⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 in 2</td>
<td>56,585</td>
</tr>
<tr>
<td>1 in 5</td>
<td>119,316</td>
</tr>
<tr>
<td>1 in 10</td>
<td>165,234</td>
</tr>
<tr>
<td>1 in 20</td>
<td>186,209</td>
</tr>
<tr>
<td>1 in 50</td>
<td>227,609</td>
</tr>
<tr>
<td>1 in 100</td>
<td>256,448</td>
</tr>
</tbody>
</table>

Flood events are thought to play important roles in the aquatic ecosystem of the Macintyre River. The frequency of overbank flow controls recharge patterns in the floodplain and anabranch billabongs. The 1996 Environmental Scan of the Border Rivers Catchment (McCosker, 1996) commented that floods in the Macintyre River system have the potential to sweep organic material into the main stream from well vegetated anabranches, floodways, and the floodplain, providing a source of energy for instream biota. The current study investigates this potential, in terms of the role of hydrological connectivity in the lower Macintyre River system, and the role of anabranch channels as sources of food energy (carbon) for the river ecosystem.

#### 4.1.6 Vegetation and fauna

The composition of the riparian zone and floodplain vegetation communities downstream of Goondiwindi is markedly different from upstream reaches (McCosker 1996; Johnson 1999; McCosker 1999; Markham 1999a; 1999b; Schiller 1999b). River red gums (*Eucalyptus camaldulensis*) dominate the fringing riparian tree communities on mid and upper banks along the main river channel. Coolabahs (*E. microtheca*) occur in association with river red gums, and are dominant on the floodplain and the banks of the anabranch channels and billabongs. Belah (*Casuarina cristata*) and weeping bottlebrush are found on the higher floodplain, and are replaced by river paperbark (*Melaleuca spp.*) on lower banks and mid channel bars. There is an understorey of river cooba (*Acacia stenophylla*) and Lignum (*Muehlenbeckia florulenta*), together with Warrego summer
grass (*Paspalidium jubiflorum*). The presence of these flood dependent species reflects the historical importance of overbank flows to the ecology of this area.

There is a general lack of aquatic macrophytes in the lower Macintyre River system. On average, 90% of the streambeds and banks are bare of vegetation. This is thought to be a consequence of high turbidity and the perhaps the presence of large numbers of European carp (McCosker 1996; Johnson 1999; McCosker 1999; Markham 1999a; 1999b; Schiller 1999b). An exception occurs after flooding, when the numerous small floodplain and anabranch billabongs support a range of emergent and floating macrophytes. Species include nardoo (*Marsilea mutica*), *Vallisneria* spp., *Myriophyllum* spp., *Azolla* spp. and duckweed (*Lemna*, *Wolffia* and *Spirodea* spp.). Other wetlands present include sedgelands in shallow depressions on the floodplain, and larger lagoons that occupy sections of abandoned river channel.

Biofilms are a primary food source in rivers that occur on submerged surfaces. Where macrophytes are lacking, they contribute the majority of benthic primary and secondary production in freshwaters. Their rate of growth is affected by temperature, nutrients and shading from riparian vegetation, while their occurrence is determined by stable substrate, favourable flows and low rates of sedimentation. Biofilm development has been rated as generally ‘moderate’ to ‘excellent’ throughout the Macintyre River catchment. Biofilm development in the main river channel at Terrewah was rated as ‘poor’ during an assessment of river condition carried out during 1998-99, but this was following a series of wet years with associated frequent high flows, which may have depressed biofilm development (McCosker 1996; Johnson 1999; McCosker 1999; Markham 1999a; 1999b; Schiller 1999b).

Macroinvertebrates, along with bacteria and fungi, facilitate the breakdown of organic debris in river systems and are food for fish and other organisms. Changes in their diversity, species composition or abundance are thought to reflect overall changes in the ecosystem. Generally, high diversity and abundance reflect good river health. Macroinvertebrate communities in the main channel of the lower Macintyre River display
lower abundance and species diversity than other reaches upstream. This has been 
attributed to less habitat diversity compared to upstream sites, with no riffles and the 
general lack of macrophytes.

Native fish species present in the main river channel include golden perch (*Macquaria 
ambigua*), silver perch (*Bidyanus bidyanus*) and Murray cod (*Maccullochella peeli*). 
Bony bream (or bony herring) (*Nematolosa erebi*) are abundant in anabranches and other 
billabongs. Bony bream occupies turbid water and can tolerate a wide range of 
temperatures, salinities and other conditions. It is an omnivore that feeds on muddy 
detritus, algae, aquatic plants, aquatic insects and crustaceans. It is therefore likely to be 
a key link for carbon cycling through the food web, being an important food source for 
golden perch and Murray cod, as well as many water bird species. Hydrological 
connection between floodplain waterbodies and the main channel is important for the 
availability of this bony bream as a food item to predators in the main channel. Mosquito 
fish (*Gambusia holbrooki*) and European carp (*Cyprinus carpio*) are exotic fish species 
that also occur in large numbers. They are tolerant of a wide range of habitat conditions 
and have been shown to adversely affect native invertebrate, fish, and macrophyte 
communities (McCosker 1996; Johnson 1999; McCosker 1999; Markham 1999a; 1999b; 
Schiller 1999b).

### 4.1.7 Water quality

Nutrients (total phosphorus and total nitrogen), electrical conductivity (salinity), turbidity 
and dissolved oxygen are monitored at several sites in the Macintyre River catchment. 
Data are of variable quality and collection often haphazard. There are conflicting reports 
regarding the nutrient status of the Macintyre River system (Bek and Robinson 1991; 
Houldsworth 1995; Powell 1999; Schiller 1999a; McGloin 2001).

Dissolved oxygen concentrations are generally within the guidelines for the prevention of 
stress to fish (>5mg/L; Table 4.8), but are variable and frequently fall below guideline
levels. Powell (1999) reported that most sites within the Macintyre River catchment exhibit ‘moderate’ to ‘poor’ water quality in terms of total phosphorus and total nitrogen concentrations, and that concentrations are usually higher than those reported by ANZECC (1992) to be a trigger for excessive algal growth. In contrast, McGloin (2001) analysed data from 1990-99 (and sometimes from 1960 onward depending on the variable) and stated that total phosphorus and total nitrogen concentrations were generally below or within the upper limits for preventing nuisance algal growth. Overall, there are few quality data concerning algae concentrations in the Macintyre River system, or how these correlate with nutrient concentrations.

Turbidity in the Macintyre River has consistently been higher than other northern NSW rivers (Houldsworth 1995). Bek and Robinson (1991) suggested an environmental turbidity guideline of less than 50 NTU for the protection of aquatic ecosystems. The Macintyre River generally has median turbidity levels below these recommended levels (Table 4.8), however readings of 800-1000 NTU are not uncommon (usually associated with floods), and turbidity levels are increasing over time at several stations. Trends in electrical conductivity (a substitute measurement for salinity) in the Macintyre River also vary depending upon location. Some tributaries display increasing salinity levels, which may be of concern for the future.

Table 4.8 Mean water quality parameters for the lower Macintyre River upstream of and adjacent to the study reach.


<table>
<thead>
<tr>
<th></th>
<th>Cond. µS/cm</th>
<th>Turbidity NTU</th>
<th>pH</th>
<th>TDS mg/L</th>
<th>TP mg/L</th>
<th>TN mg/L</th>
<th>DO mg/L</th>
</tr>
</thead>
<tbody>
<tr>
<td>Goondiwindi</td>
<td>299</td>
<td>51</td>
<td>8.12</td>
<td>170</td>
<td>0.093</td>
<td>0.632</td>
<td>8.99</td>
</tr>
<tr>
<td>Terrewah</td>
<td>215</td>
<td>83</td>
<td>7.58</td>
<td>127</td>
<td>N/A</td>
<td>N/A</td>
<td>N/A</td>
</tr>
</tbody>
</table>
4.1.8 **Land and water use**

The Macintyre River catchment has experienced large-scale changes in land use over the last 50 years. Originally dominated by sheep farming, cattle were introduced after massive sheep losses from large floods. Dryland cropping (and associated vegetation clearance) started to increase in the 1950’s, followed by summer cropping during the 1970’s and 80’s, and from the early 1980’s onward, rapid development of irrigation, particularly for cotton growing in the lower Macintyre River. Irrigated agriculture, especially cotton production, is now the most economically important land use in the Macintyre River system.

Three dams collect and regulate discharge in the catchment: Glenlyon Dam on Pike Creek (253 000 ML storage capacity; 1976); Coolmunda Dam (75 000 ML, 1968); and Pindari Dam (35 500 ML, 1969). Pindari Dam was enlarged in 1994 to 312 000 ML. Other secondary barriers for water supply within the lower Macintyre River include Goondiwindi Weir (storage capacity 1 800 ML); Boggabilla Weir, (5 850 ML); and Boomi Weir (354 ML).

In addition to dams and weirs, on-farm (or ‘off-stream’) earthen storages capture water from large floods that the upstream dams cannot contain. They may be filled either from overland flow, or more commonly by pumping water from the river during high flows. Total storage of river and flood water by these facilities in the lower Macintyre River floodplain is significant, and has increased rapidly over the last 15 years, together with the number and volume of water abstractions. Thus land and water resource developments may have resulted in significant alterations to a number of flow statistics.

Irrigation storages or dams can change the hydrological regime in rivers by generating short-term variable flows during peak demand and constant flows at other times. This is because they capture water from large rainfall events in the catchment to allow for later controlled release. This causes long-term reductions in flows by trapping water that would have caused hydrological connection and flooding downstream and increasing evaporation losses from the system. It can also dramatically alter the seasonality of flows.
(although change in seasonality is not an issue in the Macintyre River system), thereby also affecting ecological responses in the system downstream.

The construction of levee banks and on-farm storages has also changed flood flow patterns across the floodplains of the lower Macintyre River, with diversion and concentration of flows along a few selected anabranch channels, and the partial or total isolation of others. A general decline in the number, size and condition of anabranch billabongs and other wetlands in the lower Macintyre River system has been directly linked to the influence of upstream dams, diversions, small weirs and on-farm storages upon discharge (Kingsford 1999). The impacts of such changes are many, complex, and above all, not well understood. The over-arching effect is one of altered connectivity across the river-floodplain landscape, both spatially and temporally. Investigation of the potential influence of these alterations upon the ecology of the Macintyre floodplain river system forms part of this thesis.
4.2 **SITE SELECTION**

The lower Macintyre River was chosen for this study for several reasons:

- It is typical of Australia’s lowland rivers. ‘Typical’ features include the fact that it is allogenic and regulated, has a predominantly semi-arid climate, low gradient, wide floodplains, complex geomorphology, and an abundance of secondary channels.
- The complex, patchy geomorphology of the lower Macintyre River, especially the variety of anabranches, makes it ideal for the application of the concepts of connectivity and fragmentation and the testing of their roles in floodplain river systems.
- The flow regulation of the Macintyre River was thought to be ideal for this study because:
  1. It provides an opportunity to examine the effects of ‘artificial fragmentation’ or water resource development
  2. It increases the probability of the occurrence of flow pulses sufficient to connect floodplain anabranche channels with the main channel. This is an important factor considering: a) the need to sample connection events; b) the duration of field work for a project such as this is limited to <3 years and c) the effects of El Nino events and natural variability may prevent connection for several years at a time.
- Several hydrological gauging stations are present along the Macintyre River.
- The lower Macintyre River has been subjected to some of the most rapid water resource and floodplain development seen in Australia, and concerned landowners, managers and the wider community are keen to see the production of useful information to contribute to the understanding and sustainable management of the river system as a whole.
4.3 **The Study Reach**

4.3.1 **Overview**

This study focuses on a 15.8 km reach of the lower Macintyre River between Goondiwindi and Boomi (Figure 4.6). This reach is located between 75 and 91 river km downstream of Goondiwindi, and is ideal for study because it contains the highest concentration of anabranch channels on the lower Macintyre River. It is also easily accessible, and the riverbanks, anabranches and riparian zone are in relatively good condition. The reach is part of the agricultural property ‘Macintyre Downs’, between ‘Callandoon South’ and ‘Riverview’. Six anabranch channels were selected for study (Sections 4.3.2 to 4.3.7), encompassing a range of geomorphic types, shapes and sizes.

The anabranch channels within the reach form a complex interconnecting maze. At a landscape scale, they are the major contributors to the patchiness and habitat heterogeneity of the river-floodplain system in this area. They create this heterogeneity vertically, horizontally and temporally. The anabranch channels in this reach vary in size and shape, but all commence to flow at low discharges. These anabranch channels (and the main river channel) have been relatively well protected for the last 20 years from the effects of stock and cropping. A buffer zone of dense riparian vegetation surrounds most of the anabranch channels. This area is lightly used for cattle grazing, and exists partially because of the presence of the anabranches as physical impediments when dry and as barriers when wet or flowing. Moving from this buffer zone in a perpendicular direction away from the channels, floodplain landuse varies from cattle pastures to general cropping to irrigation channels, cotton fields and on-farm storages.

In general, the climatic, physical, hydrological and biological characteristics of this reach are consistent with those described for the western Plains Zone of the lower Macintyre River and its catchment. Discharges throughout the lower Macintyre River are generally referred to using the Goondiwindi town gauge. However there is a gauging station within
the study reach, at the property ‘Terrewah’, on the NSW side of the river opposite Macintyre Downs (Figure 4.6). A combined discharge and stage height hydrograph for Terrewah during the study period is presented in Figure 4.7. This is followed by a stage height hydrograph indicating the timing of fieldwork undertaken for this study (Figure 4.8). Some attenuation of flow occurs between the Goondiwindi and Terrewah gauging sites during flow and flood events, and this is accounted for during analyses, wherever relevant.

Riverbed sediments in the reach vary from silty sand to sand, with some gravel deposits. Bank sediments are generally silty clay or fine clay, with moderate stability, however as the river is active in this reach, some areas are naturally eroding. Floodplain areas are dominated by cracking clay soils and black earths, with all of the characteristics described in Section 4.1.4. Anabranch bed sediments are dominated by fine clay or silty clay, with some sandy deposits, while anabranch bank sediments are generally fine or silty clay.

All of the anabranches in this reach are disconnected from the main river channel 95% of the time (Southwell 2002; Thoms et al. 2005). However, most of them hold water in the form of small ephemeral waterbodies (billabongs) for up to a year, depending on local rainfall, evaporation, and flooding conditions. These frequently dry up entirely. These billabongs are often located in bends of the anabranch channels, suggesting that they originate and perhaps persist because of local scouring during flood events. The depth, shape and size of the billabongs vary, but they are generally very shallow, and much wider than they are deep.
Figure 4.6 Aerial photograph of the study reach.
The Macintyre River in blue and the anabanches in green. The approximate location of the Terrewah river gauge is indicated by a star.
Figure 4.7 Daily discharge and stage height at the Terrewah gauge, Macintyre River, for the duration of the study period (1/6/2000 – 1/6/2003).

Figure 4.8 Timing of field sampling trips (arrows and ellipses), superimposed upon stage height at the Terrewah gauge for the duration of the study period.
Sediments in the anabranch billabongs are soft and deep, composed of particularly fine clay. There are very few macrophytes of any kind, however *Azolla* spp. and *Pseudoraphis* spp. are often present, along with scattered individuals of *Eleocharis* spp. Depending on their location, they are usually heavily shaded by trees (coolabahs, river coobas and river red gums), and are also highly turbid. Despite this, benthic, pelagic and surface algae proliferate throughout the year, as do macroinvertebrates, especially crustaceans. They are thought to act as refuges or ‘nurseries’ for several species of fish, such as bony bream, and the larger anabranch billabongs are used as feeding and nesting sites by many species of waterbird.

There is an abundance of large woody debris (fallen trees, logs, branches, sticks etc.) in the lower Macintyre River system, however this is particularly apparent in the study reach. Debris accumulation is particularly dense in anabranch channels, often forming significant dams, which over time can block anabranches and create cut-offs containing ephemeral wetlands or billabongs. Large woody debris is known to actively participate in the development of anabranching systems, and it has been shown that anabranching river reaches store much more wood than bar braided or other reaches (Gurnell and Petts 2002; Gurnell *et al.* 2002). Debris dams form gradually over time, usually on the concave banks of anabranch channels or at their breakout points, and also during large high-energy flood events, which are more capable of carrying large loads.

The anabranches sampled for this study are of substantial size and surface area relative to the parent river channel reach that they intersect (Table 4.9 and Table 4.10). Cross-sections indicate that the anabranches commence to flow (CTF) at low to medium river stage heights (Table 4.11). The anabranches are highly complex in both planform and cross-section (e.g. Figure 4.9 – 4.12), and this complexity has important implications for connectivity in terms of flow pattern and duration during and after floods. Hence flow direction can depend on more than just the CTF threshold, and can vary with connection phase (Table 4.12).
### Table 4.9 Bankfull parameters for each anabranch channel studied (means).

<table>
<thead>
<tr>
<th>Anabranch</th>
<th>Bankfull width (m)</th>
<th>Bankfull depth (m)</th>
<th>Bankfull area (m²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>21.97</td>
<td>2.41</td>
<td>26.58</td>
</tr>
<tr>
<td>2</td>
<td>46.24</td>
<td>1.18</td>
<td>23.02</td>
</tr>
<tr>
<td>3</td>
<td>19.33</td>
<td>2.78</td>
<td>29.13</td>
</tr>
<tr>
<td>4</td>
<td>16.18</td>
<td>1.61</td>
<td>14.85</td>
</tr>
<tr>
<td>5</td>
<td>40.35</td>
<td>4.62</td>
<td>119.54</td>
</tr>
<tr>
<td>6</td>
<td>24.93</td>
<td>1.70</td>
<td>35.41</td>
</tr>
</tbody>
</table>

### Table 4.10 Geomorphological parameters for each anabranch channel studied (means).

<table>
<thead>
<tr>
<th>Anabranch</th>
<th>Length (m)</th>
<th>Wetted perimeter (m)</th>
<th>Channel area (m²)</th>
<th>Width:Depth Ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>1180</td>
<td>22.95</td>
<td>27085</td>
<td>9.29</td>
</tr>
<tr>
<td>2</td>
<td>5831</td>
<td>46.44</td>
<td>270806</td>
<td>59.10</td>
</tr>
<tr>
<td>3</td>
<td>3959</td>
<td>20.47</td>
<td>81051</td>
<td>6.94</td>
</tr>
<tr>
<td>4</td>
<td>885</td>
<td>16.77</td>
<td>14844</td>
<td>11.11</td>
</tr>
<tr>
<td>5</td>
<td>1348</td>
<td>42.11</td>
<td>56760</td>
<td>8.86</td>
</tr>
<tr>
<td>6</td>
<td>939</td>
<td>25.47</td>
<td>23913</td>
<td>13.13</td>
</tr>
</tbody>
</table>

### Table 4.11 Commence-to-flow (CTF) values for each anabranch channel studied.

<table>
<thead>
<tr>
<th>Anabranch</th>
<th>CTF discharge (ML day⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Entry 977</td>
</tr>
<tr>
<td></td>
<td>Exit 8616</td>
</tr>
<tr>
<td>2</td>
<td>Entry 19369</td>
</tr>
<tr>
<td></td>
<td>Exit 2716, 10696, 14000</td>
</tr>
<tr>
<td>3</td>
<td>Entry 9556</td>
</tr>
<tr>
<td></td>
<td>Exit timing 4527, 11573</td>
</tr>
<tr>
<td>4</td>
<td>Entry 22956</td>
</tr>
<tr>
<td></td>
<td>Exit (cutoff) 1586</td>
</tr>
<tr>
<td>5</td>
<td>Entry 1418</td>
</tr>
<tr>
<td></td>
<td>Exit 422</td>
</tr>
<tr>
<td>6</td>
<td>Entry N/A</td>
</tr>
<tr>
<td></td>
<td>Exit 25284</td>
</tr>
</tbody>
</table>

### Table 4.12 Flow direction within anabranches during connection phases.

<table>
<thead>
<tr>
<th>Anabranch</th>
<th>Partial connection</th>
<th>Complete connection</th>
<th>Draining phase</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Entry, then exit</td>
<td>Entry to exit</td>
<td>Entry and exit, then exit</td>
</tr>
<tr>
<td>2</td>
<td>Exit, then entry</td>
<td>Entry to exit</td>
<td>Entry and exit, then exit</td>
</tr>
<tr>
<td>3</td>
<td>Entry and exit similar</td>
<td>Entry to exit</td>
<td>Entry and exit, then exit</td>
</tr>
<tr>
<td>4</td>
<td>Entry to exit</td>
<td>Entry to exit</td>
<td>Entry and exit, then entry</td>
</tr>
<tr>
<td>5</td>
<td>Exit then entry</td>
<td>Entry to exit</td>
<td>Entry and exit, then exit</td>
</tr>
<tr>
<td>6</td>
<td>Exit to entry</td>
<td>Exit to entry</td>
<td>Exit only</td>
</tr>
</tbody>
</table>
Figure 4.9 Aerial photographs of the six anabranches used in this study.
Anabranches in blue; Macintyre River in heavy black.
4.3.2 **Anabranch 1**

Anabranch 1 was the anabranch sampled most thoroughly and consistently over the study period. This is because it was relatively easily accessible during all of the connection phases and in most weather conditions. It also had few ‘complications’, excepting a drainage channel from a nearby ‘ring-tank’ (on-farm water storage) that enters this anabranch near the middle transect, but is rarely used. This anabranch will consequently be described in more detail than the remaining five.

The planform of Anabranch 1 is simple, with a single entry site and a single exit (Figure 4.9), making it a ‘Type 1’ anabranch (Figure 4.2). The channel varies in cross-sectional form throughout its length, even within short distances (e.g. Figure 4.10 and Figure 4.11). In long profile, Anabranch 1 has a waterhole inside the entry, ‘downstream’ of which the gradient increases, so that floodwater has to effectively flow ‘uphill’ to reach the middle transect (Figure 4.12). The remainder of the anabranch is either dry or contains a chain of shallow ephemeral billabongs, the deepest of which occurs at the middle transect (Figure 4.13). A cleared track crosses the anabranch near the entry transect. The middle transect abuts cleared cropland, however the anabranch itself is fenced off, and the adjacent fields were fallow for the entire study period. The exit transect is more remote from surrounding landuse and rarely disturbed except occasionally by cattle during drought. The vegetation throughout the anabranch is mature open eucalypt woodland (river red gum; *E. camaldulensis*) with a mixed grass and shrub understorey. Vegetation cover in all strata increases from entry to exit.
Figure 4.10 Cross sections across the entry point of Anabranch 1 (A1E).

(a) A1EB is taken parallel to the parent river channel, directly across the breakout point (i.e. along the river bank).  (b) A1E1 is taken approximately 30 m from the breakout/entry point inside the anabranch channel, through the end of a large billabong/pool.  (c) A1E2 is taken approximately 10 m further inside the anabranch, where the channel constricts into a bottleneck. Beyond A1E2 the channel again opens out.
Figure 4.11  Cross-sections of the middle and exit points of Anabranch 1 (A1M & X).

A1M is taken approximately halfway along the entire anabranch.  (b) A1X is taken within the anabranch.  (c) A1XB is taken parallel to the parent river channel, directly across the breakout point (i.e. along the river bank).
Figure 4.12 Cross-section through the river channel and entry point of Anabranch 1.  
Note the increase in gradient within the anabranch (A) after the initial drop into the waterhole (B), and the commence to flow or breakout level.
4.3.3 **Anabranch 2**

Anabranch 2 is the largest and the most complex anabranch of the six in planform. It is a ‘Type 4’ anabranch, which begins as a single channel, but after joining with Anabranch 3 briefly at one point, spreads out across the floodplain (almost bifurcating at its apex), becomes a single channel again, and then has several exit channels that divide and fan out just before rejoining the main river channel (Figure 4.9). In cross-section this anabranch has slightly greater channel widths than others, but more importantly most of it is far shallower than other anabranch channels, especially in the open paddocks (Figure 4.14). Despite beginning and ending in riparian woodland, most of this anabranch flows through cleared and sown paddocks used predominantly for grazing; hence tree cover and shading are minimal. Coolibah, coobah and lignum are the dominant vegetation types after grasses. Cattle use the billabongs of Anabranch 2 more than others, and faecal contamination (and associated nutrient input) is correspondingly higher.

4.3.4 **Anabranch 3**

Anabranch 3 is the most sinuous of the six anabranches. In cross-section it is the deepest and narrowest, with steep well-vegetated banks. It flows for its entire length through relatively dense riparian vegetation, and its billabongs are generally either clear or heavily tannin-stained (Figure 4.15). This channel is a combination ‘Type 3’ and ‘Type 4’ anabranch. It is briefly connected with Anabranch 2 at one point, and has two exit channels, one of which has a CTF value much lower than the other and therefore is the exit surveyed in this study. This exit point empties into a short semi-cutoff loop of the main channel that flows at very low discharges. The point where the exit joins this loop is approximately 50 metres from where the loop rejoins the main channel.
4.3.5 **Anabranch 4**

Anabranch 4 is the smallest of the anabranches studied, and follows the path of the main river channel closely. It has a small entry point and a well-defined channel for most of its length, but channel shape changes at its exit, and it flows out through a broad well-vegetated depression rather than a clear-cut channel (Figure 4.16). This anabranch empties into the same short semi-cutoff loop of the main channel that Anabranch 3 joins – making it a ‘Type 3’ anabranch. It is relatively deep and narrow for most of its length, and is heavily shaded by eucalypts, with small, shallow, clear, black or heavily tannin-stained billabongs.

4.3.6 **Anabranch 5**

This anabranch is actually a short, recently formed cut-off bend of the river that consequently has an extremely low commence-to-flow level. In cross-section it is very similar to the main river channel. As an anabranch it would be classed as ‘Type 1’. Its exit is usually hydrologically connected to the river during the disconnection phase by either surface or subsurface water. This anabranch is gradually filling with sediment, but retains many of the features of the main river channel in terms of morphology. It is deeper, wider and more u-shaped than the anabranch channels studied, with a more open canopy, and is inundated much more frequently. The island between this channel and the main river is heavily vegetated, as is the floodplain at the entry and exit transects. At the middle transect, clearing for crops and stock access has left that section of the channel relatively bare, unshaded and more turbid (Figure 4.17).

4.3.7 **Anabranch 6**

Anabranch 6 is a ‘Type 2’ anabranch - it fills and empties only through its narrow exit. The ‘entry’ point is barely distinguishable from the riverbank – i.e. there is no clear-cut channel and flows over bankfull would be required for water to enter via the entry. This
anabranch is dominated by a single open, wide, very shallow and highly turbid ephemeral billabong (Figure 4.18). The billabong is replenished most often with rain (sometimes overflowing during prolonged rainfall), and occasionally with floodwater, however relatively large discharges are necessary for complete inundation. It has very fine sediments, limited shading, and despite its turbidity is highly productive, supporting dense populations of invertebrates, fish and waterbirds. The billabong is used occasionally by cattle, and is a focal point for local and migrant wildlife.
The ‘entry’ of Anabranch 1 during a connection phase, facing the main river channel from inside the anabranch.

A section of the small billabong at the ‘middle’ of Anabranch 1.

The exit of Anabranch 1 during the draining phase.

Figure 4.13  Examples of the entry, middle and exit sites of Anabranch 1.
The ‘middle’ of Anabranch 2, the only site in open paddocks.

A semi-permanent billabong behind the ‘exit’ of Anabranch 2.

The ‘exit’ of Anabranch 2, viewed from the main river channel facing into the anabranch.

Figure 4.14 Examples of the entry, middle and exit sites of Anabranch 2.
The ‘entry’ of Anabranch 3, facing into the anabranch.

A site near the ‘middle’ of Anabranch 3.

The ‘exit’ of Anabranch 3 during the draining phase.

Figure 4.15 Examples of the entry, middle and exit sites of Anabranch 3.
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<th>The 'entry' of Anabranch 4.</th>
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<td>![Image of the 'exit' of Anabranch 4.]</td>
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Figure 4.16  Examples of the entry, middle and exit sites of Anabranch 4.
Figure 4.17  The ‘middle’ of Anabranch 5, a cutoff loop of the main river channel.

Figure 4.18  The billabong at the ‘middle’ of Anabranch 6.
4.4 **SUMMARY**

The lower Macintyre River downstream of Goondiwindi is characterised by a complex landscape with a low gradient, highly sinuous channel and an extensive floodplain. Much of the spatial complexity of this landscape results from extensive anabranching, with multiple channels of various sizes dissecting the floodplain. The area is predominantly dryland, with annual evaporation far exceeding precipitation, highlighting the importance of surface flow connection between patches for ecosystem function in this riverine landscape. However variability in both precipitation and flows from upstream creates variability in hydrological connectivity. The anabranche channels are hydrologically disconnected from the main channel for most of the year (though many retain bodies of still water for several months) and commence to flow at a range of discharges below bankfull. Hence they have the potential to play a unique role in the landscape, compared to other patches such as the river channel and the wider floodplain. The anabranche in this reach are complex in terms of their geomorphology and hydrology, and provide an opportunity to conduct an interdisciplinary enquiry into the influences of natural and artificial connectivity and fragmentation upon the ecological functioning of the system.
CHAPTER FIVE: THE SPATIAL DISTRIBUTION OF MAJOR CARBON SOURCES
IN A DRYLAND, ANABRANCHING RIVER LANDSCAPE ............................... 122

5.1 INTRODUCTION ...................................................................................... 122

5.2 METHOD .................................................................................................. 124
  5.2.1 Study design ......................................................................................... 124
  5.2.2 Variables measured ............................................................................. 125
  5.2.3 Field methods ....................................................................................... 128
  5.2.4 Laboratory techniques ......................................................................... 130
  5.2.5 Data analysis ........................................................................................ 132

5.3 RESULTS ................................................................................................... 133
  5.3.1 Patch scale: Anabranches, riverbanks and floodplain....................... 133
      Sediment total carbon .............................................................................. 133
      Leaf litter .................................................................................................. 133
      Dissolved organic carbon ....................................................................... 136
      Phytoplankton .......................................................................................... 138
      Benthic metabolism ................................................................................ 138
      Water quality ............................................................................................ 143
  5.3.2 Individual anabranch scale ................................................................. 146
      Sediment total carbon .............................................................................. 146
      Leaf litter .................................................................................................. 146
      Dissolved organic carbon ....................................................................... 149
      Phytoplankton .......................................................................................... 149
      Benthic metabolism ................................................................................ 151
      Water quality ............................................................................................ 153
  5.3.3 Site scale ............................................................................................. 155
      Sediment total carbon .............................................................................. 155
      Leaf litter .................................................................................................. 157
      Dissolved organic carbon ....................................................................... 157
      Phytoplankton .......................................................................................... 159
      Benthic metabolism ................................................................................ 160

5.4 DISCUSSION ............................................................................................ 166
  5.4.1 Anabranches, riverbanks and floodplain ......................................... 166
  5.4.2 Individual anabranches ....................................................................... 170
  5.4.3 Sites .................................................................................................... 172

5.5 Summary ................................................................................................ 174
CHAPTER FIVE: THE SPATIAL DISTRIBUTION OF
MAJOR CARBON SOURCES IN A DRYLAND,
ANABRANCHING RIVER LANDSCAPE

5.1 INTRODUCTION

The landscape of a floodplain-river ecosystem can be viewed as a complex array of patches. A patch is defined as any area that differs from its surroundings in nature or appearance (Turner 1989), and in floodplain river systems may be described in ecological, geomorphological or hydrological terms. Examples in floodplain river systems include such features as levees, scroll swales, oxbows, and secondary or anabranch channels, as well as the river channel itself and its banks, bars and islands. Patches may differ in size, shape, spatial arrangement and quality, these being products of interactions at various scales between past and present geomorphology, climate and biological characteristics. Depending on the research perspective, patch quality has been measured in many ways, including in terms of plant biomass (Karrenberg et al. 2002), and soil productivity and nutrient status (Ogden and Thoms 2002).

Few studies have specifically examined the distribution of carbon sources across river landscapes and their patches (Pinay et al. 1992; Klopatek et al. 1998; Gurnell and Petts 2002; Gurnell et al. 2002). Yet the importance of variability in carbon distribution to the ecological character and functioning of river systems is often acknowledged, both implicitly and explicitly (Pinay et al. 1990; Thoms and Sheldon 1997; Amoros and Bornette 2002; Leuven and Poudovigne 2002; Robinson et al. 2002; Woodward and Hildrew 2002). Floodplain river systems contain diverse terrestrial and freshwater habitat patches, each with characteristic carbon pools and other physical, chemical and biological features. This complexity, together with varying degrees of isolation and connection across patches, enhances and maintains biodiversity (Robinson et al. 2002).
This chapter examines the spatial distribution of carbon across the dryland, anabranching river landscape of the lower Macintyre River, and asks the question ‘are carbon pools different in anabranch channels compared to other patches in dryland river landscapes?’

If carbon distribution does vary between patches in this landscape, this allows identification of which patches are potentially more important to the ecosystem as a whole in terms of the quantity and quality of carbon supply. Such variation would shed some light upon the ecological roles of physical heterogeneity and hydrological connectivity in the dryland landscape, since different patches experience different connection regimes.

Anabranch channels, the main river channel, and the surrounding floodplain are readily distinguishable as distinct landscape patches in terms of geomorphology. However this distinction is presently not as clear in terms of their carbon pools and hence ecological function. If carbon pools are different in anabanches compared to other patches, then in terms of carbon storage and supply during hydrological connection, they may be relatively more important to the dryland river ecosystem than other patches. They would therefore deserve more scientific and management attention than they have received in the past (Gurnell and Petts 2002), and their particular spatial and temporal patterns of hydrological connection and disconnection would warrant further examination, especially in terms of their influence on the main river system. Acknowledgement of not only their existence but also their hydrological and ecological roles would become essential, ideally followed by integration into current and future river ecosystem models as important features of the riverine landscape, physically, hydrologically and ecologically.

The hypothesis addressed by this chapter is that the quantity and quality of carbon sources vary significantly among and within major geomorphic patches in dryland river landscapes, and more specifically, that both quantity and quality of carbon sources are greater in anabanch channels compared to adjacent floodplain and river channel patches.
5.2 **Method**

5.2.1 **Study design**

The collection and analysis of data for this study was conducted at three spatial scales:

1. Patch type (anabranch, riverbank, floodplain)
2. Individual anabranch (1-6)
3. Site (entry, middle, exit)

Patch type was determined from aerial photographs and field inspection. The major features identified were the main river channel, anabranch channels, and the surrounding floodplain, and these were selected as the primary patches for study. Six individual anabranches (A1-A6) were selected for study based on their low to medium commence-to-flow stage heights, minimum alteration by humans and livestock, and accessibility.

Each anabranch with its adjacent areas of main river channel and floodplain forms an anabranch-river-floodplain ‘set’ (described in Chapter 3). Each set was further subdivided into three sites – entry, middle and exit sites. The ‘entry’ corresponds to the ‘upstream’ end of the anabranch, while the ‘exit’ corresponds to the downstream end, with respect to the river, regardless of flow direction within the anabranch. The ‘middle’ is located approximately halfway between the ‘entry’ and the ‘exit’ points, usually at the planform apex of the anabranch channel. A minimum of three replicate samples and measurements were taken at each site at each visit, the exact number depending on the variable examined, the site, and conditions at the time.

Sampling was conducted at approximately three-monthly intervals over two years. Three month intervals were chosen in order to include all seasons; more frequent sampling was not possible for logistical reasons. Sampling was also conducted opportunistically during flow connection events (yielding a total of ten trips; see Figure 5.1 for exact timing and Chapter 6 for results pertaining to connection events). Not all trips sampled all variables (Table 5.1). This chapter will focus on results derived from sampling during the disconnection phase, when anabranch channels are disconnected from the other patches,
but may hold billabongs (waterbodies). Essentially it describes the static state of anabranch channels, and the adjacent floodplain and river channel, rather than their responses to flow connection events.

5.2.2 Variables measured

Four major carbon pools were sampled: total carbon in surface sediments and surface leaf litter, and dissolved organic carbon and phytoplankton. Benthic metabolism was also measured in order to estimate the production and consumption of carbon (and hence the trophic state) of billabongs and the littoral zone of the main river channel. Terrestrial carbon pools (total carbon in surface sediments and surface leaf litter) were measured for each patch type – anabranch, riverbank, and floodplain. Aquatic carbon pools (phytoplankton, dissolved organic carbon, and benthic metabolism) were measured for anabranch billabongs and the littoral zone of the main river channel.

As context for the carbon distribution analyses, water quality parameters were measured using a Hydrolab MiniSonde Multiprobe, where and when water was present. Parameters included water temperature, pH, turbidity, total dissolved solids, salinity, and specific conductivity. Sediment grain size distribution and its relationship with organic matter content were also investigated via intensive surface sediment sampling focused within Anabranche 1.
Figure 5.1 Timing of data collection, superimposed upon Macintyre River stage height and discharge at the Terrewah gauge for the duration of the study period. Individual trips indicated by shaded blocks.
Table 5.1 Connection phases, patches, and parameters measured during each sampling trip, indicated by shaded boxes.

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5.2.3 Field methods

Total carbon in surface sediment

At each site, between three and eight random surface sediment samples were collected. The number of replicate samples varied depending on the sampling occasion for logistical reasons. Surface sediment samples were collected from within the same quadrats used for surface leaf litter sampling. Each sample consisted of approximately $250\text{cm}^3$ ($5\times5\times10\text{cm}$) of sediment, collected with a clean trowel to a depth of 10cm, placed in a clean sample bag, labelled and sealed.

Surface leaf litter

At each site, between three and eight (depending on the sampling occasion) random surface leaf litter samples were collected. Each sample was collected using a $0.25\text{m}^2$ quadrat, from which all leaf litter was cleared by hand, including nuts, seeds, bark, sticks and twigs, placed in a clean sample bag, labelled and sealed. Large logs and branches crossing the quadrats were excluded from the samples and analyses for logistical reasons.

Dissolved organic carbon

Water samples were collected from the top 0.3 m of the littoral zone whenever there was water within a site (riverbanks and anabranch billabongs) using two new, pre-rinsed 600 ml Nalgene bottles, and were refrigerated ($<4^\circ\text{C}$) until return to the field base station. Subsamples from each bottle (30 ml) were then filtered into sterile glass vials using 0.45 um Minisart sterile syringe filters and refrigerated, and the remaining water was used for phytoplankton filtering.

Phytoplankton

Water samples were filtered for phytoplankton (chlorophyll $\alpha$) in the field using a handheld vacuum pump and standard Whatman GC glass fibre filters (0.45 $\mu$m porosity, 47 mm diameter). The filters were wrapped in foil, labelled and frozen until analysis.
**Benthic metabolism**

Benthic metabolism rates were measured in the field using clear plastic domes (benthic chambers) equipped with circulation pumps and dissolved oxygen and temperature probes, and installed in the sediment of the riverbanks and anabranch billabongs for 24 hours. Either six or twelve chambers were installed, depending on the trip. Chambers were placed in pairs, with usually one pair at each site.

Monitoring of oxygen flux in a closed system microcosm such as a benthic chamber allows calculation of gross primary production (GPP) and respiration (R24) in the enclosed benthic community (Dyrssen *et al.* 1984; Bott *et al.* 1985; Maran *et al.* 1995; Bott 1996; Dodds and Brock 1998). From these figures, the production to respiration ratio (P/R ratio) can be derived, which indicates the trophic state of the microcosm – a P/R ratio $>1$ indicates autotrophy, with most production being derived from local water column (autochthonous) sources; and a P/R ratio $<1$ indicates heterotrophy, with most production being derived from external (allochthonous) sources. Oxygen units can also be converted into carbon units, by assuming a molar ratio of 1:1 and multiplying oxygen production or respiration by 0.375. This allows estimation of the amount of carbon being produced and consumed by the benthic community over a specified area of sediment (Bott 1996).

Where the benthic chamber is approximately the same depth as the water body being monitored, production and respiration values also provide an estimate of combined pelagic and benthic community metabolism and hence trophic state. Hence benthic metabolism rates measured in the anabranch billabongs can represent the metabolism of the entire combined benthic and pelagic community, because the billabongs are often so shallow that the tops of the chambers used were frequently within 10 cm of the water surface. At the same time, the rates measured in the river channel are representative only of the benthic community on the riverbanks at up to 1.0 m depth – not of the entire channel.
Sediment grain size and organic matter content

Anabranch 1 was sampled intensively for sediment grain size and organic matter content distribution analyses in November 2001. A nested sampling design was used, with each anabranch site (entry, middle, and exit) split into five sub-sites, with nine replicates randomly sampled from each sub-site (135 samples in total). Each sample consisted of approximately 250 cm$^3$ (5*5*10 cm) of sediment, collected with a clean trowel to a depth of 10 cm, placed in a clean sample bag, labelled and sealed.

5.2.4 Laboratory techniques

Total carbon in surface sediments

Surface sediments were oven-dried at 40°C for a minimum of 48 hours, homogenised with a mortar and pestle and subsampled. Subsamples were then ground to a powder using a Rocklab crushing machine. Known weights of the resultant powder were analysed for total carbon content using a Total Organic Carbon Analyser (O.I.Analytical 1997). This method measures the carbon dioxide released following complete oxidation of all carbon present in a sample. Each sample is catalytically combusted in an oxygen/compressed air atmosphere at 900°C, and the resulting CO$_2$ detected by a Non-Dispersive InfraRed (NDIR) detector. Results are expressed as percent (%) total carbon content.

Surface leaf litter

Leaf litter was oven-dried at 40°C for 24 hours, and total weight per quadrat recorded. Samples were then divided into two components: ‘Leaves’ - including freshly abscised and aged leaves, grasses, sedges and other soft detritus; and ‘Bark’ – including bark of all textures, twigs, sticks, nuts and seeds. Division of components was necessary in order to estimate the relative proportions of material that is rapidly decomposed (‘Leaves’), and material that may take longer to break down (‘Bark’).
Dissolved organic carbon

Filtered water samples were warmed to room temperature and analysed using a Total Organic Carbon Analyser Autosampler (O.I.Analytical 1996). This method acidifies each sample, purges it of total inorganic carbon (TIC), and adds a strong oxidiser (sodium persulfate, Na$_2$S$_2$O$_8$). This oxidant reacts quickly with organic carbon in the sample at 100°C to form CO$_2$. The CO$_2$ is then purged from solution and quantified by a NDIR detector. The resulting carbon mass, in the form of CO$_2$, is equivalent to the mass of organic carbon originally in the sample.

Phytoplankton

Phytoplankton concentration was measured via chlorophyll $\alpha$ concentrations, using the standard spectrophotometric method (A.P.H.A. et al. 1999). Chlorophyll $\alpha$ pigments were extracted from the plankton concentrate on the filters with aqueous acetone, and the optical density (absorbance) of the extract determined with a spectrophotometer (A.P.H.A. et al. (1999); Section 10200 H).

Sediment grain size and organic matter content

Grain size of the Anabranch 1 sediments was determined by wet sieving. Fines (silt and clay) were classified as particles <0.063mm. Organic matter content was measured for oven-dry (60°C; 24 hrs), 5g subsamples via Loss on Ignition (LOI; 600°C; 2.5hrs), after homogenisation with a mortar and pestle.
5.2.5 **Data analysis**

Data were analysed at each of the three spatial scales (patch type, anabranch and site). Summary statistics were derived for each parameter for the disconnection phase during individual field trips or seasons. Data from all the trips (disconnection only) were then combined for each parameter, and descriptive statistics derived for each scale – patch type, individual anabranch, and site. Fixed general linear model univariate analysis of variance (GLM univariate ANOVA) was performed using SPSS for each dataset to identify statistical significance of differences. This model was used because it is robust to unbalanced sample sizes and minor violations of assumptions. Log$_{10}$ transformations were performed when necessary, in order to comply with the assumptions of the ANOVA, and are identified where appropriate. Tukey’s Honestly Significant Difference (HSD) multiple comparison procedures were then used to determine where differences occurred (significance value $\alpha = 0.05$). When ranges and variability were so great as to prevent formal statistical analysis of variance, trends and differences were identified using summary statistics and box plots.

Box plots were used to present data and statistical values. For the purposes of this dissertation, the boundary of the box closest to zero indicates the 25th percentile, a **solid line within the box marks the median**, a **dashed line marks the mean**, and the boundary of the box farthest from zero indicates the 75th percentile. Whiskers above and below the box indicate the 90th and 10th percentiles. Outlying points are graphed as dots. A minimum number of data points are required to compute each set of percentiles. At least three points are required to compute the 25th and 75th percentiles, five points to compute the 10th percentile, and six points to compute the 5th, 90th, and 95th percentiles. If these requirements are not met, that set of points is not drawn.
5.3 RESULTS

5.3.1 Patch scale: Anabranches, riverbanks and floodplain

Sediment total carbon

Total carbon content in surface sediments was variable (range 0 – 11.71%), and there were significant differences between each of the three landscape patches (Figure 5.2; F = 68.685; df = 2, 459; p<0.005). Multiple comparisons based on the Tukey’s HSD procedure (α = 0.05) indicated that riverbank sediments contained significantly less total carbon (median 1.31%) than both the anabranth channels (3.45%) and the floodplain, while floodplain sediments contained the greatest concentrations (5.67%). However this pattern varies depending upon the anabranch-river-floodplain set examined (Figure 5.3).

Leaf litter

Leaf litter loads were also highly variable (range 0 – 1543 g m$^{-2}$), yet clear differences also existed between the three landscape patches for this carbon pool (Figure 5.4). These differences were statistically significant, as demonstrated by a GLM univariate ANOVA applied to log$_{10}$-transformed values (F = 97.55; df = 49,138; p<0.005). Multiple comparisons (Tukey’s HSD) confirmed that each patch was significantly different from each of the other patches. Litter loads in the anabranch channels were generally twice those on the riverbanks (anabranch median 53.66 g m$^{-2}$ and riverbank median 24.92 g m$^{-2}$ respectively), but the largest loads occurred on the floodplain (median 299.72 g m$^{-2}$; between four and ten times greater than the other patches). The same overall pattern of leaf litter loads occurred regardless of which anabranch-river-floodplain set was examined (Figure 5.5).

In terms of the composition of this litter, anabranches and the floodplain had proportionally more ‘bark’ material by weight (approx. 20% of the total) than the riverbanks (approx. 11% of the total). Overall, leaves were the dominant component of the surface organic litter (Figure 5.6).
Figure 5.2 Total carbon content in the surface sediment of three landscape patches of the lower Macintyre River system.

Figure 5.3 Total carbon content in the surface sediment of three landscape patches of the lower Macintyre River system, presented by anabranch-river-floodplain set (A = anabranch; R = river; F = floodplain).
Figure 5.4 Vegetative litter loads on the ground surface of three landscape patches of the lower Macintyre River system, June 2002.

Figure 5.5 Vegetative litter loads on the ground surface of three landscape patches of the lower Macintyre River system, June 2002, presented by anabranche-river-floodplain set.
Figure 5.6  Relative composition (%) of vegetative litter loads on the ground surface of three landscape patches of the lower Macintyre River system, June 2002. Median values indicated inside bars.

Dissolved organic carbon

During the disconnection phase, dissolved organic carbon (DOC) concentrations in the anabranch billabongs were significantly greater than those recorded in the river channel (log$_{10}$ transformed data; $F = 86.17$; df = 1,193; $p<0.005$). Median DOC concentrations in the anabranch billabongs were approximately double those in the river (14.33 and 7.73 ppm respectively; Figure 5.7). Maximum concentrations also differed substantially (anabranch billabongs 52.78 ppm, river channel 17.39 ppm). Data separated into separate sampling occasions or months showed larger differences between median concentrations in the two patches of between 4 and 7 ppm (Figure 5.8). Maximum concentrations during individual trips differed between the patches by 7 to 45 ppm.
Figure 5.7 Dissolved organic carbon concentrations in anabranch billabongs and the main river channel during the disconnection phase.

Figure 5.8 Dissolved organic carbon concentrations in anabranch billabongs and the main river channel during the disconnection phase, presented for individual months (sampling occasions).
**Phytoplankton**

Chlorophyll α concentrations ranged from 0 – 169.81 mg m⁻³. There were statistically significant differences in chlorophyll α concentrations between anabranch billabongs and the river channel (log₁₀ transformed data; F = 24.90; df = 1,35; p<0.005). Median chlorophyll α concentrations in the anabranch billabongs were nearly triple those in the river (30.44 and 11.32 mg m⁻³ respectively; Figure 5.9). These differences were similar for individual sampling occasions or months, with gaps ranging from 15 mg m⁻³ (June 2002) to 37 mg m⁻³ (July 2001; Figure 5.10).

**Benthic metabolism**

During the disconnection phase, benthic production was statistically significantly greater in the littoral zone of the river channel than in the anabranch billabongs (F = 30.89; df = 1,127; p<0.005; Figure 5.11), while respiration was not significantly different between patch types (F = 0.004; df = 1,127; p = 0.949; Figure 5.12). Hence, benthic P/R ratios on the riverbanks were significantly greater than those in the anabranch billabongs (F = 39.34; df = 1,126; p<0.005; Figure 5.13). Importantly, the P/R ratios on the riverbanks were generally greater than one (median 2.60), while the ratios in the anabranch billabongs were usually less than one (median 0.90). This indicates that benthic metabolism in the littoral zone of the river was autotrophic, while metabolism in the anabranch billabongs was heterotrophic (using carbon derived from external sources).
Figure 5.9 Chlorophyll $\alpha$ (phytoplankton) concentrations in anabranch billabongs and the main river channel during the disconnection phase.

Figure 5.10 Chlorophyll $\alpha$ (phytoplankton) concentrations in anabranch billabongs and the main river channel during the disconnection phase, presented for individual months (sampling occasions).
Figure 5.11 Benthic production in anabranch billabongs and the littoral zone of the main river channel during the disconnection phase.

Figure 5.12 Benthic respiration in anabranch billabongs and the littoral zone of the main river channel during the disconnection phase.
Focusing on the disconnection phase during individual months, benthic production was greater on the riverbanks than in the anabranch billabongs (Figure 5.14), however benthic respiration varied greatly from month to month and between patch types, in terms of both absolute and relative magnitude (Figure 5.15). This was particularly evident in February 2002 (summer), when benthic respiration in the anabranch billabongs far exceeded that on the riverbanks. This variability was reflected in P/R ratios for individual months (Figure 5.16). July 2001 was the only occasion on which both anabranch and river ratios were generally less than one. For the remaining months, P/R ratios on the riverbanks were generally above one and exceptionally high (range 0.6 to 9.2), with means and medians well above those in the anabranch billabongs, which ranged between 0.5 and 1.5 but were most commonly less than one.
Figure 5.14  Benthic production in anabranch billabongs and the littoral zone of the main river channel during the disconnection phase in different months. Jun/Jul = Winter; Oct = Spring; Feb = Summer.

Figure 5.15  Benthic respiration in anabranch billabongs and the littoral zone of the main river channel during the disconnection phase in different months. Jun/Jul = Winter; Oct = Spring; Feb = Summer.
Figure 5.16  Benthic P/R ratios in anabranch billabongs and the littoral zone of the main river channel during the disconnection phase in different months. The solid line at ratio 1.0 indicates the threshold between autotrophy (>1) and heterotrophy (<1).

Water quality

Water quality parameters influence carbon dynamics in aquatic ecosystems, and vice versa. Consequently concurrent conditions such as temperature, pH and turbidity must be taken into account when investigating pattern and process in terms of carbon across the riverine landscape. These and other parameters were measured as part of this study whenever carbon sampling was conducted.

Within any month, average water temperatures differed between the river and the anabranches by 0.1 to 0.5°C. River and anabranch pH values were also similar for both the river and anabranches (~7.4) with differences ranging between 0.01 and 0.34 pH units.
Dissolved oxygen (DO) readings were highly variable at all scales, with differences between average concentrations in the anabranches and the river ranging from 8 to 68%. Average DO concentrations in the anabranches across all months ranged from 17% to 90%. Average concentrations in the river ranged from 43% to 93%. The overall average DO concentration in anabranch billabongs was 63%, compared to 82% for the river. That is, DO concentrations in anabranch billabongs are on average 19% lower than those in the river (Table 5.2).

Average anabranch turbidity values exceeded those of the river in all months by between 27 and 305 NTU. Over all months, average anabranch turbidity was 168 NTU compared to 35 NTU in the river. Turbidity values in the anabranches ranged from 18.5 to 947 NTU, while in the river values ranged from 11.6 to 373 NTU. Anabranch and river average TDS values differed by between 0.00 and 0.06 g L$^{-1}$ within individual months. Overall, anabranch TDS averaged 0.19 g L$^{-1}$, while river TDS averaged 0.18 g L$^{-1}$. Concentrations in the anabranches ranged from 0.03 to 0.60 g L$^{-1}$. Concentrations in the river ranged from 0.12 to 0.18 g L$^{-1}$. Reflecting these values, average secchi depths in the river (28 cm) were double those in the anabranch billabongs (14 cm), indicating far greater clarity in river water (Table 5.2). Secchi depths in anabranches ranged from 2 to 30 cm, while those in the river ranged from 25 to 35 cm.

There was little difference in specific conductivity between anabranch billabongs and the river channel. Within individual months, average differences in specific conductivity between anabranch billabongs and the river ranged from 0.04 to 0.09 mS cm$^{-1}$. Over all months, the average level in the river channel was 0.26 mS cm$^{-1}$, compared to 0.29 mS cm$^{-1}$ in anabranch channels. Salinity levels in anabranches were generally slightly higher than those in the river channel. Average salinity levels within months differed between anabranches and the river by between 0.02 and 0.06 ppt. Over all months, average anabranch salinity was 0.14 ppt, while average river salinity was 0.12 ppt. Salinity levels in anabranches ranged from 0.01 to 0.26 ppt. Salinity levels in the river ranged from 0.08 to 0.15 ppt.
Table 5.2  Mean water quality values for the river channel and anabranch billabongs during the disconnection phase.

<table>
<thead>
<tr>
<th></th>
<th>Anabranches</th>
<th>River</th>
</tr>
</thead>
<tbody>
<tr>
<td>DO (mg/L)</td>
<td>4.48</td>
<td>5.91</td>
</tr>
<tr>
<td>DO (%)</td>
<td>53.43</td>
<td>71.24</td>
</tr>
<tr>
<td>pH</td>
<td>7.45</td>
<td>7.62</td>
</tr>
<tr>
<td>Salinity (ppt)</td>
<td>0.13</td>
<td>0.12</td>
</tr>
<tr>
<td>Spec. cond. (mS cm(^{-1}))</td>
<td>0.26</td>
<td>0.25</td>
</tr>
<tr>
<td>TDS (g/L)</td>
<td>0.16</td>
<td>0.17</td>
</tr>
<tr>
<td>Turbidity (NTU)</td>
<td>207.38</td>
<td>42.59</td>
</tr>
<tr>
<td>Water temp. ((^\circ)C)</td>
<td>20.65</td>
<td>21.75</td>
</tr>
<tr>
<td>Secchi depth (cm)</td>
<td>16.71</td>
<td>28.50</td>
</tr>
</tbody>
</table>
5.3.2 Individual anabranch scale

Sediment total carbon

There was no significant difference between anabranches in terms of total carbon in surface sediments ($F = 2.62; \text{df} = 5,289; p = 0.25$), with all anabranches averaging around 3% total carbon (Figure 5.17). Surface sediments from anabranches 3, 4, and 6 had very slightly higher total carbon contents than 1, 2 and 5, probably reflecting vegetation type, vegetation density and sediment texture differences. Anabranch 5, which had the lowest mean concentration (2.67%), differs from the other channels in that it is a cut-off loop of the main river channel that has a significantly lower commence-to-flow discharge than other anabranch channels. This anabranch retains many of the features of the main river channel in terms of morphology and sediment, and hence may be expected to retain total carbon concentrations nearer to the low levels observed for the river channel.

Leaf litter

In contrast to total carbon concentrations in sediment, litter loads were statistically different between anabranch channels ($F = 6.34; \text{df} = 5,308; p<0.005$; Figure 5.18). Multiple comparisons (Tukey’s HSD) indicated that anabranch 5 had significantly lower litter loads than all other anabranches, except anabranch 4. Anabranch 4 in turn had significantly lower litter loads than anabranches 1 and 3. The anabranches with the highest median litter loads were anabranch 6 (77 g m$^{-2}$) and anabranch 1 (73 g m$^{-2}$), followed by anabranches 4, 3, and 5 (59, 48 and 41 g m$^{-2}$ respectively). Anabranch 2 had the lowest median litter load (29 g m$^{-2}$).

Litter composition also varied, but to a lesser degree, and did not match the pattern found for total litter (Figure 5.19). Anabranch 3 contained the largest median proportion of ‘bark’ material (29 % of the total), followed by Anabranches 6 and 1 at 23 % of the total. Anabranches 4 and 5 contained proportionately less ‘bark’ material than other anabranches (17 and 16 % of the total), while Anabranch 2 contained an intermediate proportion (20 %).
Figure 5.17  Total carbon content in surface sediment of individual anabranches.

Figure 5.18  Vegetative litter loads on the ground surface of six anabranche channels of the lower Macintyre River system, June 2002.
Figure 5.19 Composition (%) of vegetative litter loads on the ground surface of six anabranchn channels of the lower Macintyre River system, June 2002. Median values indicated inside bars.
**Dissolved organic carbon**

When billabongs were present in anabranches during the disconnection phase, median dissolved organic carbon concentrations ranged from 13 – 20 ppm (Figure 5.20). Concentrations were statistically significantly different between anabranches (log$_{10}$ transformed data; $F = 3.607; df = 5,98; p<0.05$). However follow-up multiple comparisons (Tukey’s HSD) indicated that the primary source of variation was the difference between anabranches 1 and 6. Dissolved organic carbon concentrations were highly variable within anabranches 6 and 2 (Figure 5.20). In particular, anabranch 6 values were skewed by high concentrations of DOC during February 2002 (53 ppm) compared to those in October 2001 and June 2002 (21 and 17 ppm respectively).

**Phytoplankton**

GLM univariate ANOVA demonstrated no significant difference in chlorophyll $a$ concentrations between the anabranches sampled during the disconnection phase (Log$_{10}$ transformed data; $F = 1.438; df = 4,17; p = 0.264$). Limited sample numbers because of dry field conditions, and some data redundancy because of laboratory technical problems, resulted in small sample sizes ($n$: 2-8), and concentrations were highly variable, limiting the utility of data analysis. Median concentrations ranged from 25.82 mg m$^{-3}$ in anabranch 1, to 102.55 mg m$^{-3}$ in anabranch 6 (Figure 5.21). Median concentrations for anabranches 2, 3, and 5 were 40.72, 83.30, and 48.99 mg m$^{-3}$ respectively.
Figure 5.20  Dissolved organic carbon concentrations in anabranch billabongs (grouped by anabranch) during the disconnection phase.

Figure 5.21  Chlorophyll α (phytoplankton) concentrations in anabranch billabongs (grouped by anabranch) during the disconnection phase. Where boxes or symbols are not plotted, either insufficient data were available or no water was present at the time of sampling.
Benthic metabolism

Median benthic production during the disconnection phase was greatest in anabranch 5 (0.33 gC m\(^{-2}\) day\(^{-1}\)), followed by anabranch 1 (0.20 gC m\(^{-2}\) day\(^{-1}\); Figure 5.22). Anabranches 2, 3, 4 and 6 had relatively low rates of benthic production (0.10, 0.12, 0.12 and 0.13 gC m\(^{-2}\) day\(^{-1}\)). Benthic respiration during disconnection was generally similar across all anabranches, ranging from 0.13 gC m\(^{-2}\) day\(^{-1}\) (anabranch 4) to 0.19 gC m\(^{-2}\) day\(^{-1}\) (anabranch 2; Figure 5.23). Median P/R ratios during disconnection were less than 1.0 for anabranches 1, 2, 3, and 6 (0.95, 0.70, 0.66 and 0.76), and greater than 1.0 for anabranches 4 and 5 (1.07 and 2.43; Figure 5.24). Thus anabranches 1, 2, 3, and 6 may be dependent upon allochthonous carbon for benthic metabolism during this phase, while anabranches 4 and 5 are capable of supporting their own benthic metabolism with autochthonous carbon.

![Figure 5.22](image)

Figure 5.22 Benthic production in anabranch billabongs (grouped by anabranch) during the disconnection phase.

151
Figure 5.23  Benthic respiration in anabranch billabongs (grouped by anabranch) during the disconnection phase.

Figure 5.24  Benthic P/R ratios in anabranch billabongs (grouped by anabranch) during the disconnection phase. The solid line at ratio 1.0 indicates the threshold between autotrophy (>1) and heterotrophy (<1).
Water quality

Average water temperature during the disconnection phase (over all months) was generally similar across anabranches (21.2 – 23.2 °C; Table 5.3), with the exception of anabranch 4, which had a lower average temperature (12.85°C), due to the fact that temperature was only measured in this anabranch during the winter months. Average pH was also generally similar between anabranches, ranging from 7.17 (anabranch 4) to 7.77 (anabranch 5). Dissolved oxygen levels were highly variable at all spatial and temporal scales. Anabranch 4 had the lowest average concentration (28%), while anabranch 1 had the highest (79%).

Specific conductivity was lowest in anabranch 4 (0.16 mS cm\(^{-1}\)), and highest in anabranch 5 (0.32 mS cm\(^{-1}\)). Salinity values reflected those of specific conductivity, with average salinity lowest in anabranch 4 (0.07 ppt), and highest in anabranch 5 (0.16 ppt). Average turbidity was by far highest in anabranch 6 (588.80 NTU). Average turbidity was lowest in anabranches 3 and 4 (56.72 and 30.87 NTU). Average concentrations of total dissolved solids were lowest in anabranches 2, 4 and 5 (0.15, 0.13 and 0.10 g/L respectively) and highest in anabranches 3, 6 and 7 (0.20, 0.20 and 0.19 g/L respectively; Table 5.3).
Table 5.3  Mean water quality values for individual anabranches during the disconnection phase.

<table>
<thead>
<tr>
<th></th>
<th>Anabranch 1</th>
<th>Anabranch 2</th>
<th>Anabranch 3</th>
<th>Anabranch 4</th>
<th>Anabranch 5</th>
<th>Anabranch 6</th>
</tr>
</thead>
<tbody>
<tr>
<td>DO (mg/L)</td>
<td>6.12</td>
<td>4.77</td>
<td>3.62</td>
<td>2.74</td>
<td>4.85</td>
<td>4.81</td>
</tr>
<tr>
<td>DO (%)</td>
<td>78.69</td>
<td>56.90</td>
<td>53.24</td>
<td>28.00</td>
<td>60.61</td>
<td>43.15</td>
</tr>
<tr>
<td>pH</td>
<td>7.46</td>
<td>7.36</td>
<td>7.22</td>
<td>7.17</td>
<td>7.77</td>
<td>7.73</td>
</tr>
<tr>
<td>Salinity (ppt)</td>
<td>0.15</td>
<td>0.12</td>
<td>0.11</td>
<td>0.07</td>
<td>0.16</td>
<td>0.14</td>
</tr>
<tr>
<td>Spec. cond. (mS cm(^{-1}))</td>
<td>0.29</td>
<td>0.27</td>
<td>0.24</td>
<td>0.16</td>
<td>0.32</td>
<td>0.30</td>
</tr>
<tr>
<td>TDS (g/L)</td>
<td>0.15</td>
<td>0.20</td>
<td>0.13</td>
<td>0.10</td>
<td>0.20</td>
<td>0.19</td>
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<td>Turbidity (NTU)</td>
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<td>134.12</td>
<td>588.80</td>
</tr>
<tr>
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<td>21.20</td>
<td>23.22</td>
<td>12.85</td>
<td>22.35</td>
<td>22.01</td>
</tr>
</tbody>
</table>
5.3.3 Site scale

Sediment total carbon

Total carbon content was statistically significantly lower in the surface sediments of the entry sites of the anabranch channels compared to the middle and exit sites ($F = 43.730$; $df = 2,292$; $p<0.005$; Tukey’s HSD). The mean concentration for entry sites was 2.03%, compared to 3.92% and 3.71% for the middle and exit sites respectively (Figure 5.25).

Two other patterns were recognizable in terms of within-anabranch total carbon distribution. The first pattern appears in anabranches 1, 4 and 5, where total carbon content increases from the entry to the exit (Figure 5.26). This result is probably linked predominantly to flow pattern (from entry to exit) and associated sediment texture gradients within each anabranch channel, in addition to fairly consistent vegetation cover and type along each channel.

The second pattern was the occurrence of the highest concentrations of carbon at the middle sites in anabranches 2, 3 and 6. There are a number of possible explanations for this result, including the presence of greater vegetation density and hence litterfall (anabranch 3), the presence of more open billabongs and hence greater algal and macrophytic carbon production (anabranch 2 and anabranch 6), and the presence of more intensive waterbird use and cattle grazing and hence greater faecal carbon input at the anabranch 2 and anabranch 6 middle sites.
Figure 5.25 Total carbon content in the surface sediment of anabranch channels, by site.

Figure 5.26 Total carbon content in the surface sediment of individual anabranch channels, split into sites.
Leaf litter

Combining data from all of the anabranches, there was no statistically significant difference in litter loads between anabranch sites ($\log_{10}$ transformed data; $F = 0.005$; df = 2,311; $p = 0.995$). However median litter loads appeared to be slightly lower at exit sites (41 g m$^{-2}$) compared to entry and middle sites (57 and 60 g m$^{-2}$ respectively; Figure 5.27). At the individual anabranch scale, patterns differed considerably from the above (Figure 5.28). In anabranches 1 and 3, median litter loads were greatest at the middle sites and lowest at the entry sites. In anabranches 4 and 6, loads decreased from entry to middle to exit. Loads were also greatest at the entry site of anabranch 2; however they were uniquely lower at the middle site than at either the entry or the exit. Anabranch 5 was also distinctive in that litter loads tended to increase slightly from entry to middle to exit. Combining data from all of the anabranches, exit sites contained approximately 15% ‘bark’ material, proportionally 5-9 % less than entry or middle sites (20 and 24 % respectively; Figure 5.29); hence exit sites contained more leaves than other sites. This compositional difference may have contributed to the overall lower litter weights found for exit sites.

Dissolved organic carbon

Individual billabongs within anabranches displayed variability in dissolved organic carbon concentrations, both spatially and temporally, and there was no consistent pattern or statistically significant difference between them ($\log_{10}$ transformed data; $F = 2.342$; df = 2,101; $p = 0.101$). Each billabong is subject to its own set of variables influencing dissolved organic carbon, including shading, width, depth, wind disturbance, vegetation type, and turbidity.
Figure 5.27 Vegetative litter loads on the ground surface of anabranch channels, by site.

Figure 5.28 Vegetative litter loads on the ground surface of individual anabranch channels, split into sites.
Figure 5.29 Composition of vegetative litter loads of anabranches, by site, June 2002.

Phytoplankton

Variation in chlorophyll α concentration among anabranch sites (billabongs) was so great that there was no statistically significant difference identifiable (Log$_{10}$ transformed data; $F = 0.226; \text{df} = 2,19; p = 0.800$). Again, limited sample numbers because of dry field conditions, and some data redundancy because of laboratory technical problems, resulted in small sample sizes, and concentrations were highly variable, limiting the utility of data analysis. Median concentrations in anabranch 1 billabongs were 38, 17, and 145 mg m$^{-3}$ (entry, middle and exit respectively; Figure 5.30). Median concentrations in anabranch 2 billabongs were 158, 75, and 30 mg m$^{-3}$ (entry, middle, and exit). Anabranch 3, 5 and 6 billabongs contained median chlorophyll α concentrations of 83, 49, and 103 mg m$^{-3}$ respectively.
Benthic metabolism

Individual billabongs within anabranches varied in benthic production and respiration rates both spatially and temporally. There was no consistent pattern at this scale, and there were no statistically significant differences in benthic production or respiration rates (GPP: F = 0.320; df = 2,77; p = 0.727. R24: F = 2.720; df = 2,77; p = 0.072). Each billabong is subject to its own set of variables influencing benthic metabolism.

Median benthic production rates in the anabranch billabongs ranged from 0.05 to 0.53 gC m\(^{-2}\) day\(^{-1}\) (Figure 5.31). They were lowest in billabongs in anabranches 1, 2, 3, and 4, at the sites 1X, 2X, 3E, and 4E. Production rates were highest in the anabranch 5 middle billabong (5M) and the anabranch 3 exit billabong (3X). Median benthic respiration rates in the anabranch billabongs ranged from 0.04 to 0.32 gC m\(^{-2}\) day\(^{-1}\) (Figure 5.32). They
were lowest in the billabongs at anabranch 2X, anabranch 4E and anabranch 5X.
Respiration rates were highest in anabranch 2E, anabranch 2M and anabranch 5M.
Median P/R ratios in the anabranch billabongs ranged from 0.44 to 2.87 (Figure 5.33).
Nine out of 15 sites had ratios less than one. They were less than one at all the middle
sites except anabranch 5M. Other sites with ratios less than one included anabranch 1X,
anabranch 2E, anabranch 2X, and anabranch 3E. Anabranch billabong sites with P/R
ratios greater than one were anabranch 1E, anabranch 3X, anabranch 4E, anabranch 4X,
anabranch 5M and anabranch 5X.

Figure 5.31  Benthic production in anabranch billabongs during the disconnection phase. Where
boxes are not plotted, insufficient data were available or no water was present at sampling.
Figure 5.32  Benthic respiration in anabranch billabongs during the disconnection phase. Where boxes are not plotted, insufficient data were available or no water was present at sampling.

Figure 5.33 Benthic P/R ratios in anabranch billabongs during the disconnection phase. Where boxes are not plotted, insufficient data were available or no water was present at sampling.
Sediment grain size and organic matter content
Detailed sediment grain size distribution analyses were confined to anabranch 1, and were intended to give an indication of within-anabranch (site scale) patterns and their associations with organic matter content. Fine grain sizes (silts and clays) dominated the surface sediments (12-99%; Figure 5.34). Overall, the distribution of sediment grain size indicated the presence of coarse fractions at the entry site, becoming progressively finer from entry, to middle, to exit, where predominantly fine fractions were present (Figure 5.35). Organic matter content (% ash-free dry weight) also increased from entry, to middle and exit (Figure 5.36). A significant correlation was found between the sediment fine fraction (<63μm) and organic matter content ($R^2$=73%; Figure 5.37).

![Figure 5.34](image-url)  Surface sediment size fractions within Anabranch 1, by site, showing increasing clay content from entry to exit.
Figure 5.35  Ternary plot of sediment size distribution for Anabranch 1, showing progressive changes in sediment size from coarse to fine from entry site to middle site to exit site.
Figure 5.36 Organic matter content of surface sediment used for particle size analysis.

Figure 5.37 The relationship between the fine silt and clay fraction (<63μm) and organic matter content ($R^2=73\%$) in surface sediments of Anabranch 1.
5.4 **DISCUSSION**

This chapter has examined the distribution of carbon across a dryland, anabranching river landscape, and has found differences at each of the three scales studied. Important distinctions can be made between patterns in terms of carbon quantity, and patterns in terms of carbon quality. Variability at all scales emphasises the role of local factors such as geomorphology, vegetation, and sediment size in determining total carbon pools. These relationships and their implications are discussed in the following sections.

5.4.1 **Anabranches, riverbanks and floodplain**

Carbon quantity and quality varied among the three major geomorphic patches in this dryland river landscape – riverbanks, anabranches and floodplain (Table 5.4, Figure 5.38). In particular, carbon pools were different in anabranch channels compared to the other patches. These differences were significant despite spatial and temporal variability in carbon pools at different scales.

Carbon **quantity** was greater in anabranch channels compared to adjacent river channel patches but not compared to the floodplain. The floodplain contained the largest pools of particulate carbon, such as total carbon and vegetative litter. Carbon **quality** was greater in anabranch channels compared to both adjacent river channel and floodplain patches. The anabranch channels contained the largest pools of dissolved and labile carbon (e.g. phytoplankton) where billabongs were present, as well as the largest quantities of living aquatic and terrestrial vegetation. The riverbanks appeared to be relatively insignificant in terms of the concentration of carbon pools when compared to anabranch channels and the floodplain. However benthic production was greater on the riverbanks than in the anabranch billabongs. Similar levels of respiration in both patch types combined with the difference in production yielded differences in production to respiration ratios. Hence, riverbank benthic communities were autotrophic during the disconnection phase (which dominates this system), while anabranch billabong communities were predominantly heterotrophic.
Table 5.4  Summary of the spatial distribution of carbon pools and water quality parameters across patch types during the disconnection phase. Concentrations of primary carbon sources in the anabranch channels significantly exceed those of the river channel in all cases.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>River</th>
<th>Anabranch</th>
<th>Floodplain</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total carbon in sediment</td>
<td>Least</td>
<td>Intermediate</td>
<td>Most</td>
</tr>
<tr>
<td>Total surface litter</td>
<td>Least</td>
<td>Intermediate</td>
<td>Most</td>
</tr>
<tr>
<td>Dissolved organic carbon</td>
<td>Least</td>
<td>Most</td>
<td>N/A</td>
</tr>
<tr>
<td>Phytoplankton (Chl α)</td>
<td>Least</td>
<td>Most</td>
<td>N/A</td>
</tr>
<tr>
<td>Specific conductivity</td>
<td>Least</td>
<td>Most</td>
<td>N/A</td>
</tr>
<tr>
<td>Salinity</td>
<td>Least</td>
<td>Most</td>
<td>N/A</td>
</tr>
<tr>
<td>Turbidity</td>
<td>Least</td>
<td>Most</td>
<td>N/A</td>
</tr>
<tr>
<td>Total dissolved solids</td>
<td>Least</td>
<td>Most</td>
<td>N/A</td>
</tr>
<tr>
<td>Temperature</td>
<td>Most</td>
<td>Least</td>
<td>N/A</td>
</tr>
<tr>
<td>pH</td>
<td>Most</td>
<td>Least</td>
<td>N/A</td>
</tr>
<tr>
<td>Dissolved oxygen (%)</td>
<td>Most</td>
<td>Least</td>
<td>N/A</td>
</tr>
<tr>
<td>Benthic production</td>
<td>Most</td>
<td>Least</td>
<td>N/A</td>
</tr>
<tr>
<td>Benthic respiration</td>
<td>No difference</td>
<td>No difference</td>
<td>N/A</td>
</tr>
<tr>
<td>Benthic P/R ratios</td>
<td>Most</td>
<td>Least</td>
<td>N/A</td>
</tr>
<tr>
<td></td>
<td>(&gt;1; Autotrophic)</td>
<td>(=/&lt;1; Heterotrophic)</td>
<td></td>
</tr>
</tbody>
</table>
Figure 5.38 Schematic diagram of where the highest values for each carbon source and water quality parameter were found across the landscape.
Consistently greater quantities of carbon in anabranch channels indicate that anabranch channels are potentially important as both sinks and sources of carbon for the river system. However the floodplain is the patch with the largest refractory carbon pools (leaf litter and sediment carbon). This may be due to an array of factors, such as fine sediment particle size, high density and variability of vegetation, greater surface roughness or complexity, and low inundation frequency. Vertically accreting floodplains such as those characterising the lower Macintyre are typically composed of fine-grained sediment such as silts and clays. These sediments adsorb relatively large amounts of carbon due to their greater surface area and mineral composition (Burford and Bremner, 1975; Oades and Ladd, 1977; Nelson et al., 1991). Carbon retention is also known to increase with roughness and substrate complexity (Wanner et al., 2002). While anabranch channels are dominated by bare sediment, the floodplain is vegetated with a variety of species, all of which deposit detritus on the sediment surface and increase roughness (McCosker, 1999). This floodplain litter is rarely inundated or flushed compared to litter in the anabranches and the river channel (Chapter 6). There is therefore more time for accumulation of litter (and sediment carbon) between flow events – hence the larger load. Yet despite such large pools of carbon, the relative infrequency of connecting flows over the floodplain may restrict its relative contribution to river ecosystem carbon dynamics. The role of the floodplain is perhaps more of a long term, intermittent carbon source. Alternatively it may act as a secondary source, supplying wind and water-washed carbon to anabranch channels, for distribution to the river channel ecosystem on a more frequent basis. Because anabranches have lower commence to flow thresholds, they are connected to the main river channel more frequently than the floodplain (Chapter 6). Consequently their role in terms of supplying carbon to the river channel has the potential to be very different to those of the other patches. The primary role of anabranch channels may be as regular suppliers in their own right, as well as transporters, and sinks or temporary storages. This role is likely to be complex, involving thresholds, spikes and different time scales of input. Their role would also vary differently between carbon quantity and carbon quality-related issues. For example, benthic metabolism values indicate a predominance of carbon consumption in anabranch billabongs, and limited community
production, indicating their potential as sinks. However the greater pools of relatively higher-quality resources such as dissolved organic carbon and phytoplankton suggest their potential as sources when connected to the main river channel. At the flow pulse scale, without overbank flooding, the relative importance of anabranch channels as patches in this landscape is greatly increased.

Patch quality is one of the central themes of landscape ecology (Wiens 2002). In terms of patch carbon quality in the Macintyre floodplain river system, the greatest concentrations of relatively labile carbon were found in the anabranch billabongs. The still-water environment of the billabongs, together with a plentiful supply of leaf litter and other detritus, provides ideal conditions for the proliferation of benthic and pelagic algal and bacterial communities, producing high concentrations of chlorophyll $\alpha$ and dissolved organic carbon. These carbon pools are readily available to riverine consumers during connection events, either in-situ or during or after transport to the river channel. Additionally, the alternate wetting and drying cycle experienced by the anabranch channels and their billabongs provides ideal conditions for the breakdown of detritus and soil carbon, and the concomitant release of carbon and nutrients to overlying water during successive connection events (Baldwin 1999; Baldwin and Mitchell 2000; O'Connell et al. 2000; Francis and Sheldon 2002; Scholz et al. 2002). Anabranches are ‘intermediate’ patches in terms of hydrological connectivity and quantitative carbon pools, however this same ‘intermediate’ character also results in their having higher quality carbon pools than the other patches.

5.4.2 Individual anabranches

In terms of particulate and refractory carbon pools, individual anabranch channels were relatively similar, although some minor differences were identifiable. Differences between anabranches became more apparent when dissolved and more labile carbon pools were examined. Anabranches 1, 3, 4 and especially 6 contained the largest pools of particulate and refractory carbon, while anabranches 2, 5, and again, especially anabranch
6, contained the largest pools of dissolved and labile carbon (e.g. phytoplankton). Primary production and respiration values generally reflected these differences.

As discussed in Chapter 4, there were several types of anabranches represented in this study. Anabranches 1, 3, 4 and 6 had slightly larger concentrations of refractory carbon. They also represent the full range of anabranch types (Types 1, 3/4, 3 and 2 respectively) and hence a range of geomorphological and hydrological conditions. The largest concentrations of labile carbon were found in Anabranches 2, 5 and 6, which are Type 4, Type 1 and Type 2 anabranches respectively. Thus it would seem that geomorphological (and hence hydrological) character of anabranches (at this scale) has little to do with the distribution of carbon. However when the data are viewed in the context of individual anabranch billabongs, their location with anabranches, and their particular geomorphological and hydrological characteristics, it is clear that a relationship does exist at the site scale.

Anabranch 6, which is a single large ‘Type 2’ anabranch billabong (with a single connection to the main river channel at its ‘exit’ or downstream end) had high loads of both refractory and labile carbon. However it had some of the lowest rates of production and the lowest median P/R ratios. There is a trend in this data where benthic metabolism seems to tell a different story to that which might be surmised from the carbon pool work. The billabongs with the highest carbon concentrations had the lowest production and P/R ratios, while the waterbodies with the lowest concentrations had the highest production and P/R ratios. There are several possible reasons for this. Excessive dissolved organic carbon concentrations are known to inhibit productivity of plankton and bacteria (Wotton 1994; Pusch et al. 1998). In addition, high loads of pelagic dissolved organic carbon and phytoplankton indicate high production in the pelagic zone, requiring good light availability, warmth, and nutrient availability – but this would restrict light in the benthic zone. High turbidity, whether from inorganic or organic particles, results in rapid diminution of light toward the benthic zone. In addition, the benthic zone in the anabranch channels is characterised by fine clay or coarse sand (depending on the channel), high organic loads, high tannin-heavy litter loads, lack of oxygen, lack of light, and...
and frequent biological disturbance. Where disturbance, litter loads, pelagic production and turbidity are high, benthic production is limited. Where disturbance, litter loads, pelagic production and turbidity are low, benthic production is relatively unrestricted.

5.4.3 Sites

The distribution of particulate and refractory carbon sources within anabranch channels appears to be linked to flow sequences or patterns (see Chapter 4 for flow patterns). In anabranch channels that flow predominantly from entry to exit during the entire connection event, total carbon pools increased from entry sites to exit sites. In anabranch channels that flow ‘backwards’, predominantly from exit to entry, or from both ends at once, carbon pools peaked at the middle sites. Salinity, specific conductivity, and turbidity were also generally greatest in billabongs at middle sites. The distribution of dissolved and labile carbon sources, as well as production and respiration rates were variable between sites (anabranch billabongs), with no clear spatial trends observable.

Within individual anabranch channels, the relatively limited sedimentary carbon evident near the entry sites may be attributed to several related factors, including the biomass of the overlying litter, flushing of leaf litter and other organic matter during flow events, and sediment grain size patterns within the anabanches. However leaf litter distribution patterns within anabanches were variable, and in general did not correspond well with sediment carbon distribution patterns. The distribution of leaf litter in these channels is inherently controlled by vegetation distribution and density, but is also partially influenced by flow dynamics. This was reflected in the distribution patterns found in anabranhes 1, 3, 5 and 6, with increases in leaf litter load in the dominant flow direction. The character of an individual flow pulse is important in determining a) whether litter is moved or buried within anabanches; b) the type and size of litter moved; c) the distance litter is moved; and d) where litter is deposited. Large woody debris dams and leaf packs were observed to increase in frequency and size with distance down anabanches in the study area, being absent at entry points and accumulating at exit points.
Grain size distribution within river channels has been shown to be a function of flow dynamics, with larger grains falling out first as the velocity of the water decreases (Wolman and Leopold 1970). Sediment grain size analysis for this chapter indicated that flow pulses through anabranches deposit coarse sandy sediment at the entry point, and progressively finer silts and clays toward the exit. Increases in sediment organic matter content corresponded closely with increases in the fine grain size fractions. Fine-grained sediments such as silts and clays have higher affinity for carbon due to their greater surface area and mineral composition – generally, the finer the sediment, the greater the carbon content (Burford and Bremner 1975; Oades and Ladd 1977; Nelson et al. 1991). This relationship appeared to have a relatively greater effect upon sediment carbon distribution within anabranches than the biomass of overlying litter. In French floodplain waterbodies connected with the main channel, sediment grain size and organic matter content have also been directly related to hydrological connection patterns. In waterbodies connected both upstream and downstream, sediments ranged from medium to coarse grained, whereas waterbodies connected at only one end had finer sediments and more organic matter (Amoros and Bornette, 2002). Similar patterns occur in the Macintyre River anabranches. Hence the interaction between geomorphology and the spatial character of hydrological connection strongly influences the spatial distribution of carbon, both directly through transport, and indirectly, through control of velocity and hence depositional patterns. The controlling influence of flow pattern within anabranch channels upon carbon distribution is also complicated by variability in the distribution of vegetation (and hence leaf litter), and also by the presence of ephemeral waterbodies (billabongs). These factors produce apparent discrepancies in pattern, such the limited correspondence observed between leaf litter distribution and sediment carbon distribution.

Again, at this scale as well as others, it is apparent that there are several interacting geomorphological, hydrological and ecological factors determining carbon distribution across this landscape. Consequently, carbon distribution is patchy in terms of both quantity and quality. This patchiness varies with scale and has implications for system functioning. For example, at the within-patch (site) scale, if the carbon within a patch is
not evenly distributed, its accessibility to connecting floodwater will vary depending upon the magnitude and extent of individual flow events. If an anabranch is only partially connected, and floodwater does not traverse the entire channel, carbon pools located spatially beyond the reach of that connection event will remain isolated and unavailable to the river. Hence it is important to understand patterns and processes within, as well as between, patches across river-floodplain landscapes.

5.5 **SUMMARY**

Geomorphic patchiness is associated with a mosaic of carbon pools across this riverine landscape of varying quantity and quality. The inherent character of this geomorphic variability is also associated with the nature of hydrological connectivity across the landscape, which in turn is a primary control of the quantity and quality of carbon sources. The two variables interact and interlink to produce a spatial pattern that ultimately has the potential to affect the functioning of the floodplain river system as a whole. These differences indicate that each of the patch types examined has the potential to play a different role in the ecosystem in terms of carbon supply. Their relative importance varies depending on the spatial and temporal scales examined.

The scale of observation influences the degree of patchiness in carbon distribution perceived across this floodplain river landscape. At the patch-type scale, there were significant differences between the river channel, anabranch channels, and the surrounding floodplain. However moving down a scale, there were no statistically significant differences between the six individual anabranches as units. Hence multiple representatives of a single patch type demonstrated a consistent character. At a yet smaller scale again, significant spatial differences were observed *within* anabranches, between sites (entry, middle and exit). Hence each individual patch, although representative of its type, may contain its own complexities that have bearing on pattern and process in the system.
These results indicate that anabranch channels may play a unique role in the dryland river ecosystem compared to other patch types. Over certain time scales (especially at the flow pulse scale) and in terms of the supply of high-quality carbon sources, they are of higher value to the floodplain river ecosystem relative to other patches. Carbon pools and processes occurring in anabranch channels are different to those occurring in the river channel and the floodplain. These differences depend upon the timing of a) seasons and b) hydrological connection events, including the size and duration of individual connection events. Therefore the role of anabranch channels and their influence upon the functioning of the ecosystem during connection events will also vary according to these factors. Different processes occurring over space at a particular moment in time will lead to different impacts at the moment of connection.

The disconnection phase examined in this chapter dominates the Macintyre River ecosystem in terms of total time (McGinness et al. 2002; Southwell 2002; Thoms et al. 2005). Accumulation and concentration of carbon sources such as litter and detritus, algae, and dissolved organic carbon (DOC) occur within each anabranch during this phase, and vary spatially. In this sense, the disconnection phase may be likened to seasonal droughts. During a drought, flow ceases, and transport of detritus and fine sediments stops, with accumulation of dissolved and particulate carbon sources and sediments (Lake 2003). Conductivity and nutrient concentrations can also increase. Shaded waterbodies may become dark brown with dissolved organic matter leached from leaves, while those in full sun are subject to high temperatures, nutrient build up and solar radiation leading to algal blooms, which in turn can create large diel changes in oxygen concentration (Lake 2003). There are the direct effects of loss of water, and indirect effects, generated by the loss of water volume, that affect water quality and resource availability that in turn affect the biota. In addition, decomposition of organic matter in dry channels occurs at a much slower rate than in wet conditions. During drought, production declines, but remaining isolated pools such as billabongs may become temporary hotspots (Lake 2003), as seen in this chapter for dissolved organic carbon and phytoplankton. As for channels in drought, anabranch channels during the disconnection phase can retain large amounts of various carbon sources, that may be exported.
downstream with storms or with hydrological connection when the drought breaks (Lake 2003). The dominance of the disconnection phase in this and other inland Australian river systems and its relationship and similarity in effect to drought (also a dominant driver) reinforce the need for more research in this area.

This chapter analysed the status of carbon pools in three landscape patches with different levels of hydrological connectivity. The results provide valuable descriptive information that forms the basis of the remaining chapters, in order to address the issue of limited understanding of the ecological importance of physical heterogeneity and hydrological connection of anabranch channels in semi-arid floodplain river systems. The patterns of carbon distribution across the riverine landscape studied suggest that hydrological connection between anabranch channels and the parent river channel may play an important role in determining the quantity and quality of carbon available for maintaining the integrity and sustainability of semi-arid, anabranching floodplain river systems. The following chapters explore that role.
Key messages:

- Physical heterogeneity in this riverine landscape significantly influences biological pattern. Carbon quantity and quality vary among major hydrogeomorphic patches in this landscape. In particular, carbon pools are different in anabranch channels compared to other patches.
  - Carbon **quantity** is greater in anabranch channels compared to adjacent river channel patches, but not compared to the floodplain.
  - Carbon **quality** is greater in anabranch channels compared to both adjacent river channel and floodplain patches.

- Scale is important – patterns vary and are distinct at multiple scales.
  - At the patch type scale – between anabranches, river channel and floodplain
  - Between individual anabranch channels
  - At the within-anabranch scale – between entry, middle and exit sites

- Anabranch channels are particularly important patches in this dryland river landscape, not only in terms of their spatial and physical characteristics, but also in terms of their potential ecological role as carbon storages and sources.
CHAPTER SIX: HYDROLOGICAL CONNECTIVITY AND MAJOR CARBON SOURCES IN A DRYLAND, ANABRANCHING RIVER LANDSCAPE

6.1 INTRODUCTION ........................................................................................................ 179

6.2 METHOD .................................................................................................................. 181
  6.2.1 Study design .......................................................................................................... 181
  6.2.2 Measurement of aquatic carbon sources ............................................................. 182
  6.2.3 Sediment and carbon deposition .......................................................................... 190
  6.2.4 Laboratory flood-simulation experiment ............................................................ 192
  6.2.5 Data analysis ....................................................................................................... 195

6.3 RESULTS ................................................................................................................... 196
  6.3.1 Hydrological connection phases and aquatic carbon sources ......................... 196
      River channel carbon pools – differences between connection phases .......... 196
      Anabranch channel carbon pools – differences between connection phases..... 199
      Differences between anabranches and river during each phase ....................... 201
      Flow event 1: The November-December 2001 Flood .................................... 204
      Flow event 2: The February 2003 Flow Pulse ................................................. 210
  6.3.2 Sediment and carbon deposition ........................................................................ 217
      Sediment deposition ............................................................................................... 217
      Total sediment-associated carbon concentrations ............................................ 220
      Total sediment-associated carbon deposition .................................................... 223
  6.3.3 Laboratory flood-simulation experiment ............................................................ 226
      Spatial patterns ...................................................................................................... 226
      Rates of release .................................................................................................... 232

6.4 DISCUSSION ............................................................................................................ 234
  6.4.1 Hydrological connection phases and the quantity, quality, production and
       respiration of carbon in the river channel ............................................................ 238
  6.4.2 Hydrological connection phases and the quantity, quality, production and
       respiration of carbon in the anabranch channels .............................................. 242
  6.4.3 Sediment and carbon deposition ....................................................................... 246
  6.4.4 Laboratory flood-simulation experiment ........................................................... 248

6.5 SUMMARY ............................................................................................................... 251
6 CHAPTER SIX: HYDROLOGICAL CONNECTIVITY AND MAJOR CARBON SOURCES IN A DRYLAND, ANABRANCHING RIVER LANDSCAPE

6.1 INTRODUCTION
Hydrological connectivity is a key element of floodplain river ecosystem functioning (Heiler et al. 1995; Tockner et al. 1999a; Amoros and Bornette 2002; Ward et al. 2002). Varying flow regimes, histories and events produce complex and variable levels of hydrological connection and natural fragmentation in floodplain river systems. However, the detailed nature of this connectivity and fragmentation and its influences on ecosystem structure and function is only beginning to be understood. During a flow pulse, hydrological connection between the main channel and adjacent floodplain patches facilitates the movement and exchange of water, sediment, biota, nutrients and carbon (Junk et al. 1989; Robertson and Hatcher 1994; Power et al. 1995; Robertson et al. 1999; Tockner et al. 1999a; Ward et al. 1999; Hein et al. 2003). These transfers are considered to be essential for the functioning and integrity of these systems (Amoros and Bornette 2002). Thus, the connectivity provided by a floodplain river’s flood pulse shapes the river channel and the floodplain, but also strongly influences habitat structure, the food web and biotic interactions (Sparks 1995; Sparks and Spink 1998).

Until recently, much of the existing information demonstrating linkages between river channels and their floodplains was derived from studies of temperate forest systems in North America and Europe and tropical forest systems such as the Amazon. While some Australian coastal systems may function in a similar manner to other temperate streams (Lake et al. 1985), the limited information that exists regarding the larger dryland systems inland suggests that they are substantially different (Walker et al. 1995; Puckridge et al. 1998; Robertson et al. 1999; Puckridge et al. 2000). Most Australian inland floodplain rivers are similar to the lowland Macintyre River studied here, in that they are allogenic, dryland complex, variable, boom and bust ecosystems (Walker et al.
1997), that require customised scientific and management approaches to understanding their function and maintaining their integrity (Thoms and Cullen 1998; Boulton et al. 2000).

Extensive dry floodplain surfaces and networks of channels that are connected only during flow pulses are important characteristics of Australian inland rivers (Walker et al. 1995; Thoms and Sheldon 2000). The combination of hydrological and geomorphological variation that is present in semi-arid anabranching river systems such as the Macintyre River provides an opportunity to investigate the roles of connectivity and fragmentation in a riverine landscape. This information is important because individualised flow in anabranches occurs during minor and moderate flow events (flow pulses); hence large amounts of water are not generally required to instigate connection and disconnection, with direct implications for both ecology and environmental flow management.

This chapter tests and reviews the temporal component of the conceptual model outlined in Chapter 3, in light of both field and experimental data. It aims to quantify the influence of different phases of hydrological connection and fragmentation upon carbon availability in anabranche channels and the parent river channel of a semi-arid system. It examines carbon sources in anabranche channels and the river channel during each of four connection phases, and asks the question ‘Does hydrological connection influence the quantity, quality, production or respiration of carbon in the main river channel and adjacent anabranche channels?’ Each connection phase has the potential to create changes or differences in the availability of carbon in both the parent river and anabranche channels. Such differences in turn may cause changes in production and respiration within the parent river channel, with possible switching between autotrophy and heterotrophy.
6.2 **Method**

6.2.1 **Study design**

This chapter focuses on the major carbon sources present in the main river channel and adjacent anabranch channels during each of the connection phases. It emphasises short-term temporal variation, as well as providing insight into the long-term influences of each connection phase on the ecology of the system. Within the temporal ‘template’ of each connection phase, the collection and analysis of data for this chapter was conducted at the same three nested spatial scales described in Chapter 5:

1. Patch type (anabranchn, riverbank, floodplain)
2. Individual anabranch (1-6)
3. Site (entry, middle, exit; see Chapter 3)

Where possible, the same six individual anabranches were used, however during flood and flow events accessibility and logistics restricted sampling to a limited number of selected anabranchn channels.

There are three primary components to this chapter, which test the conceptual model described in Chapter 3:

1. Measurement of aquatic carbon pools during two flow events: the first in November-December 2001, and the second in February 2003. This component tests the conceptual model by making direct measurements of aquatic carbon sources in the anabranch channels and adjacent river channel during each connection phase. It aims to detect changes in primary carbon pools and link these changes to the characteristics and sequence of each phase.

2. Measurement of sediment and associated carbon deposition during a third flow event (March-April 2002). This component tests the conceptual model by measuring the accumulation of sediment and associated carbon during a connection event encompassing all four phases. It provides data useful in
distinguishing whether the role of anabranches (e.g. are they sinks or sources of carbon) differs according to the quality of carbon studied (e.g. sediment carbon vs. dissolved carbon).

3. Measurement of dissolved organic carbon release from sediments artificially flooded in the laboratory. This component tests the conceptual model by allowing controlled measurement of one of the primary processes occurring during connection events – the release of carbon from freshly inundated sediments. It balances the second component (sediment deposition) by providing an estimate of the amounts of dissolved organic carbon made available during inundation of sediments from different patches.

The three components are interlinked, with the latter two providing examples of ‘static’, detailed measurements of the influence of hydrological connection upon two key processes – deposition and release – while component one provides a ‘moving’, in-situ estimate of the status of carbon sources in the ever-changing environment of flow connection events. In addition, they help to clarify the links between different carbon transfers – for example, is the spatial pattern of sedimentary carbon deposition in anabranches related to a spatial pattern of potential dissolved organic carbon supply?

6.2.2 Measurement of aquatic carbon sources

Sampling during the two flow events focused on three aquatic carbon sources: phytoplankton (Chl α), dissolved organic carbon (DOC), and carbon produced by benthic production (GPP) and consumed by benthic respiration (R24). These were measured in anabranch billabongs and the littoral zone of main river channel during each of the four connection phases, in the same manner as that described in Chapter 5.

Analysis of individual flow connection events is desirable for accurate representation of differences between connection phases, however an overall perspective is also useful to identify general trends. This general view is presented first, with all available data.
analysed separately for the main river channel and the anabranch channels, in order to detect significant differences in concentrations associated with connection phase. A summary of connection phases, anabranches and aquatic parameters sampled over the duration of the study is presented in Table 6.1.

During large flood events, concentrations of carbon in the river channel are influenced by movement of the hydrograph flow peak and its associated dissolved and particulate loads, as well as potential anabranch input. For this reason, dissolved organic carbon and benthic metabolism results are also presented individually for the two flow event case studies; the November-December 2001 flood, and the February 2003 flow pulse.

Phytoplankton samples (chlorophyll $\alpha$) were collected during the partial connection, complete connection, and draining phases of the November-December 2001 flood event, and during July 2001 (disconnection), October 2001 (disconnection/partial connection), and February 2002 (disconnection/partial connection). Phytoplankton samples were not collected during the February 2003 flood event. Temporal changes in phytoplankton concentrations during the November – December 2001 flood event mirrored those represented by the aggregated data, but the dataset was not as complete, so for the purposes of this dissertation, phytoplankton results are presented as part of the aggregated overview section, and not as part of the case study of the November-December 2001 flow event.
Table 6.1  Connection phases, patch types, and aquatic parameters measured during each sampling trip, indicated by shaded boxes.

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<td>Complete connection</td>
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<tr>
<td>River phytoplankton</td>
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<tr>
<td>River benthic metabolism</td>
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<tr>
<td>Water quality parameters</td>
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Flow event 1: The November-December 2001 Flood

The November-December 2001 event resulted in extensive overbank inundation and had an average recurrence interval (ARI) of approximately 1 in 3 years. Discharge peaked at 53,697 Ml day$^{-1}$ and 7.67 metres at Goondiwindi on the 29$^{th}$ of November 2001. This event had a relatively rapid rate of rise, discharge increasing from 911 Ml day$^{-1}$ on the 26$^{th}$ to 13,975 Ml day$^{-1}$ on the 27$^{th}$ of November. The flood was effectively over at Goondiwindi by the 7$^{th}$ of December, when flows had dropped to 1358 Ml day$^{-1}$ but were still falling. At Terrewah, 95 river kilometres downstream of Goondiwindi, and eight river kilometres downstream of the exit of anabranch 1, the main anabranch sampled (A1; Figure 6.1), the flood event peaked 5 days later on the 4$^{th}$ of December, at 10,546 Ml day$^{-1}$ and 6.77 metres. The flood hydrograph at Terrewah is attenuated compared to that at Goondiwindi, with elevated stage heights and discharge over a longer period, between the 28$^{th}$ November and 12$^{th}$ December. Because of this attenuation, flow duration above the anabranch commence-to-flow thresholds was increased.

Sampling of this flood was opportunistic, beginning during the partial connection phase and continuing through to the end of the draining phase. Initially, four anabranches were sampled - anabranches 1, 2, 3 and 5 – however sampling of the latter three anabranches was soon abandoned due to overbank flooding impeding access. Anabranches 4 and 6 were not sampled at all due to flooding-related lack of access. Dissolved organic carbon, and phytoplankton (chlorophyll $\alpha$) measurements were taken at the entry and exit sites of each anabranch, as well as in the river channel above and below each entry and exit point. Duplicate samples were taken once daily between 27/11/2001 and 9/12/2001 (Table 6.2).

During the November-December 2001 Flood, benthic metabolism measurements were focused on the riverbanks adjacent to anabranch 1 (Table 6.2). Two chambers were positioned at each of 3 sites: upstream of the entry (RAE), downstream of the entry (RBE), and downstream of the exit (RBX). Monitoring took place on 6 occasions (27$^{th}$ November, and 1$^{st}$, 3$^{rd}$, 6$^{th}$, 8$^{th}$, and 10$^{th}$ December 2001), from the partial connection phase through complete connection to the draining phase.
Flow event 2: The February 2003 Flow Event

The February 2003 event was a flow pulse (average recurrence interval approximately 1 in 2 years) that was much smaller than the November-December 2001 event. Discharge peaked at 19,714 Ml day\(^{-1}\) and 5.03 metres at Goondiwindi on the 25\(^{th}\) of February 2003. Discharge remained below bankfull, yet completely inundated the anabranch channels. Consequently this event may be more useful for identifying possible influences of phases of connection between anabranches and the river. Two anabranch channels (A1 and A2) and their adjacent river reaches were sampled continuously throughout the hydrograph (Table 6.3; Figure 6.1).

Previously, discharge at Goondiwindi had reached a low of 66 Ml day\(^{-1}\) on the 19\(^{th}\) February, gradually rose to 256 Ml day\(^{-1}\) by the 23\(^{rd}\) February, and then rose to peak within 2 days. The flood was effectively over at Goondiwindi by the 2\(^{nd}\) of March, when flows had dropped to 1596 Ml day\(^{-1}\), but were still falling. At Terrewah, the same flood peaked 3 days later on the 28\(^{th}\) of February, at 7,402 Ml day\(^{-1}\) and 6.05 metres. Terrewah discharge began to rise at the same time as discharge peaks in Goondiwindi. The flood hydrograph at Terrewah was again attenuated compared to that for Goondiwindi. The flood was over at Terrewah by the 3\(^{rd}\) March, with flows of 1946 Ml day\(^{-1}\) (3.44 m).

All comparisons were made after adjusting the Terrewah hydrograph for each site according to its distance from the gauge (river km) and a flood moving at 1.32 river km per hour (based on hydrograph calculations of the time taken for the flood peak to travel from Goondiwindi to Terrewah). Sampling of this flood began during the disconnection phase and continued through to the end of the draining phase. Anabranches 1 and 2 were selected for sampling based on logistical concerns as well as previous experience regarding access to the other anabranches. Dissolved organic carbon measurements were taken at the entry and exit sites of each anabranch, as well as in the river channel above each entry, between the entry and exit points, and below the exit point. Duplicate samples were taken thrice daily between 25/2/2003 and 3/3/2003 (Table 6.3).
Table 6.2 Sites and parameters monitored during Flow Event 1 (November-December 2001).

<table>
<thead>
<tr>
<th>Anabranch and site</th>
<th>22nd Nov - 11th Dec 2001</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Parameters ($n$ replicates)</td>
</tr>
<tr>
<td>Anabranch 1</td>
<td></td>
</tr>
<tr>
<td>Entry</td>
<td>A1E</td>
</tr>
<tr>
<td>Middle</td>
<td>A1M</td>
</tr>
<tr>
<td>Exit</td>
<td>A1X</td>
</tr>
<tr>
<td>River above entry</td>
<td>A1RAE - DOC (2 day -1), Chl (2 day -1), sediment TC (3, pre + post event)</td>
</tr>
<tr>
<td>River below entry</td>
<td>A1RBE - DOC (2 day -1), sediment TC (3, pre + post event)</td>
</tr>
<tr>
<td>River above exit</td>
<td>A1RAX - DOC (2 day -1), Chl (2 day -1), sediment TC (3, pre-event)</td>
</tr>
<tr>
<td>River below exit</td>
<td>A1RBX - DOC (2 day -1), sediment TC (3, pre-event)</td>
</tr>
<tr>
<td>Anabranch 2</td>
<td>Water sampling only on 28th Nov (lack of access)</td>
</tr>
<tr>
<td>Entry</td>
<td>A2E - DOC (2 day -1), Chl (2 day -1), sediment TC (3, pre + post event)</td>
</tr>
<tr>
<td>Exit</td>
<td>A2X</td>
</tr>
<tr>
<td>River above entry</td>
<td>A2RAE - DOC (2 day -1), Chl (2 day -1)</td>
</tr>
<tr>
<td>River below entry</td>
<td>A2RBE - DOC (2 day -1), Chl (2 day -1)</td>
</tr>
<tr>
<td>River above exit</td>
<td>A2RAX - DOC (2 day -1), Chl (2 day -1)</td>
</tr>
<tr>
<td>River below exit</td>
<td>A2RBX - DOC (2 day -1), Chl (2 day -1)</td>
</tr>
<tr>
<td>Anabranch 3</td>
<td>Water sampling only on 28th Nov (lack of access)</td>
</tr>
<tr>
<td>Entry</td>
<td>A3E - DOC (2 day -1), Chl (2 day -1), sediment TC (3, pre + post event)</td>
</tr>
<tr>
<td>Middle</td>
<td>A3M</td>
</tr>
<tr>
<td>Exit</td>
<td>A3X</td>
</tr>
<tr>
<td>River above entry</td>
<td>A3RAE - DOC (2 day -1), Chl (2 day -1)</td>
</tr>
<tr>
<td>River below entry</td>
<td>A3RBE - DOC (2 day -1), Chl (2 day -1)</td>
</tr>
<tr>
<td>River above exit</td>
<td>A3RAX - DOC (2 day -1), Chl (2 day -1)</td>
</tr>
<tr>
<td>River below exit</td>
<td>A3RBX - DOC (2 day -1), Chl (2 day -1)</td>
</tr>
<tr>
<td>Anabranch 4</td>
<td>Water not sampled due to lack of access</td>
</tr>
<tr>
<td>Entry</td>
<td>A4E</td>
</tr>
<tr>
<td>Middle</td>
<td>A4M</td>
</tr>
<tr>
<td>Exit</td>
<td>A4X</td>
</tr>
<tr>
<td>Anabranch 5</td>
<td>Water sampling only on 22nd and 25th Nov (lack of access)</td>
</tr>
<tr>
<td>Entry</td>
<td>A5E - DOC (2 day -1), Chl (2 day -1), sediment TC (3, post-event)</td>
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<td>Middle</td>
<td>A5M</td>
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</tr>
<tr>
<td>River above entry</td>
<td>A5RAE - DOC (2 day -1), Chl (2 day -1)</td>
</tr>
<tr>
<td>River below entry</td>
<td>A5RBE - DOC (2 day -1), Chl (2 day -1)</td>
</tr>
<tr>
<td>River below exit</td>
<td>A5RBX - DOC (2 day -1), Chl (2 day -1)</td>
</tr>
<tr>
<td>Anabranch 6</td>
<td>Not sampled due to lack of access</td>
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</tbody>
</table>
Table 6.3 Sites and parameters monitored during Flow Event 2 (February 2003).

<table>
<thead>
<tr>
<th>Anabranch and site</th>
<th>25th Feb - 3rd Mar 2003</th>
<th>Parameters (n replicates)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Anabranch 1</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Entry</td>
<td>A1E</td>
<td>DOC (2 reps* 3 per day), benthic metabolism chambers (4), water quality (3 day$^{-1}$)</td>
</tr>
<tr>
<td>Exit</td>
<td>A1X</td>
<td>DOC (2 reps* 3 per day), benthic metabolism chambers (4), water quality (3 day$^{-1}$)</td>
</tr>
<tr>
<td>River above entry</td>
<td>A1RAE</td>
<td>DOC (2 reps* 3 per day), benthic metabolism chambers (4), water quality (3 day$^{-1}$)</td>
</tr>
<tr>
<td>River above exit</td>
<td>A1RAX</td>
<td>DOC (2 reps* 3 per day), water quality (3 day$^{-1}$)</td>
</tr>
<tr>
<td>River below exit</td>
<td>A1RBX</td>
<td>DOC (2 reps* 3 per day), benthic metabolism chambers (4), water quality (3 day$^{-1}$)</td>
</tr>
<tr>
<td><strong>Anabranch 2</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Entry</td>
<td>A2E</td>
<td>DOC (2 reps* 3 per day), water quality (3 day$^{-1}$)</td>
</tr>
<tr>
<td>Exit</td>
<td>A2X</td>
<td>DOC (2 reps* 3 per day), water quality (3 day$^{-1}$)</td>
</tr>
<tr>
<td>River above entry</td>
<td>A2RAE</td>
<td>DOC (2 reps* 3 per day), water quality (3 day$^{-1}$)</td>
</tr>
<tr>
<td>River above exit</td>
<td>A2RAX</td>
<td>DOC (2 reps* 3 per day), water quality (3 day$^{-1}$)</td>
</tr>
<tr>
<td>River below exit</td>
<td>A2RBX</td>
<td>DOC (2 reps* 3 per day), water quality (3 day$^{-1}$)</td>
</tr>
</tbody>
</table>
Figure 6.1 Locations of sites sampled during the November 2001 and February 2003 flow events.
6.2.3 **Sediment and carbon deposition**

Carbon associated with sediment may be directly available to bacteria and other consumers, and may also be dissolved or released to the water column upon inundation of the sediment. Field observation in the Macintyre River system suggested that a great deal of sediment is deposited in anabranch channels during flow connection events, burying leaf litter and grasses. This sediment has the potential to bear carbon loads that may be of significance to the ecosystem. Anabranches may function as sinks for particulate carbon but as sources of dissolved carbon. If this is the case, the movement of sediment within and between these landscape patches may be of primary importance to the functioning of the ecosystem. Investigation of the loads of sediment and associated carbon deposited in anabranch channels, compared with those deposited on riverbanks, may help to clarify the role of anabranches.

Artificial grass mats of a known area have been used in other studies (Asselman and Middelkoop 1995; Middelkoop and Asselman 1998; Asselman 1999; Ogden and Thoms 2002) to estimate sediment deposition on in-channel benches and floodplains. In the present study, three replicate synthetic grass mats measuring 0.5 x 0.5m were placed during the disconnection phase (February 2002) at the entry, middle, and exit sites of each of the six anabranches previously studied. Three mats were also placed on the adjacent riverbanks of each anabranch upstream of the entry site.

The mats were inundated by a flow event during March-April 2002 (Figure 6.2), and retrieved during June 2002. The flow event lasted eight days, peaking on the 31st of March at Goondiwindi (13231 Ml day⁻¹) and the 3rd of April at Terrewah (6471 Ml day⁻¹; 5.8 m). The anabranches were completely inundated (except anabranch 6, which had two of its three sites inundated), and the floodwater did not go ‘overbank’. Of the 72 mats, three were lost and therefore not retrieved from the riverbanks, and four were lost from the anabranch channels. The entry site of anabranch 6 was not inundated; hence there are no data for these three mats.
The sediment mats and all sediment deposited on them were individually placed into large plastic bags, labelled and sealed for transportation to the laboratory. In the laboratory each bag with its mat and sediment was opened and oven-dried at 30°C for 7 days, then weighed. The sediment for each mat was then mixed and 50 g subsamples were taken and homogenised using a mortar and pestle for total carbon content analysis (see Chapter 5 for precise method). Mats and bags were then washed, dried and weighed, and their weights subtracted from the total mat/bag/sediment weight to yield total dry weight of sediment.
6.2.4 Laboratory flood-simulation experiment

Wetting of sediments and leaf litter in anabranch channels releases quantities of dissolved organic carbon (DOC) that can be readily assimilated into aquatic food webs (Baldwin and Mitchell 2000). The high total carbon content of surface sediments, and the large loads of litter present in anabranches of the Macintyre River system indicate that release of dissolved organic carbon may be an important carbon source during connection phases. For example, on the lower Balonne Floodplain, Australia (a neighbouring catchment), the average amount of DOC released from surface sediments upon wetting (in the laboratory) was equivalent to 2.28 kg (0.002 tonnes) per hectare per day (McGinness and Thoms 2002). The importance of dissolved organic carbon release from sediments upon wetting is magnified in dryland floodplain river systems such as the Macintyre River, because of the limited vegetation and hence dominance of the bare-earth environment within sites. It is important to know a) how much carbon is actually released to the water column during connection events; b) which patch type releases the most; and c) how release varies from upstream to downstream within anabranches.

In addition, an El Nino event beginning in winter 2002 resulted in less rainfall than usual, with associated reduced flows and the onset of drought. This resulted in an unexpected lack of small flow connection events, which are usually common in the study area. Thus sampling of an ‘in-channel’ complete connection event in the field was thought likely to be unachievable. To compensate for this, and to explore the issues raised above regarding potential DOC supply, intact sediment sods were collected during December 2002 for a laboratory experiment to simulate the effects of a flood event in the study area. This experiment was conducted during January 2003, and provides quantitative information regarding the release of dissolved organic carbon to the water column from the sediments of various floodplain landscape patches during inundation.
The objectives of the laboratory experiment were:

1. To determine the amount of dissolved organic carbon (DOC) released from dry surface sediments of the lower Macintyre River system following inundation
2. To determine if the amount of DOC released differs between sediments from the three primary patch types: anabranch channels, the main river channel and the surrounding floodplain
3. To determine how DOC concentrations change over time in water overlying surface sediments

Anabranch 3 was chosen for sampling because it has a commence-to-flow (CTF) offtake below 7000 Ml day\(^{-1}\) (Chapter 4), and is therefore frequently connected to the main channel. It also has a clearly separate floodplain; and offers easy access to riverbanks. Samples were collected in December 2002 from the entry, middle and exit sites of the dry anabranch channel, the adjacent floodplain sites, and corresponding sites in the main river channel. Replicate samples comprised intact surface sediment sods measuring 110 x 110 x 50 mm that were collected using a square metal frame, placed in opaque two-litre plastic containers (basal area 110 x 110 mm) and sealed.

Chapter 5 demonstrated variability in total carbon content of surface sediments according to position within the anabranch. To account for this variation, five replicate samples were collected at each site. Floodplain samples were taken approximately 20 m perpendicular from the anabranch channel (anabranch 3), avoiding disturbed or tilled ground. River samples were taken on the banks upstream of the entry point, between the entry and exit, and downstream of the exit point. These samples were taken level with the anabranch offtake or commence-to-flow height, and approximately 20 m from the nearest anabranch entry or exit point. At each site, separate sediment samples were also collected immediately adjacent to the sods for later analysis of carbon content.

Comparisons were also made to determine how the amount of DOC released and its flux over time differs with the use of a) distilled water and b) river water to inundate the sediments, however these results are not presented as part of this dissertation. Extra
replicate samples were taken from the middle anabranch, floodplain and river sites for experiments comparing release of dissolved organic carbon to different water types. River water was collected upstream of the anabranch in 20 L opaque plastic containers just before the return trip, and kept refrigerated in the dark until commencement of the experiment.

In the laboratory, live and dead organic matter was removed after recording the percentage cover of each sod. The sods were then placed in random order into dark incubation chambers set at 30°C during the day (12 hours) and 20°C at night (12 hours). After 24 hours, two litres of distilled water was sprinkled into each container, minimising physical disruption, until the sod was covered to a depth of at least 20 mm. Four empty containers were placed in each incubator as controls – two filled with two litres of distilled water, and two with river water.

The water in each container was sampled after 2, 6, 12, 24, 48, 72, 96, 120, and 144 hours, simulating a 6-day inundation event. Using a sterile syringe, 25 ml was withdrawn from the water overlying the centre of each sod, taking care not to disturb the sediment or take up solid matter. The sample was then immediately filtered through a 0.45um syringe filter into a glass vial, sealed and placed into a cooled, darkened container. Used filters were discarded. Between each sample, the syringe was rinsed three times with Milli-Q water. Samples were analysed within 24 hours for carbon content according to the method described in Chapter 5.
6.2.5 **Data analysis**

Fixed general linear model univariate analysis of variance (GLM univariate ANOVA) was performed for each dataset to identify statistical significance of differences. Log\textsubscript{10} transformations were performed when necessary, in order to comply with the assumptions of the ANOVA, and are identified where appropriate. Tukey’s Honestly Significant Difference (HSD) multiple comparison procedures were then used to determine where differences occurred (significance value [$\alpha$] = 0.05). Box plots were used to present data and statistical values. The boundary of the box closest to zero indicates the 25th percentile, a solid line within the box marks the median, a dashed line marks the mean, and the boundary of the box farthest from zero indicates the 75th percentile.

The effect of flow connection phase was investigated first by analysing data from each patch type (river channel and anabranch channel) for each of the four phases. This analysis gave an indication of the changes occurring within a patch from one phase to the next. This was followed by analysis of the differences between patches within each connection phase – as conducted for the disconnection phase in Chapter 5, but here extended to the partial connection, complete connection, and draining phases. This analysis gave an indication of the relative status of each patch type during each phase, in terms of carbon, production and respiration. Analysis was first conducted using aggregated data from all sampling trips. This was followed by analysis of data within two individual flow events (November 2001 and February 2003), to more accurately highlight differences.
6.3 RESULTS

6.3.1 Hydrological connection phases and aquatic carbon sources

River channel carbon pools – differences between connection phases

Dissolved organic carbon
Aggregating all available data, dissolved organic carbon (DOC) concentrations in the main river channel differed significantly between connection phases (log$_{10}$ transformed data; $F = 49.20; \text{df} = 3,264; p<0.005$; Figure 6.3). Multiple comparisons based on Tukey’s HSD ($\alpha = 0.05$) indicated that the only phases not significantly different from each other were disconnection and partial connection (medians approx. 8 and 9 ppm). All other phases were significantly different from these and from each other. During complete connection median concentrations in the river were 13 ppm, compared to draining phase concentrations of 14 ppm. Maximum DOC concentrations in the river ranged from 14 ppm (partial connection) to around 17-18 ppm (draining and complete connection).

Phytoplankton
After aggregating all available data, phytoplankton concentrations in the river differed significantly between connection phases (log$_{10}$ transformed data; $F = 15.23; \text{df} = 3,52; p<0.005$), with concentrations during the draining phase significantly lower than all other phases (Tukey’s HSD; $\alpha = 0.05$; median 0.93 mg m$^{-3}$). Variability was high, however the greatest concentrations were recorded during the disconnection phase (median 9.13 mg m$^{-3}$), while the partial and complete connection phases had generally similar concentrations (5.55 and 6.41 mg m$^{-3}$ respectively; Figure 6.4). Maximum concentrations of phytoplankton in the river ranged from 8.81 mg m$^{-3}$ during the draining phase, to a high of 110.31 mg m$^{-3}$ during the disconnection phase. The complete connection phase also had a relatively high maximum concentration of 35.18 mg m$^{-3}$, while partial connection showed a relatively low maximum concentration of 15.49 mg m$^{-3}$.
**Benthic metabolism**

**River GPP**

After aggregating all available data, benthic production rates in the main river channel differed significantly between each of the different connection phases ($F = 22.14; \text{df} = 3, 91; p<0.005$; Figure 6.5). Multiple comparisons using Tukey’s HSD indicated that benthic production was significantly lower during complete connection, dropping to a median of 0.06 gC m$^{-2}$ day$^{-1}$. Production during the draining phase (median 0.12 gC m$^{-2}$ day$^{-1}$) was significantly higher than that in the complete connection phase, but significantly lower than that during disconnection and partial connection. Disconnection and partial connection production rates in the river were similar, although slightly lower during partial connection (medians 0.35 and 0.28 gC m$^{-2}$ day$^{-1}$ respectively).

**River R24**

After aggregating all available data, benthic respiration rates on riverbanks differed significantly between each of the connection phases ($F = 4.09; \text{df} = 3,91; p<0.05$; Tukey’s HSD $\alpha = 0.05$; Figure 6.6). In particular, benthic respiration rates on the riverbanks were significantly higher during disconnection and partial connection (medians 0.14 gC m$^{-2}$ day$^{-1}$ and 0.21 gC m$^{-2}$ day$^{-1}$ respectively), than those during the complete connection and draining phases (medians 0.08 gC m$^{-2}$ day$^{-1}$).

**River P/R ratios**

On the riverbanks median benthic P/R ratios were greater than 1.0 for all phases except complete connection (0.61). The P/R ratios on the riverbanks were statistically significantly different between all connection phases ($F = 4.85; \text{df} = 3,91; p<0.05$; Tukey’s HSD $\alpha = 0.05$). Ratios were highest during the disconnection phase (median 2.68), followed by partial connection (1.92), then draining (1.29) and complete connection (0.61).
Figure 6.3 Dissolved organic carbon concentrations in the river channel, by phase.

Figure 6.4 River chlorophyll α by connection phase.

Figure 6.5 Benthic production in the river channel during each connection phase.

Figure 6.6 Benthic respiration in the river channel during each connection phase.

Figure 6.7 Benthic P/R ratios in the river channel during each connection phase. The solid line at ratio 1.0 indicates the threshold between autotrophy (>1) and heterotrophy (<1).
Anabranch channel carbon pools – differences between connection phases

**Dissolved organic carbon**

After aggregating data from all trips, DOC concentrations in the anabranch channels were also significantly different between different connection phases, but to a greater degree than in the river (lg$_{10}$; F = 12.97; df = 3,219; p<0.005). The disconnection phase had the highest concentrations (median 15 ppm); statistically significantly greater than the complete and partial connection phases (Tukey’s HSD; $\alpha$ = 0.05; medians 13 ppm and 11 ppm respectively). The onset of the partial connection phase resulted in significantly lower DOC concentrations in the anabranch channels than all other phases (Tukey’s HSD; $\alpha$ = 0.05). This was followed by significant increases during the complete connection and draining phases (Figure 6.8; draining phase median 14 ppm). Maximum DOC concentrations in the anabranch channels also varied between phases, with the maximum concentration in the billabongs during disconnection being more than triple those found in other connection phases (66 ppm vs. 16-29 ppm).

**Phytoplankton**

After aggregating data from all trips and anabranches, anabranch channel phytoplankton concentrations were significantly different during different connection phases (log$_{10}$ transformed data; F = 12.04; df = 3,46; p<0.005). Trends were different to those found in the river (Figure 6.9). The disconnection phase in anabranches displayed significantly higher mean, median and maximum concentrations of phytoplankton than all other phases (Tukey’s HSD; 68.31, 33.31 and 708.62 mg m$^{-3}$ respectively). Median concentrations of phytoplankton in the anabranches were lower during partial connection (11.56 mg m$^{-3}$), and lowest during the complete connection phase (4.17 mg m$^{-3}$). This was followed by a substantial increase in concentrations during the draining phase (median 22.29 mg m$^{-3}$). Maximum phytoplankton concentrations in the anabranches ranged from 24.76 mg m$^{-3}$ during complete connection, to 708.62 mg m$^{-3}$ during disconnection. Partial connection and draining phases showed maximum concentrations of 50.80 and 36.58 mg m$^{-3}$ respectively.
Benthic metabolism

Anabranch GPP
After aggregating data from all trips, median benthic productivity in the anabranch channels was not statistically different between connection phases (F = 1.130; df = 3,97; p = 0.341; Figure 6.10). In general, productivity in anabranch channels appeared to be lowest during complete connection (median 0.13 gC m$^{-2}$ day$^{-1}$), and highest during the draining phase (median 0.23 gC m$^{-2}$ day$^{-1}$), compared to the disconnection and partial connection phases (medians 0.15 and 0.18 gC m$^{-2}$ day$^{-1}$ respectively).

Anabranch R24
Differences in anabranch benthic respiration between connection phases were not statistically significant (F= 1.56; df = 3,97; p = 0.204). Examination of the plotted data (Figure 6.11) indicates that respiration rates were highest during the disconnection phase (median 0.15 gC m$^{-2}$ day$^{-1}$), and lowest during complete connection (0.08 gC m$^{-2}$ day$^{-1}$). Respiration during the partial connection and draining phases was similar (0.11 gC m$^{-2}$ day$^{-1}$).

Anabranch P/R ratios
In the anabranches, median benthic P/R ratios were greater than 1.0 for all phases except disconnection (0.91; Figure 6.12). Differences in P/R ratios between all connection phases were statistically significant (F = 4.270; df = 3,96; p <0.05). The highest median P/R ratio in the anabranches occurred during the draining phase (2.04), followed by partial connection (1.84) and complete connection (1.75).
Differences between anabranches and river during each phase

The several statistically significant differences between river and anabranch channels during the disconnection phase were described fully in Chapter 5. During the partial connection phase, dissolved organic carbon concentrations were significantly greater in anabranch channels (median 11 ppm) compared to the river channel (9 ppm; Table 6.4). Benthic respiration on the riverbanks (median 0.21 gC m\(^{-2}\) day\(^{-1}\)) significantly exceeded that of anabranch channels (median 0.11 gC m\(^{-2}\) day\(^{-1}\)) during this phase. There were no other statistically significant differences between the patches during the partial connection phase. During the complete connection phase, no statistically significant differences between the river and the anabranch channels were recorded for any parameter. However during the draining phase, phytoplankton (chlorophyll \(\alpha\)) concentrations were significantly different between patches (Table 6.4). Median anabranch chlorophyll \(\alpha\) concentrations were 22.29 mg m\(^{-3}\) during this phase, while median river concentrations were 0.93 mg m\(^{-3}\).
The image contains figures illustrating various ecological data as follows:

**Figure 6.8** Anabranch dissolved organic carbon concentrations, by connection phase.

**Figure 6.9** Anabranch chlorophyll α by connection phase.

**Figure 6.10** Benthic production in anabranch channels during connection phases.

**Figure 6.11** Benthic respiration in anabranch channels during connection phases.

**Figure 6.12** Benthic P/R ratios in anabranch channels during connection phases. The solid line at ratio 1.0 indicates the threshold between autotrophy (>1) and heterotrophy (<1).
Table 6.4  Statistical significance (GLM univariate ANOVA) of dissolved organic carbon (DOC), phytoplankton (Chl α), and benthic metabolism (R24, GPP, P/R ratio) differences between anabranch and riverbank patches during connection phases.

<table>
<thead>
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<th>df</th>
<th>p value</th>
</tr>
</thead>
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<tr>
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<tr>
<td></td>
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<tr>
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<tr>
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<td>1,16</td>
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</tbody>
</table>
Flow event 1: The November-December 2001 Flood

*Dissolved organic carbon – differences between connection phases*

During the November-December 2001 flood event, DOC concentrations in anabranch 1 and the river channel rose and peaked at about the same time as discharge, then remained elevated during and after flood recession. The disconnection phase was not sampled immediately before this flow event, therefore only the partial connection, complete connection and draining phases are presented here.

Focusing on an individual anabranch (A1), sampled throughout the hydrograph, DOC concentrations were significantly greater in the anabranch during the completely connected and draining phases compared to the partial connection phase (F = 5.167; df = 2,26; p<0.05; Tukey’s HSD; Figure 6.13). Concentrations began rising quickly with partial connection (approx. 10 ppm in 7 days), peaking at around 17 ppm, and then falling gradually in both the anabranch and the river as the river stage height dropped (Figure 6.14). However DOC concentrations remained elevated within the anabranch exit (A1X) for several days after peak discharge had passed. Indeed, when complete connection ceased and the anabranch began to drain, concentrations at the anabranch exit (A1X) and also at the other sites (notably A1RBE) actually rose, or at least ceased falling temporarily (Figure 6.15). Consequently, the progression of the flow pulse was associated with an increase in the range of DOC concentrations across the floodplain river landscape, both spatially and temporally.

<table>
<thead>
<tr>
<th>Patch type</th>
<th>Variable</th>
<th>Treatment</th>
<th>Result</th>
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<th>df</th>
<th>p value</th>
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</thead>
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<td>Anabranch</td>
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<td>DOC</td>
<td>Phase</td>
<td>SIG</td>
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<td>3.59</td>
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</tbody>
</table>
River DOC concentrations varied over time but not spatially, reflecting the passage of the flood peak with associated elevated concentration of dissolved and particulate matter (Figure 6.16). Again, DOC concentrations were significantly greater during the complete connection and draining phases compared to those present during the partial connection phase ($F = 14.19; \text{df} = 3,59; p<0.005$; Tukey’s HSD).

![Figure 6.13 Dissolved organic carbon concentrations in anabranch channels and the river channel during the partial, complete, and draining phases of the Nov-Dec 2001 flood. Symbol meanings are explained in section 6.2.5.](image)

205
Figure 6.14 Dissolved organic carbon concentrations in anabranch 1 (A1E = entry site and A1X = exit site) and the adjacent river sites (A1RAE, RBE, RAX and RBX), plotted with the river stage height hydrograph for Terrewah during the November-December 2001 Flood. RAE = River above entry; RBE = River below entry; RAX = River above exit; RBX = River below exit. Where values are similar, symbols may overlap.
Figure 6.15 Dissolved organic carbon concentrations in anabranch channels over the duration of the November-December 2001 Flood. Sampling was discontinuous for some anabranches, and in these cases lines are not shown. Where values are similar, symbols may overlap.

Figure 6.16 Dissolved organic carbon concentrations in the main river channel over the duration of the November-December 2001 Flood. Sampling was discontinuous for some anabranches, and in these cases lines are not shown. Where values are similar, symbols may overlap.
Benthic metabolism – differences between connection phases

Benthic metabolism rates were spatially variable within and between sites during the November-December 2001 flow event. In general, respiration, production and P/R ratios decreased with complete connection, and then increased again slightly during draining.

Benthic production on the riverbanks during this flood was highest during the partial connection phase, and fell rapidly and significantly (F = 14.55; df = 2,23; p<0.005) with the onset of complete connection. During the draining phase production was significantly greater than during complete connection, but still significantly lower than that of the partial connection phase (Figure 6.17). Benthic production during each of the three phases monitored during this flood event was significantly different from that of each other phase (Tukey’s HSD; α = 0.05).

Changes in benthic respiration rates between each connection phase were also significant (F = 4.581; df = 2,23; p <0.05; Tukey’s HSD; α = 0.05), again falling rapidly with complete connection (Figure 6.18). However unlike the pattern observed for benthic production, respiration continued to decrease during the draining phase.

At the beginning of partial connection P/R ratios were greater than one for three of the four sites. With the onset of complete connection, ratios generally dropped to less than one. During draining P/R ratios increased, with 3 of the 4 sites again recording ratios greater than one (Figure 6.19). These changes were not statistically significant (F = 1.66; df = 2,23; p = 0.211).

Differences between anabranches and river during each phase

Within-phase differences in dissolved organic carbon concentration between the anabranches and the river during this flow event were not statistically significant for any phase (Table 6.6;Figure 6.13). Benthic metabolism was measured only in the river during this event; hence no patch comparison is possible for GPP, R24 and P/R ratios.
Table 6.6  Statistical significance (GLM univariate ANOVA) of dissolved organic carbon (DOC) differences between anabranch and riverbank patches during connection phases of the November-December flow event.

<table>
<thead>
<tr>
<th>Phase</th>
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<th>Result</th>
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<th>df</th>
<th>p value</th>
</tr>
</thead>
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</tr>
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<td>Complete connection</td>
<td>DOC</td>
<td>NS</td>
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<td>1,47</td>
<td>0.79</td>
</tr>
<tr>
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<td>DOC</td>
<td>NS</td>
<td>1.393</td>
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</table>

Figure 6.17  Benthic production in the river channel, by connection phase, Nov-Dec 2001 flood.

Figure 6.18  Benthic respiration in the river channel, by connection phase, Nov-Dec 2001 flood.

Figure 6.19  Benthic P:R ratios in the river channel, by connection phase, Nov-Dec 2001 flood. Symbol meanings are explained in section 6.2.5.
Flow event 2: The February 2003 Flow Pulse

*Dissolved organic carbon – differences between connection phases*

Patterns of dissolved organic carbon concentration during this flow event were similar to those observed in November-December 2001, despite this event being a pulse (remaining in-channel) rather than an overbank flood (Figure 6.20). There were significant differences in anabranch DOC concentrations between phases ($F = 10.64; df = 3,68; p<0.005$). Concentrations dropped slightly but not significantly in the anabranch channels from disconnection to partial connection, as water levels began to rise, and remained relatively low through the rising limb of the hydrograph (Figure 6.21 and Figure 6.22). Concentrations then increased slightly but not significantly from partial connection to complete connection at about the time of the peak discharge. The greatest increase in concentrations occurred during the draining phase (flood recession; Tukey’s HSD), when concentrations were significantly greater than those recorded in the partial and complete connection phases. Concentrations then continued to rise, and remained elevated, after the flow pulse had passed.

In the river channel, significant differences in DOC concentration also occurred from phase to phase ($F = 12.88; df = 3,102; p<0.005$). Tukey’s HSD multiple comparisons showed that DOC concentrations during the draining phase were significantly greater than those in the partial and complete connection phases. Concentrations during the complete connection phase were significantly lower than those in the disconnection and draining phases.
Figure 6.20  Dissolved organic carbon concentrations in anabranch channels and the river channel during the disconnection, partial, complete, and draining phases of the February 2003 flow event. Symbol meanings are explained in section 6.2.5.
Figure 6.21 Discharge hydrograph and dissolved organic carbon concentrations over time in Anabranch 1 and the adjacent river during the February 2003 flood.
Figure 6.22  Discharge hydrograph and dissolved organic carbon concentrations over time in Anabranch 2 and the adjacent river during the February 2003 flood.
**Benthic metabolism – differences between connection phases**

During the February 2003 flow pulse, benthic production increased between complete connection and the draining phase at all sites but one, by between 0.012 and 0.398 gC m$^{-2}$ day$^{-1}$ (Figure 6.23). This increase in production averaged 0.1 g m$^{-2}$/day between phases, and was not statistically significant for either the river sites ($F = .2.50; df = 1,13; p = 0.138$) or the anabranch sites ($F = 4.003; df = 1,5; p = 0.102$).

Between complete connection and the draining phase, benthic respiration increased by between 0.007 and 0.258 gC m$^{-2}$ day$^{-1}$ at some sites, while at others it decreased by between 0.003 and 0.084 gC m$^{-2}$ day$^{-1}$ (Figure 6.24). These differences were not statistically significant for either the river sites ($F = 0.365; df = 1,13; p = 0.556$) or the anabanch sites ($F = 2.37; df = 1,5; p = 0.185$). The average increase was greater than the average decrease (0.096 gC m$^{-2}$ day$^{-1}$ vs. 0.032 gC m$^{-2}$ day$^{-1}$). The actual location of the chambers did not bear any relationship to whether an increase or a decrease in respiration rates was recorded.

Benthic P/R ratios generally increased from complete connection to draining (Figure 6.25), but differences between phases were not statistically significant for either the river ($F = 0.127; df = 1,13; p = 0.727$) or the anabranch sites ($F = 0.677; df = 1,5; p = 0.448$). The majority of sites had P/R ratios greater than one during both phases, however three of the chambers recorded ratios less than one during both phases (A1RBX, A1RAE and a second A1RBX), and one chamber (at A1E) started with a ratio >1 but finished with a ratio <1. The increases recorded ranged from 0.1 to 33.4, and averaged 5.9. Decreases were recorded for three chambers (one chamber at A1E and two at A1RBX; decreases of 1.7, 0.5, and 5.9; average 2.7). Again, the actual location of the chambers did not bear any relationship to whether an increase or a decrease in P/R ratio was recorded.
Figure 6.23  Benthic production in anabranches and the river by connection phase, Feb 2003.

Figure 6.24  Benthic respiration in anabranches and the river by connection phase, Feb 2003.

Figure 6.25  Benthic P:R ratios in anabranches and the river by connection phase, Feb 2003. Symbol meanings are explained in section 6.2.5.
Differences between anabranches and river during each phase

There were no statistically significant differences in dissolved organic concentration between anabranches and the river channel during any phase of this connection event (Table 6.7; Figure 6.20). In terms of benthic production, respiration and P/R ratios, there was no statistically significant difference between anabranches and the riverbanks, within either the complete connection or draining phases of this flow event (Table 6.7).

Taking this into consideration, examination of the plotted data (Figure 6.23) suggests that benthic production rates were greater in the anabranche channels than on the riverbanks during both connection phases. Benthic respiration rates during the draining phase also appeared to be greater in the anabranch channels than on the riverbanks (Figure 6.24). During complete connection benthic production in the anabranches averaged 0.109 gC m\(^{-2}\) day\(^{-1}\), and ranged from 0.046 to 0.143 gC m\(^{-2}\) day\(^{-1}\). On the riverbanks, production averaged 0.067 gC m\(^{-2}\) day\(^{-1}\), and ranged from 0.025 to 0.203 gC m\(^{-2}\) day\(^{-1}\). During the draining phase, benthic production in the anabranches averaged 0.270 gC m\(^{-2}\) day\(^{-1}\), and ranged from 0.134 to 0.442 gC m\(^{-2}\) day\(^{-1}\). On the riverbanks during the draining phase production averaged 0.149 gC m\(^{-2}\) day\(^{-1}\), and ranged from 0.021 to 0.443 gC m\(^{-2}\) day\(^{-1}\).

Table 6.7 Statistical significance (GLM univariate ANOVA) of dissolved organic carbon (DOC) and benthic metabolism (R24, GPP, P/R ratio) differences between anabranch and riverbank patches during connection phases of the February 2003 flow event.

<table>
<thead>
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<th>df</th>
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6.3.2 Sediment and carbon deposition

Sediment deposition

Sediment deposition during the March-April 2002 event in terms of weight per square metre was highly variable. Overall, sediment deposition was significantly higher on the riverbanks (median 6758 g m\(^{-2}\)) than in the anabranch channels (median 5720 g m\(^{-2}\); F = 4.38; df = 1,63; p < 0.05; Figure 6.26). Within the anabranch channels, weights ranged from 1203 g m\(^{-2}\) (1.2 kg m\(^{-2}\)) to 20493 g m\(^{-2}\) (20.5 kg m\(^{-2}\)), while on the riverbanks weights deposited ranged from 3897 g m\(^{-2}\) (3.9 kg m\(^{-2}\)) to 22049 g m\(^{-2}\) (22.1 kg m\(^{-2}\)).

There were no significant differences in sediment deposition between anabranch channels (F = 1.19; df = 5,44; p = 0.330; Figure 6.27). Median values were greatest in anabranch 3 (7447 g m\(^{-2}\)), followed by anabranches 4 and 5 (6692 and 5773 g m\(^{-2}\)), and smallest in anabranch 1 (2721 g m\(^{-2}\)), followed by anabranches 2 and 6 (4157 and 3965 g m\(^{-2}\)).

Combining all anabranches, site differences in deposition are apparent (Figure 6.28) but are not statistically significant (F = 1.893; df = 4,60; p = 0.123). Overall, entry sites accumulated the greatest median load of sediment (8054 g m\(^{-2}\)), while middle sites accumulated the least (median 4157 g m\(^{-2}\)). Riverbanks appeared to accumulate more sediment than the exit points of anabranches (median 6758 g m\(^{-2}\)).

When site deposition patterns are examined within individual anabranches, four different spatial patterns emerge (Figure 6.29). In anabranches 1 and 5, sediment deposition was substantially greater at the entry, and decreased from entry to exit. In anabranches 2 and 3, deposition decreased from entry to middle, but was greatest at the exit. In anabranch 4, deposition was greatest at the middle site, and lowest at the exit. Finally, in anabranch 6, deposition was similar at both the middle and exit sites (the entry was not flooded). Deposition was relatively similar at all of the riverbank sites, with the exception of A2RAE (upstream of the entry point of A2), where approximately 4 kg m\(^{-2}\) more sediment was deposited than at the other river sites.
Figure 6.26  Sediment mass deposited in anabranch channels and the adjacent river channel during the March-April 2002 flow event.

Figure 6.27  Sediment mass deposited in individual anabranch channels during the March-April 2002 flow event.
Figure 6.28 Sediment mass deposited among sites during the March-April 2002 flow event.

Figure 6.29 Sediment mass deposited among sites within individual anabanch channels during the March-April 2002 flow event. Symbol meanings are explained in section 6.2.5.
Total sediment-associated carbon concentrations

Total carbon concentrations in the deposited sediments ranged from 0 to 13.05%. On the riverbanks concentrations ranged from 0 to 2%, while in the anabranches concentrations ranged from 0.69 to 13.05%. Overall, carbon concentrations in sediment deposited in the anabranchn channels were significantly higher than those in sediment deposited on the riverbanks (F = 15.49; df = 1,60; p < 0.005; means 3.70% and 0.74% respectively; medians 2.94 vs. 0.41% respectively; Figure 6.30).

Carbon concentrations in deposited sediment were not significantly different between individual anabranchn channels (F = 0.588; df = 5,42; p = 0.709). Median carbon concentrations in the anabranchn channels were greatest in anabranchn 6 (4.21%) and anabranchn 4 (3.70%), and lowest in anabranches 3 and 5 (2.52 and 2.44% respectively; Figure 6.31).

Combining all anabranches, site differences in carbon concentration are apparent (Figure 6.32). In contrast to the pattern observed for total weights, sediment deposited at the middle sites contained significantly greater concentrations of total carbon than all other sites (F = 14.48; df = 4,57; p < 0.005; median 5.33%). Sediment deposited at the exit sites contained the least carbon (0.41%), while the entry and riverbank sediment contained relatively similar amounts to each other (2.65 and 2.51%).

Again, when distribution of carbon concentrations is examined within individual anabranches, patterns vary (Figure 6.33). In anabranches 1, 2, 3 and 6 the spatial pattern of carbon content was opposite to that of total sediment weight deposited, while in anabranchn 4 the patterns match those of total weight. In anabranches 2, 3, 4, and 6 carbon contents were highest at the middle sites. In anabranches 1, 3 and 4 carbon contents were lowest at the entry sites. In anabranchn 5, total carbon content was similar throughout the anabranchn.
Figure 6.30 Carbon content of sediment deposited in anabranch channels and the adjacent river channel during the March-April 2002 flow event.

Figure 6.31 Carbon content of sediment deposited in individual anabranch channels during the March-April 2002 flow event.
Figure 6.32 Carbon content of sediment deposited among sites during the March-April 2002 flow event.

Figure 6.33 Carbon concentrations in sediment deposited among sites within individual anabranch channels during the March-April 2002 flow event. Symbol meanings are explained in section 6.2.5.
**Total sediment-associated carbon deposition**

Total carbon (TC) deposited by the flood in sediments was calculated using the %TC data and the total weight data to yield gTC m$^{-2}$. Loads ranged from 0 to 439 gTC m$^{-2}$ in the anabranch channels, and 0 to 212 gTC m$^{-2}$ on the riverbanks (Figure 6.). Overall, carbon mass deposited by the flow event in the anabranch channels was significantly greater than that deposited on the riverbanks ($F = 12.95; df = 1,61; p<0.005$; 178 and 55 gTC m$^{-2}$ respectively; medians 150 and 32 gTC m$^{-2}$).

Carbon loads among the anabranches were not statistically different ($F = 0.87; df = 5,43; p = 0.510$). Median values were greatest in anabranch 3 (201 gTC m$^{-2}$), and least in anabranch 1 (90 gTC m$^{-2}$; Figure 6.35). The remaining anabranches had median carbon loads ranging between 147 and 160 gTC m$^{-2}$.

Combining data from all anabranches (Figure 6.36), the middle anabranch sites accumulated significantly greater loads of total carbon ($F = 4.23; df = 4,58; p < 0.05$) than the river sites (medians 174 gTC m$^{-2}$ and 134 gTC m$^{-2}$ respectively), but were not significantly different from the entry and exit sites (Tukey’s HSD; $\alpha = 0.05$).

Within individual anabranches, two major depositional patterns are evident (Figure 6.37): in the first, carbon loads deposited decrease from entry to middle to exit (anabranches 1, 5, 6). In the second, carbon loads deposited peak at the middle sites (anabranches 3 and 4). Anabranch 2 was unique in that carbon loads deposited were relatively similar across sites, with slightly lower loads at the middle site and slightly higher loads at the exit site.
Figure 6.34 Carbon mass per unit area deposited in anabranche channels and the adjacent river channel during the March-April 2002 flow event.

Figure 6.35 Carbon mass per unit area deposited in individual anabranche channels during the March-April 2002 flow event.
Figure 6.36  Carbon mass per unit area deposited among sites during the March-April 2002 flow event.

Figure 6.37  Carbon mass per unit area deposited among sites within individual anabanch channels during the March-April 2002 flow event.
6.3.3 **Laboratory flood-simulation experiment**

**Spatial patterns**
Release of dissolved organic carbon (DOC) from surface sediments of the Macintyre River landscape varied spatially at both of the scales sampled – patch scale and site scale – and in terms of both quantities and rates of release. At the patch scale, there were significant differences in the total quantity of DOC released by the riverbank, anabranch channel, and floodplain patches (Table 6.8). Variation in DOC release was also significant at the site scale (Table 6.8).

**Differences between river, anabranches and floodplain**
Over the flood period, floodplain sediments released significantly more dissolved organic carbon (DOC; 23-129 ppm), than the river (18-61 ppm) and anabranch sediments (15-44 ppm; Figure 6.38; Table 6.8). Average concentrations over floodplain sediments (69 ppm) were more than double those over anabranch sediments (29 ppm), and more than 40% higher than those over river sediments (41 ppm; Figure 6.38).

Over time, anabranch and river sediments released dissolved organic carbon in similar amounts for the first 48 hours of inundation, after which average concentrations over river sediments increased relative to those over anabranch sediments, and then stabilised at around 60 ppm before dropping to 49 ppm after 144 hours (Figure 6.38). After an initial average release of 12 – 23 ppm immediately after inundation, average DOC concentrations over anabranch sediments stabilised rapidly at around 30 to 40 ppm, increasing only slightly over the flood period.

Temporal patterns of average DOC release over floodplain sediments were different to those of river and anabranch sediments. Average DOC concentrations over floodplain sediments increased rapidly, peaking after 48 hours at 129 ppm. Concentrations then fell to a low after 96 hours (84 ppm) however this was followed by another small rise after 120 hours (96 ppm) before dropping rapidly to a final low after 144 hours (29 ppm).
This overall pattern changed at the site scale. Sediments from the floodplain, river and anabranch near the ‘entry’ and ‘exit’ sites of the anabranch released carbon in similar proportions to those observed overall (Figure 6.39 and Figure 6.41). However at the middle sites, anabranch sediments released significantly more DOC than both floodplain and river sediments (Figure 6.40). Over the ‘flood’ period, mean concentrations over anabranch sediments ranged from 16 to 56 ppm, with those over floodplain sediments at 12 - 32 ppm, and those over river sediments at 8 – 18 ppm.
Table 6.8 Statistical significance of spatial patterns of dissolved organic carbon release from sediment. Univariate GLM ANOVA results with Tukey’s HSD multiple comparisons ($\alpha=0.05$). Log$_{10}$ transformed data.

<table>
<thead>
<tr>
<th>VARIABLE</th>
<th>DATA</th>
<th>TREATMENT</th>
<th>RESULT</th>
<th>F value</th>
<th>df</th>
<th>p value</th>
<th>TUKEY’S HSD</th>
</tr>
</thead>
<tbody>
<tr>
<td>LG10 DOC RELEASE</td>
<td>2HRS</td>
<td>Patch type</td>
<td>NS</td>
<td>2.563</td>
<td>2,41</td>
<td>0.089</td>
<td>Floodplain vs. anabranch</td>
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<td>SIG</td>
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<td>Floodplain vs. anabranch</td>
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<td>SIG</td>
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<td>&lt;0.05 (=0.010)</td>
<td>Middle vs. entry</td>
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<td>Middle vs. entry &amp; exit</td>
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<td>SIG</td>
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<td>Site</td>
<td>NS</td>
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<td>0.136</td>
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<td>Middle vs. entry &amp; exit</td>
</tr>
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<td>Site</td>
<td>SIG</td>
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<td>Middle vs. entry &amp; exit</td>
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<td>Site</td>
<td>SIG/NS</td>
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<td>2,12</td>
<td>&lt;0.05 (=0.049)</td>
<td>Middle vs. entry &amp; exit</td>
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<td>Site</td>
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<td>Site</td>
<td>SIG</td>
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<td>Middle vs. entry &amp; exit</td>
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<td>Site</td>
<td>SIG</td>
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<td>2,6</td>
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<td>Site</td>
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<td>0.338</td>
<td>1,3</td>
<td>0.602</td>
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</tr>
<tr>
<td>RIVER</td>
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<td>Site</td>
<td>SIG</td>
<td>16.099</td>
<td>2,12</td>
<td>&lt;0.005</td>
<td>RAX vs. RAE &amp; RBX</td>
</tr>
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<td>Site</td>
<td>SIG</td>
<td>13.882</td>
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<td>&lt;0.005 (=0.001)</td>
<td>RAX vs. RAE &amp; RBX</td>
</tr>
<tr>
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<td>Site</td>
<td>SIG</td>
<td>8.877</td>
<td>2,12</td>
<td>&lt;0.05 (=0.004)</td>
<td>RAX vs. RAE &amp; RBX</td>
</tr>
<tr>
<td>RIVER</td>
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<td>Site</td>
<td>SIG</td>
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<td>&lt;0.05 (=0.020)</td>
<td>RAX vs. RBX</td>
</tr>
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<td>Site</td>
<td>SIG</td>
<td>18.551</td>
<td>2,12</td>
<td>&lt;0.005</td>
<td>RAX vs. RAE &amp; RBX</td>
</tr>
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<td>RIVER</td>
<td>72HRS</td>
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<td>&lt;0.005</td>
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<tr>
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<td>96HRS</td>
<td>Site</td>
<td>SIG</td>
<td>17.681</td>
<td>2,12</td>
<td>&lt;0.005</td>
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</tr>
<tr>
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<td>Site</td>
<td>SIG</td>
<td>6.84</td>
<td>2,6</td>
<td>&lt;0.05 (=0.012)</td>
<td>RAX vs. RAE</td>
</tr>
<tr>
<td>RIVER</td>
<td>144HRS</td>
<td>Site</td>
<td>SIG</td>
<td>5.908</td>
<td>2,6</td>
<td>&lt;0.05 (=0.038)</td>
<td>RAX vs. RAE</td>
</tr>
</tbody>
</table>
Figure 6.38  Average DOC concentrations in distilled water over river, anabranch and floodplain patches over time.

Figure 6.39  Average DOC concentration over time by patch type, entry sites only.

Figure 6.40  Average DOC concentration over time by patch type, middle sites only.

Figure 6.41  Average DOC concentration over time by patch type, exit sites only.
**Differences between sites**

Anabranch sediments from the middle site released significantly more DOC (37 ppm; Table 6.8) than those from the entry and exit sites, which were almost identical to each other in both pattern and average concentration (24 and 25 ppm respectively; Figure 6.42). Conversely, floodplain sediments from the middle site released significantly less DOC on average (58 ppm) than those from the entry and exit sites (219 and 265 ppm respectively; Figure 6.43; Table 6.8).

There were also significant differences in DOC release between the river sediments from each site (Figure 6.44; Table 6.8). River sediments from near the middle site (RAX) released significantly less DOC than the other river sites (mean 17 ppm), while an average of 51 ppm was released from river sediments downstream of the anabranch exit and upstream of the anabranch entry. Generally, river sediments near the entry and exit points of the anabranch released more carbon upon inundation than river sediments distant from the anabranch connection points.
Figure 6.42 Average DOC concentrations over time by site, anabranch sediments only.

Figure 6.43 Average DOC concentrations over time by site, floodplain sediments only.

Figure 6.44 Average DOC concentrations over time by site, riverbank sediments only.
Rates of release

Rates of release of dissolved organic carbon (DOC) from surface sediments of the Macintyre River landscape varied temporally at both of the scales sampled. At the patch scale, there were substantial differences in the rates of release of DOC from the floodplain sediments compared to the riverbank and anabranch channel sediments (Figure 6.45).

The fastest rate of DOC release occurred within two to three hours of inundation for all sediments (Figures 6.45-6.48), when wetting stimulated an immediate flush of carbon into the water column from the sediments. Following this initial flush, rates of DOC release decreased rapidly and generally stabilised or reached zero after approximately 96 hours. Anabranch and riverbank sediments behaved in a similar fashion in terms of temporal patterns and rates of DOC release, however floodplain sediments were different. Rates of DOC release from floodplain sediments fluctuated markedly over time compared to other patch types (Figure 6.45).

Anabranch sediments from different sites exhibited slightly different initial release rates, however these fell rapidly and became virtually uniform (averaging 1 ppm hr⁻¹) within 24 hours (Figure 6.46). Anabranch sediments from the middle site had the greatest initial rate of release (9 ppm hr⁻¹), followed by exit site sediments (7 ppm hr⁻¹) and finally entry site sediments (6 ppm hr⁻¹). Rates of DOC release from floodplain sediments from different sites varied over time, and to a greater degree than anabranch sediments (Figure 6.47). Rates of release were greatest from floodplain sediments at the entry and exit sites (15 and 13 ppm/hour), and substantially lower for floodplain sediments from the middle site (6 ppm/hour). Rates of DOC release from riverbank sediments were highest at the entry and exit sites during the initial flush, and substantially lower at the middle site (RAX; Figure 6.48). However river sediments from the middle site released a second flush of DOC after 24 hours that the other sites did not experience. Rates of release from sediments from all three sites fluctuated but remained at very low levels for the remainder of the experiment.
Figure 6.45 Rates of DOC release from anabranch, floodplain and riverbank sediments.

Figure 6.46 Rates of DOC release for anabranch sediments from entry, middle and exit sites.

Figure 6.47 Rates of DOC release for floodplain sediments from entry, middle and exit sites.

Figure 6.48 Rates of DOC release for riverbank sediments from entry, middle and exit sites.
Hydrological connectivity is a primary factor determining sedimentation, erosion and production processes in floodplains, and hence also the sources (authochthonous or allochthonous) and availability of carbon in the river and surrounding landscape patches (e.g. anabranches and floodplain waterbodies; (Heiler et al. 1995; Tockner et al. 1999a; Thoms and Sheldon 2000; Amoros and Bornette 2002; Hein et al. 2003)). The biogeochemical flux of matter across the floodplain river landscape is coupled to hydrological flow paths (Pusch et al. 1998), and trophic linkages form, break and change in strength as environmental conditions change (Power et al. 1995). Although it is known that these fluxes can have a significant impact upon the biogeochemistry and food webs of temperate and tropical floodplain-river ecosystems (Hamilton et al. 1992; Spink et al. 1998; Hein et al. 2003), more data are required regarding their controls and effects in arid and semi-arid systems (Robertson et al. 1999; Bunn et al. 2003; Bunn et al. 2006).

This chapter searched for associations between different phases of hydrological connection and carbon availability, in anabranch channels and the parent river channel of a semi-arid system. It examined carbon sources in anabranch channels and the river channel during each of four connection phases, and asked the question ‘Does the quantity, quality, production or respiration of carbon change in the river channel and the anabranch channels during different phases of hydrological connection? The results show that each connection phase was associated with differences in the availability of carbon in both the main channel of the Macintyre River and adjacent anabranch channels. Changes in production and respiration within the main river channel were also detected, with some apparent switching between autotrophy and heterotrophy.

The first part of this chapter tested the temporal component of the conceptual model (Chapter 3) by making in-situ, direct measurements of carbon sources in the anabranch channels and adjacent river channel during flow events. It aimed to detect changes in primary carbon pools and link these changes to the characteristics and sequence of each phase. It found that hydrological connection is associated with changes in the ecological
state of both anabranches and the adjacent river channel of the lower Macintyre River system. This influence is apparent in terms of quantity and quality of carbon, as well as benthic metabolism. Individual connection phases can be related to distinct differences in carbon pools and benthic metabolism in both the anabranch channels and the parent river channel. Many of the differences observed agree with the conceptual model as proposed – others do not.

The passing of a flow pulse controls local hydraulic characteristics such as volume, inundation extent, duration, velocity, turbulence, as well as overall turbidity and suspended and dissolved loads, which all in turn influence biological processes. Consequently, stationary sampling such as that used in this study records the passing of the pulse of water and the materials that it carries, as well as local inputs. For example, in a wide range of running waters in different biomes, DOC concentration increases with discharge, although there are exceptions (Spitzy and Leenheer 1991; Hope et al. 1994). The increase in DOC concentrations observed in both the river and the anabranch channels of the Macintyre River during the complete connection phase is dominated by this relationship. The homogenising effect of large overbank flow events was also reflected in the carbon data from the November-December 2001 flow event. However during the smaller February 2003 flow event, differences in carbon concentrations related to the heterogeneity provided by anabranch channels in the landscape are distinguishable. Thus during flow pulses, connectivity with anabranch channels has the potential to influence the DOC-discharge relationship in rivers at larger spatial and temporal scales.

The relationship between DOC concentration and discharge during a flood or storm event can vary between the rising and falling limbs of the hydrograph and over time, depending upon the preceding conditions (Spitzy and Leenheer 1991; Hope et al. 1994; Robertson et al. 1999). The most common situation reported is a clockwise hysteresis, whereby DOC concentrations at a given discharge are higher on the rising than the falling limb (Hope et al. 1994). However the increase in DOC concentrations observed in both the river and the anabranch channels of the Macintyre River during the complete connection and draining phases of this study does not correspond to the clockwise hysteresis usually
observed. In fact during both of the flow events examined in the case studies, DOC concentrations were higher during the *falling* limb, rather than the rising limb of the hydrograph (Figure 6.49). The major differences between the Macintyre River system and the systems that have been reported to exhibit clockwise hysteresis are a) it is a lowland allogenic system, with a predominantly semi-arid climate; b) the presence and high frequency of floodplain anabranch channels; and c) the domination of the disconnection phase. This emphasises the unique importance of anabranch channels for Australian floodplain river systems as storage areas or sinks for carbon during disconnection, and as sources of carbon during connection phases, particularly during the draining phase. Permanently disconnecting or isolating anabranch channels from the main river channel thus has implications for large scale patterns and processes, and hence for the resilience of the ecosystem as a whole.
Figure 6.49  Hysteresis patterns of dissolved organic carbon concentrations against discharge. Anabranch and river channels plotted separately for the November-December 2001 flood event (a,b) and the February 2003 flow pulse (c,d). Arrows indicate the direction of hysteresis.
6.4.1 **Hydrological connection phases and the quantity, quality, production and respiration of carbon in the river channel**

In the river channel, the most striking pattern observed between connection phases was the elevation of dissolved organic carbon (DOC) during the complete connection phase and the draining phase (Table 6.9). Peaking DOC concentrations in the river during the draining phase rather than the complete connection phase suggest progressive concentration of DOC within anabranches as draining commences, and the subsequent injection of the concentrated water-DOC solution into the river channel. Rising DOC concentrations in a side channel of the Danube River during complete surface connection with the river were attributed by Tockner *et al.* (1999) to mobilization of soluble organic matter that had accumulated in the side channel during low water conditions (the disconnection phase). These results indicate a similar role for the Macintyre River anabranchn channels: DOC concentrations were generally low during the disconnection and partial connection phases, and the onset of complete connection with anabranchn channels appears to mobilize significant quantities of DOC and to release carbon into the river channel during the draining phase. The key difference for this system, and its significance for other inland Australian systems, is that anabranches are inundated at significantly lower discharges than those required to inundate the surrounding floodplain – hence the organic matter they accumulate is potentially more physically ‘available’ over time in terms of both their ecology and potential flow management.
Table 6.9 Median values for carbon sources measured in the river channel and anabranch channels during hydrological connection phases. Shading indicates the phase with the highest median value.

<table>
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<th>PHASE</th>
</tr>
</thead>
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<td>Disconnection</td>
</tr>
<tr>
<td><strong>RIVER</strong></td>
<td></td>
</tr>
<tr>
<td>Dissolved organic carbon (ppm)</td>
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</tr>
<tr>
<td>Chlorophyll a (mg m-3)</td>
<td>9.13</td>
</tr>
<tr>
<td>Production (g C m-2 day-1)</td>
<td>0.35</td>
</tr>
<tr>
<td>Respiration (g C m-2 day-1)</td>
<td>0.14</td>
</tr>
<tr>
<td>P/R ratio</td>
<td>2.68</td>
</tr>
<tr>
<td><strong>ANABRANCHES</strong></td>
<td></td>
</tr>
<tr>
<td>Dissolved organic carbon (ppm)</td>
<td>14.84</td>
</tr>
<tr>
<td>Chlorophyll a (mg m-3)</td>
<td>33.31</td>
</tr>
<tr>
<td>Production (g C m-2 day-1)</td>
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</tr>
<tr>
<td>Respiration (g C m-2 day-1)</td>
<td>0.15</td>
</tr>
<tr>
<td>P/R ratio</td>
<td>0.91</td>
</tr>
</tbody>
</table>

The conceptual model for the Macintyre River (Chapter 3) suggested that during draining, phytoplankton concentrations in the river would rise, because of assumed decreasing turbidity and turbulence as the flow peak receded, together with the increased availability of nutrient resources for phytoplankton production. In fact chlorophyll a (phytoplankton) concentrations in the river reached their lowest point during draining rather than complete connection. Most phytoplankton prefer a stable water column with good light penetration (low turbidity), warm temperatures and abundant nutrients (Bukaveckas et al. 2002). These conditions were not met during the draining phase (e.g. turbidity and turbulence remained relatively high in the river channel), so phytoplankton production did not recover as predicted, and concentrations of chlorophyll α continued to decline due to flushing, consumption and degradation. Phytoplankton concentrations in side channels of the Danube River have been reported to be affected by these factors, plus the water retention time (which can be correlated to connection phases in the present study), and other abiotic parameters controlled by the hydrological regime of the river (Hein et al. 1999). However in contrast, Hein et al. (2003) observed a dominance of ‘terrestrial’ carbon input during the complete connection phase, and of phytoplankton-related carbon input during the draining and disconnection phases. In the main channel of the Danube River, connection with secondary channels increases the available area of
relatively shallow, warm habitats, and therefore increases the potential for phytoplankton production, however this potential is greatest during phases with low water velocity (i.e. phases other than complete connection). Thus hydrological connection may shift the function of secondary channels to sources of autochthonous organic matter, which may then support riverine food webs (Hein et al. 2003), however this function is partially controlled by the connection phase. Anabranch channels and billabongs of the semi-arid Macintyre River have the potential to perform a similar function in an ephemeral, short term sense. However their role in this sense is more restricted than that of the side-channels of the Danube River, because the duration of flow pulses and individual connection phases is considerably shorter in a dryland system.

These results indicate that the conceptual model (Chapter 3) describes conditions in the river during the disconnection phase accurately. The model also describes differences in the river between all of the phases correctly for GPP. However differences between predicted and observed patterns become apparent as hydrological connection with anabranch channels commences during the partial connection phase, through complete connection to the draining phase. These include the following:

- R24 was at its highest during the partial connection phase rather than the draining phase
- P/R ratios were at their lowest during the complete connection phase rather than the draining phase
- Benthic metabolism in the river switches from autotrophy to heterotrophy during the complete connection phase rather than the draining phase, and then actually switches back to autotrophy during the draining phase

Benthic production on the riverbanks varied substantially in comparison to benthic respiration, creating differences in P/R ratio in each phase. Respiration reached its greatest levels during partial connection rather than during draining. This was probably related to inundation of dry sediments on both riverbanks and in the anabranches, releasing an initial flush of dissolved organic carbon and nutrients, which are rapidly
utilized by the benthic community, resulting in increased respiration rates (Qui and McComb 1994; 1996; Neilsen and Chick 1997; Mitchell and Baldwin 1998; O'Connell et al. 2000; Francis and Sheldon 2002; Scholz et al. 2002). It was thought that the greatest effect of this release would occur during the draining phase because this is when the greatest amount of sediment has been inundated and the largest quantities of DOC and nutrients would be available. However it is likely that the labile carbon sources mobilized during inundation are utilized virtually immediately by the benthic community (Pusch et al. 1998; Findlay and Sinsabaugh 1999), and that those sources remaining to be washed into the river channel, despite their high quantities, are dominated by more refractory components, and hence are lower in quality.

Benthic P/R ratios were at their lowest on the riverbanks during the complete connection phase rather than the draining phase. Complete connection was also the only phase in which the median P/R ratio was less than one. This means that benthic production of carbon on the riverbanks exceeds respiration (consumption of carbon) most of the time, however when complete connection occurs, the situation is reversed and respiration exceeds production. Hence benthic metabolism appears to switch from autotrophy to heterotrophy during the complete connection phase rather than during the draining phase. This was because of relatively reduced production, rather than increased respiration, however it may indicate that allochthonous carbon is of some importance for benthic metabolism in the riverbanks during this phase. Spatial and temporal switching between heterotrophy and autotrophy is thought to be a characteristic of large rivers in a range of biomes (Thorp and Delong 2002; Woodward and Hildrew 2002; Hein et al. 2003). A floodplain secondary channel of the Danube River was observed to shift from autotrophy during disconnection and a seepage or ‘partial connection’ phase, to heterotrophy during and after flooding (Hein et al. 1999; Tockner et al. 1999a). Thus a pattern observed in a heavily altered temperate river system is reproduced (at least in the benthic community) in the semi-arid Macintyre River system. This switching appears to be driven by changes in production rather than respiration in the Macintyre River, and because of this is likely to be related to extremes in turbidity and hence changing light conditions. The potential role of increased DOC inputs from anabranches in changing river trophic states is at this
stage unknown. The possible relationship between trophic switching in the Macintyre River channel itself and hydrological connection with floodplain anabranch channels is an issue worthy of further research, as it has fundamental implications for our understanding of the importance of these secondary channels and their influence upon the functioning of the river ecosystem as a whole.

6.4.2 Hydrological connection phases and the quantity, quality, production and respiration of carbon in the anabranch channels

Hydrological connection between the river and its floodplain has been suggested to determine the importance of floodplains and their features for carbon dynamics at the whole-river scale (Hein et al. 2003). Anabranch channels translate river channel flow regimes, histories and events into complex and variable levels of hydrological connection and natural fragmentation across floodplain river landscapes. However their responses to hydrological connection, and indeed their ecological roles in semi-arid floodplain river systems, have generally not been quantified. The conceptual model described in Chapter 3 framed some possible answers to these questions, while the results of this component of the thesis provide some insight into the influence of connection phases on the ecology of anabranch billabongs, the adjacent river channel, and potentially the whole system.

The conceptual model as originally proposed described conditions in the anabranches during the complete and partial connection phases more accurately than those for disconnection or draining. The conceptual model accurately described relative changes in DOC and phytoplankton (chlorophyll a) concentrations in the anabranches for all of the phases. The disconnection phase in the anabranch channels resulted in the highest concentrations of DOC and phytoplankton. Similarly, at low water levels (corresponding to the disconnection phase in the present study) in the Danube system, the side channels were characterized by high plankton biomass compared to the river (Hein et al. 1999). Phytoplankton biomass was also elevated in the Danube side channels during the period corresponding to the draining phase in the present study. The lowest phytoplankton biomass was found to occur during the ‘partial’ and ‘complete’ connection phases (low
Phytoplankton in side channels of the Danube were affected by both water retention time (which can be correlated to connection phase in the present study), and other abiotic parameters such as turbidity and nutrient concentrations, which are controlled by the hydrological regime of the river (Hein et al. 1999). Low phytoplankton concentrations during the connection phase in the anabranch channels of the Macintyre River system are likely due to high turbidity, velocities and turbulence associated with the passage of the discharge peak. Increases in these factors associated with the flood hydrograph are well established for floodplain river systems (Richey et al. 1986; Hein et al. 1999; Golladay et al. 2000; Amoros and Bornette 2002; Hein et al. 2003).

During disconnection, anabranch water samples were taken from stationary billabongs, which contained substantially higher median DOC concentrations than the river during this phase (15 ppm vs. 8 ppm respectively). However partial connection appeared to result in anabranch median DOC concentrations much closer to, although still slightly higher than, those found in the river, probably due to dilution and perhaps export and consumption. Anabranch DOC concentrations at entry and exit sites rose during the complete connection and draining phases, and this appeared to cause increased river DOC concentrations downstream of these connection points.

Differences between expected and observed patterns in the anabranches occurred for the benthic metabolism parameters (GPP, R24 and P/R). The differences apparent for the benthic metabolism parameters include:

- GPP was highest in the anabranches during the draining phase rather than the disconnection phase
- R24 was highest during the disconnection phase rather than the draining phase
- P/R ratios were highest during the draining phase and lowest during the disconnection phase, rather than vice versa (opposite to predicted pattern)
- Heterotrophy occurs during the disconnection phase rather than the draining phase
Benthic GPP, R24 and P/R ratios in the anabranch channels displayed the opposite patterns to those expected. Benthic respiration in the anabranch channels remained relatively stable through each connection phase; however GPP varied substantially, thereby also inducing differences in P/R ratio in each phase. Anabranch benthic GPP being highest in the draining phase rather than during disconnection may be explained by greater water clarity and hence light penetration following flushing of the billabongs, deposition of fresh sediment loads due to reduced water velocities, and the increased availability of nutrient resources due to release from freshly inundated sediments and leaf litter and decomposition processes. Dry leaves and sediments have low bacterial, fungal and microbial activity levels, and with submersion the abundances of bacteria and aquatic hyphomycetes and of levels of microbial activity rapidly rise (Pusch et al. 1998). Anabranch benthic R24 being slightly higher during disconnection rather than draining indicates that allochthonous sources of carbon are more important to the anabranch billabong ecosystems than than during other phases. Degradation of detritus (and associated benthic respiration) may be expected to decrease with increasing depth (i.e. as connection progresses from disconnection to partial to complete phases), because water temperature and microbial concentrations would both be likely to decrease as depth increases (Power et al. 1995). In addition, in retentive stream reaches, massive input of organic matter may lead to oxygen depletion in sediments, and thus generate sediment patches that are anaerobic, where organic matter is processed by fermentation. These anaerobic pathways are prevalent in lowland streams with fine sediments (Pusch et al. 1998).

P/R ratios in anabranch channels were highest during the draining phase and lowest during the disconnection phase, rather than vice versa. Indeed, the disconnection phase was the only phase with a ratio of less than one - i.e. during the disconnection phase in the anabranes, respiration (consumption of carbon) exceeds production of carbon. This indicates that during the disconnection phase heterotrophy dominates, with perhaps primarily allochthonous sources of carbon supporting benthic metabolism, while during other phases autotrophy dominates and autochthonous carbon plays a more significant role. In the Danube system, increasing water retention time in the side-channels resulted
in a shift from primary production (autotrophy) towards prevailing bacterial secondary production (heterotrophy; (Hein et al. 1999; Hein et al. 2003). Similarly, in the anabranch channels of the Macintyre River system, lentic conditions (disconnection, billabongs) were associated with heterotrophic metabolism, while lotic conditions (partial connection, complete connection, draining) were autotrophic. Benthic metabolism on the banks of the lotic river channel was also predominantly autotrophic, except during the complete connection phase (and possibly draining phase), when benthic metabolism switched to heterotrophy, possibly because of reduced light availability (high turbidity). The major reasons for the differences between expected and observed changes include hydrograph-related temporal and spatial patterns of turbidity (and hence light penetration), hydrological turbulence/velocity, and inundation extent and duration. Overall, benthic production on the riverbanks appears to be depressed during a flood event, while benthic production in the anabranches becomes relatively elevated, at least during the draining phase (Table 6.10).

<table>
<thead>
<tr>
<th>RIVER</th>
<th>Production</th>
<th>Respiration</th>
<th>P/R ratio</th>
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<tr>
<td></td>
<td>Maximum</td>
<td>Decreasing values</td>
<td>Minimum</td>
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<tr>
<td>Production</td>
<td>Disconnection</td>
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<td>Respiration</td>
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<td>P/R ratio</td>
<td>Disconnection</td>
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<td>Draining</td>
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</tbody>
</table>

<table>
<thead>
<tr>
<th>ANABRANCHES</th>
<th>Production</th>
<th>Respiration</th>
<th>P/R ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Maximum</td>
<td>Decreasing values</td>
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<td>Production</td>
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</tr>
<tr>
<td>Respiration</td>
<td>Disconnection</td>
<td>Draining</td>
<td>Partial</td>
</tr>
<tr>
<td>P/R ratio</td>
<td>Draining</td>
<td>Partial</td>
<td>Complete</td>
</tr>
</tbody>
</table>

These results have revealed differences between field observation and the conceptual predictions of the proposed model (Chapter 3). Acknowledgement and incorporation of these differences aids better understanding of the implications of the configuration of this
floodplain river landscape for ecological function. In addition to these adjustments, the conceptual model would also be improved by further testing to evaluate the consistency and predictability of these patterns in the field. The model would also benefit significantly from the inclusion of data for the following parameters: turbidity; temperature; light data (photosynthetically active radiation and photic depth); nutrient data; open-water metabolism measurements (although the anabranch measurements incorporated the full depth of the anabranch billabongs during the disconnection, partial connection and draining phases); detailed hydraulic modelling of turbulence and residence time; and sediment and leaf litter suspension, transport and deposition.

6.4.3 **Sediment and carbon deposition**

Although inundation can release carbon and thereby reduce its stores in surficial sediments, carbon is also deposited during floods. Suspended sediment and detritus particles settle out of the water column in areas of reduced flow competence, making secondary channels, pools, eddies, backwaters and floodplains major sites of sediment and carbon accumulation (Wolman and Leopold 1957; 1970; Walling and Bradley 1989; Nicholas and Walling 1997; Amoros and Bornette 2002; Richards *et al.* 2002). For example, average deposition rates in a Danube floodplain side channel were 23 kg m\(^{-2}\) year\(^{-1}\) for suspended sediments and 0.29 kg m\(^{-2}\) year\(^{-1}\) for particulate organic carbon (Tockner *et al.* 1999b). In contrast, deposition rates of suspended matter ranging from 2.2 to 29.3 kg m\(^{-2}\) during single floods have been found in the floodplain of the River Adour, France (Brunet and Astin 1997). These rates are comparable to those measured for the single flood in the Macintyre River system focused on by this component. Within the anabranch channels deposited sediment weights ranged from 1.2 kg m\(^{-2}\) to 20.5 kg m\(^{-2}\), while on the riverbanks weights deposited ranged from 3.9 kg m\(^{-2}\) to 22.1 kg m\(^{-2}\).

This second component measured sediment and associated carbon deposition in anabranch channels of the Macintyre River during a single flow event (March-April 2002). It found that despite overall sediment deposition by weight being greater on the riverbanks compared to the anabranch channels, more total carbon was deposited in the
anabranches, elevating their potential importance as patches. This was most likely related to the well-known associations between sediment carbon content, sediment size, and flow velocity. The variation in sediment and carbon deposition patterns observed at each scale (particularly at the site scale) can be explained by the geomorphology and hydrology of each site relative to one another, and their effects upon sediment size distributions. In anabranches 1 and 5, sediment deposition was substantially greater at the entry, and decreased from entry to exit. These anabranches are more like the river channel than any of the other anabranches in terms of hydrology and geomorphology, with flow occurring primarily in one direction from entry to exit (downstream).

Anabranch 5 is in fact an abandoned section of river channel that is filling with sediment. In anabranches 2 and 3, deposition decreased from entry to middle, but was greatest at the exit. These are the largest anabranches of the six, and consequently their middle sites are more distant from the breakout points (entry and exit). In addition, their exit points are larger and have lower commence to flow discharges than their entry points. In anabranch 4, deposition was greatest at the middle site, and lowest at the exit. At the exit of this site there is no clear-cut channel, and flow is distributed over a wide area, with concomitant widespread distribution of the sediment load. The entry point is narrow and chute-like, preventing significant deposition, and effectively pushing floodwater and its associated loads through to the wider, low-gradient shallow channel found at the middle site. In anabranch 6, deposition was similar at both the middle and exit sites (entry not flooded). The middle site of this anabranch is dominated by a large, shallow billabong, while the exit site is a relatively short, narrow and steep chute through which water both enters and exits during rainfall and flow events.

This chapter demonstrates that although DOC concentrations in anabranch and river water may increase during flood events, the system is also highly retentive of carbon (sensu (Pusch et al. 1998). Floodplains and anabranch channels that experience different phases of connection act as temporary carbon reservoirs, slowing the transport of particulate carbon to the oceans and acting as important processing agents for the entire river system. However carbon reservoirs in anabranch channels are relatively more accessible than those in surrounding floodplains, spatially and temporally, and this
intermediate ecological role has important implications for the sustainability and management of the systems of which they are an integral part.

6.4.4 Laboratory flood-simulation experiment

This component tested the conceptual model by allowing controlled measurement of one of the primary processes occurring during connection events – the release of dissolved organic carbon from newly inundated sediments. It balances the second component (sediment deposition) by providing an estimate of the amounts of dissolved organic carbon supplied from anabranch sediments during inundation. This experiment focused on a single anabranch (anabranch 3), and hence only patch and site scale are represented, however noteworthy comparisons can be made between its results and those of other components.

Between-phase patterns in DOC concentration in overlying ‘flood’ water were similar for both field data and experimental data. Experimental rates of DOC release from sediments indicate that initial inundation during partial connection is the peak release time, however due to the limited area of sediment inundated in the field during this phase, concentrations remained low. As DOC continues to be released from inundated sediments, leaf litter, and related metabolic processes, concentrations build as seen in both the field data and the experimental data, peaking during the draining phase. It is at this point that anabranches may begin to play a significant role in carbon dynamics of the river system. Robertson et al. (1999) estimated that the export of DOC from billabongs to the main channel of the Murrumbidgee River in south-eastern Australia during a single flood event was sufficient to support in-channel respiration for approximately 20 days. However many processes interact to produce the final concentrations measured.

At the within-anabranch or site scale, patterns of DOC release matched the patterns of sediment total carbon concentrations and total carbon deposition. Again, the middle site has the greatest potential in terms of carbon resources. Compared to entry and exit sites, anabranch sediments at the middle site a) consistently had greater concentrations of total
carbon during the disconnection phase; b) had greater concentrations of carbon deposited during a flow pulse; and c) released substantially more DOC than sediments from the entry and exit sites. This focusing of resources is influenced by the interactions between geomorphology and hydrology, and those interactions’ effects upon hydraulics, sediment size, inundation frequency, and vegetation density and type. In terms of influences other than the sediment size-carbon relationship described in previous sections, partial connection, though experienced frequently by entry and exit sites, is rare at sites midway through the anabranches, allowing greater time for carbon accumulation through litter decomposition and other detritus. Another influence would be the greater vegetation density at the middle site of this anabranch.

High concentrations of DOC release measured in the laboratory as well as in the field can give a misleading impression of its role and importance, because the material may have been recycled a number of times within the food web before measurement or uptake, and may consequently be of less value. Turnover of DOC is intense and often rapid, and it is readily immobilized (Pusch et al. 1998). Immobilisation of DOC can occur as a purely physical process involving physical sorption to mineral surfaces such as iron, aluminium oxides and clay. In addition, most wetted sediment surfaces are colonized by microbial biofilms which efficiently remove DOC from the water column (Findlay and Sinsabaugh 1999). One of the reasons DOC concentrations were observed to rise through each consecutive phase is the increasing area inundated, in addition to metabolic processes that also release DOC. Inundation of sediments can restart biochemical transformations that had ceased because of the depletion of a specific substrate or terminal electron acceptor during disconnection (Pusch et al. 1998). However in the field, labile DOC would be utilized almost as soon as it was released from sediments – thus restricting or preventing the accumulation of DOC in the water column. In addition, DOC released from anabranch channel sediments and litter may be recycled several times within the food web before it reaches the main river channel, thus reducing its quality. There are also differences between the uptake and release of labile DOC and refractory DOC (Pusch et al. 1998). This chapter has no data to show of what quality the DOC in the water column of the Macintyre River and its anabranches during each phase is, and hence cannot
establish what effect this may have. Dilution also plays a role – which is partly why DOC concentrations were highest in anabranch billabongs during the disconnection phase.

Overall, however, these results indicate that one of the roles of anabranch channels may be to act as a sink or reserve of sediment-associated and particulate carbon. This reserve appears to then act as a source for dissolved organic carbon when re-inundated. However this role changes with scale and will also change with the spatial and temporal nature of hydrological connectivity in the system. For example, if most carbon tends to be deposited in the middle of the anabranch channels, then lack of complete connection throughout the anabranches will eliminate or isolate that resource – i.e. Partial connection would not provide access to that resource. Between the threshold transitions of partial connection and draining, changes in discharge and anabranch length, width and depth can also affect the deposition, storage and potential supply of carbon sources. Together with the other parts of this chapter, this data suggests a possible dual role for anabranches: 1) as sinks for particulate and relatively refractory carbon, such as that adsorbed to sediment and 2) as sources for dissolved or more labile carbon.
6.5 SUMMARY

There are four defined phases of hydrological connection between the main channel and anabranch system during a flood pulse. These are the disconnection phase or dry period between intervening flow events; the partial connection phase when floodwaters begin to enter anabranch channels and wet the surface; complete flow of water through the entire anabranch channel; and the draining phase during the recession of the flow pulse. Each connection phase frames changes or differences in the availability of carbon in both the parent river and anabranch channels. At the same time, changes occur in production and respiration within the parent river channel, with switching between autotrophy and heterotrophy. The influence of each connection phase and its characteristics at any moment in time also vary with scale, from patch (river vs. anabranch vs. floodplain), to individual anabranch (1-6) to within-anabranch or site scale. Hydrological connection also facilitates both storage and release of carbon in the landscape, with anabranch channels apparently acting as key locations for these processes. The ‘intermediate’ nature of anabranch channels in terms of geomorphology, hydrological connectivity and carbon storage and supply emphasises their importance as components of the landscape and of the ecosystem as a whole. Each of the interlinked components of this chapter accentuates the dependence of both the conceptual model and the results upon the interaction between the spatial and temporal characteristics of hydrological connection events, the physical characteristics of the landscape and its patches, and the scales of observation. Changes to the character of each phase (e.g. in terms of its frequency or duration) may result in changes in ecological functioning of the river system as a whole.
Key messages:

- Different phases of hydrological connection between anabranch channels and the main river channel are associated with differences in the availability of carbon sources
  - Draining of water from anabanches to the river (the draining phase) is associated with relatively high concentrations of dissolved organic carbon (DOC) and low concentrations of phytoplankton in the river channel. Conversely, the disconnection phase is associated with relatively low concentrations of DOC and high concentrations of phytoplankton in the river channel.
  - In anabranch channels and their waterbodies, the disconnection and draining phases are associated with high concentrations of both DOC and phytoplankton. Concentrations of these carbon sources are lowest in anabanches during the partial and complete connection phases.

- Different hydrological connection phases are also associated with changes in trophic status in the aquatic components of the landscape.
  - On the riverbanks, relatively low rates of benthic production and respiration during the complete connection phase resulted in a P/R ratio less than one, indicating heterotrophy. The remaining phases appeared to be autotrophic. Benthic production on riverbanks was greatest during the disconnection phase, and respiration was greatest during the partial connection phase.
  - In the anabranch channels, rates of production and respiration were similar during the disconnection phase, but resulted in a P/R ratio slightly less than one, indicating heterotrophy in the anabranch waterbodies. The remaining phases appeared to be autotrophic. Respiration was greatest in anabanches during the disconnection phase, and production was greatest during the draining phase. Both production and respiration were lowest during complete connection.

- These differences and changes vary according to the landscape patch examined (parent river vs. anabanch channels)

- Anabanch channels act as both sinks and sources of carbon in this landscape
  - Sinks for large quantities of sediment-associated carbon, facilitated by high rates of sediment deposition
  - Sources for dissolved organic carbon, particularly via inundation-stimulated release from surface sediments

- At the flow pulse scale, anabanch channels play a unique role in the landscape of this dryland river ecosystem compared to other patch types.

- Hydrological connectivity between anabanch channels and the main river channel influences the distribution and quality of available carbon sources in this landscape
# Chapter Seven: Stable Isotope Analysis – Linking Carbon Sources and Consumers

## 7.1 Introduction

### 7.1.1 The Method

### 7.1.2 Advantages

### 7.1.3 Assumptions

### 7.1.4 Potential Problems

### 7.1.5 Aquatic Carbon Isotope Signatures

- Dissolved inorganic carbon
- Dissolved organic carbon
- Suspended particulate organic matter
- Algae
- Macrophytes

### 7.1.6 Summary

## 7.2 Why Use Stable Carbon Isotope Analysis for This Study?

## 7.3 Aims, Hypotheses and Rationale

## 7.4 Methods

- Carbon sources – sampling and preparation
- Consumers – sampling and preparation
- Laboratory procedure

## 7.5 Results

- Carbon sources
- Consumers
- Linking potential food sources and consumers
- Signature ranges

## 7.6 Discussion

## 7.7 Summary
7 CHAPTER SEVEN: STABLE ISOTOPE ANALYSIS – LINKING CARBON SOURCES AND CONSUMERS

7.1 INTRODUCTION

The analysis of stable carbon and nitrogen isotopes is an increasingly popular method for tracing energy flow through food webs. A clear relationship between an organism’s stable isotope value and its diet has led to stable isotope analysis becoming a ‘standard analytical tool’ in studies of energy flow and food webs (O'Reilly et al. 2002). Stable carbon isotopes are often used in conjunction with stable nitrogen isotopes to determine trophic relationships. Generally, carbon isotopes can help determine the primary energy source (e.g. autotrophic phytoplankton vs. allochthonous leaf litter), while nitrogen isotopes help discriminate between trophic levels and clarify differences between sources.

Stable carbon isotope analysis uses differences in the natural abundances of $^{13}$C and $^{12}$C, which move with little or predictable alteration through food webs, to reveal hidden carbon pathways and accurately distinguish carbon sources (Rounick and Winterbourn 1986). The ratio of $^{13}$C to $^{12}$C in a consumer’s tissue ‘effectively summarizes an animal’s recent feeding history’ (Fry and Arnold 1982), and is sometimes termed its carbon isotope ‘signature’ or ‘signal’. In a basic sense, the $C^{13}/C^{12}$ ratio in a consumer’s tissue is generally the same or very similar to the ratio in the food it has assimilated. The carbon isotope ‘signature’ of the food source is imprinted into the tissue of the consumer, giving the consumer a very similar carbon isotope ‘signature’.

The carbon isotope composition of organic matter is determined by the amount of fractionation that occurs during the biological fixation of CO$_2$. The resultant isotopic composition of plants is associated with their photosynthetic pathways. The two most common are the ‘C$_3$’ and ‘C$_4$’ pathways. C$_3$, or Calvin pathway plants, incorporate atmospheric CO$_2$ by carboxylation of ribulose biphosphate (RuBP), producing first a three-carbon molecule. C$_4$ plants, in contrast, use the Hatch-Slack pathway and
incorporate CO$_2$ by carboxilation of phosphoenol pyruvate (PEP), producing an initial four-carbon molecule. The different carboxylase enzymes discriminate differently toward $^{13}$C in the two pathways, and as a result, the $\delta^{13}$C values of C$_3$ plants generally range from $-32 \, ^\circ/oo$ to $-22 \, ^\circ/oo$, whereas those of C$_4$ plants range from $-23 \, ^\circ/oo$ to $-9 \, ^\circ/oo$ (Rounick and Winterbourn 1986). These differences can be used to trace the sources and fates of carbon in different environments – for example, the application of C$_4$ cattle dung to a C$_3$ grass pasture has been used to quantify the fate of cattle dung in the soil environment (Bol et al. 2000).

The differences in photosynthetic pathway between C$_3$ and C$_4$ plants enable C$_4$ plants to tolerate higher temperatures and more arid conditions than C$_3$ plants, however they are also more sensitive to cold than C$_3$ plants (Thain and Hickman 1994). The other major pathway, crassulacean acid metabolism (CAM), is also adapted to arid conditions. In terms of Australian grasses, C$_4$ species are most numerous where the summer is hot and wet and C$_3$ species are most common where the spring is cool and wet. In other words, C$_4$ species numbers decline with decreasing temperature and/or decreasing summer rainfall; while C$_3$ species numbers decline with increasing temperature and/or decreasing spring rainfall (Hattersley 1983).

Chemical, physical and biological fractionation processes can alter natural stable carbon isotope abundances. These can occur during photosynthesis, biosynthesis and catabolic reactions during respiration, decomposition and remineralisation (Hellings et al. 1999). They involve complex and interacting factors, including the origin of the carbon, changes in diffusive resistance across plant surfaces and the presence of C$_3$, C$_4$ or CAM metabolic pathways (Keeley and Sandquist 1992). In addition, small, incremental increases in animal $\delta^{13}$C occur concurrently with increases in trophic level (Rounick and Winterbourn 1986).

Concise introductions to the reasoning behind and benefits of using the stable carbon isotopes $^{13}$C and $^{12}$C to trace carbon flow through food webs are provided by Rounick and Winterbourn (1986) and Peterson and Fry (1987). The following is a brief introduction to
the method, its advantages, and potential problems. The aims and hypotheses of this chapter are then outlined, along with the specific methods employed, the results, and a discussion of the implications for this thesis.

7.1.1 The method

The stable isotopes of carbon, $^{13}$C and $^{12}$C, occur on Earth in an approximate ratio of 98.9 to 1.1. Physical and chemical fractionation processes resulting from differences in reaction rates involving atoms of dissimilar size and mass can change this ratio. Consequently, organic materials exhibit a range of $^{13}$C/$^{12}$C ratios (Rounick and Winterbourn 1986). The $^{13}$C/$^{12}$C ratio is generally measured by mass spectrometry, and expressed as $\delta^{13}$C in parts per thousand ($^{0}$/oo). It is either enriched in $^{13}$C and depleted in $^{12}$C (more positive) or depleted in $^{13}$C and enriched in $^{12}$C (more negative) relative to an international standard. Another way of expressing this is that material that is enriched in the heavy isotope ($^{13}$C) is described as ‘heavier’, with $^{13}$C values that are ‘higher’ or ‘less negative’ than that of the standard. Material that is depleted in the heavier $^{13}$C is ‘lighter’, and has ‘lower’ or ‘more negative’ $^{13}$C values. Biological samples are usually depleted in $^{13}$C relative to the standard and so have negative $^{13}$C values, ranging from $-50^{0}$/oo to $-5^{0}$/oo. The $\delta^{13}$C values of land plants are significantly lower than that of their inorganic carbon source, atmospheric CO$_2$, which has a $\delta^{13}$C value of $-7^{0}$/oo.

During analysis, organic samples are combusted and carbonates are acidified to produce CO$_2$, which is compared to a CO$_2$ standard, usually ‘PDB’. PDB is the international limestone standard, which has an arbitrary value of zero, and is prepared from the fossil skeleton of a Cretaceous belemnite, Belemnitella Americana, an extinct cuttlefish found in South Carolina’s Pee Dee formation (Rounick and Winterbourn 1986: citing Craig 1957).

The formula for the $\delta^{13}$C$_{\text{PDB}}$ calculation is

$$\delta^{13}$C$_{\text{PDB}} = \frac{^{13}$C/$^{12}$C sample - $^{13}$C/$^{12}$C$_{\text{PDB}}$ standard}{^{13}$C/$^{12}$C$_{\text{PDB}}$ standard} \times 1000$$

256
The accuracy of $\delta^{13}$C determinations of organic samples routinely measured in most studies is about ± 0.2‰ (Rounick and Winterbourn 1986).

Storage and preservation of samples can significantly affect stable isotope signatures (Lochmann and Perschbacher; Kaehler and Pakhomov 2001). Freeze-drying and oven-drying are more reliable methods of sample preservation than the use of formalin and alcohol. Formalin and ethanol have been shown to decrease and increase $\delta^{13}$C values of marine organisms respectively, and to slightly increase $\delta^{15}$N values (Kaehler and Pakhomov 2001). The effects of preservatives vary greatly between species and studies, and methods should be selected carefully.

Most studies recommend temporary confinement of consumer organisms in order to void their guts before sacrifice, to avoid interference from recently ingested material in carbon isotope signatures. However KAehler and Pakhomov (2001) found that such confinement significantly affected stable isotope signatures of littorinid snails. They could not explain the changes they observed, but suggested that it may be due to the metabolism of lipids. They concluded that ‘samples intended for isotope analysis should be frozen, freeze-dried or oven-dried, preservatives should be used only for $\delta^{15}$N analysis and organisms should be sacrificed immediately after collection.’

7.1.2 Advantages

Determining which carbon sources are the most important in terms of supporting the food web has always been a difficult task. Carbon pathways are complex and often invisible. Traditional methods used to measure the use of carbon sources by consumers include gut contents analysis, feeding observations, and the use of tracers such as the radioisotopes $^{14}$C and $^{32}$P (Rounick and Winterbourn 1986; Woodward and Hildrew 2002). More recent methods include C:N ratios, fatty acid, sterol, lignin-phenol and loliolide biomarkers, and plant pigment biomarkers (Bianchi et al. 1997a; Bianchi et al. 1997b; Bodineau et al. 1998; Muller and Mathesius 1998; Muller and Voss 1998). A major
advantage of stable isotope analysis in comparison to these is that it is able to detect
dietary sources integrated over time, rather than simply reflecting recent feeding events.
In addition, stable carbon isotope data reflect only materials actually assimilated and
incorporated into tissue, as opposed to total materials ingested (providing guts are voided
or the investigator removes their contents from the animals before analysis; Rounick and
Winterbourn 1986). Stable carbon isotope procedures are faster than traditional gut
content and faecal analyses, and their results are considered to be relatively conservative
in comparison with nitrogen isotope values or C:N ratios (Muller and Voss 1998).

Simple gut contents analysis, feeding observations or radio tracing are often insufficient
or misleading when investigating carbon sources and pathways (Rounick and
Winterbourn 1986). This is particularly true in aquatic systems, where the importance of
food sources that are relatively amorphous (e.g. filamentous algae, soft-bodied prey,
biofilm, detritus) can be difficult to quantify (Woodward and Hildrew 2002).
Consequently, these sources have often been overlooked or underestimated. There are
many organic carbon sources in aquatic systems, including diatoms, benthic algae,
epilithic algae, pelagic algae (phytoplankton), macrophytes, and terrestrially-derived
organic matter such as leaf litter, seeds and pollen. Both the quantity and quality of these
sources may influence the feeding habits and productivity of primary consumers (Zah et
al. 2001).

Stable carbon isotope analysis helps to discriminate between carbon inputs to streams and
rivers that become primary carbon sources for consumers (Rounick and Winterbourn
1986). For example, allochthonous plant material and autochthonous algae were shown
to be isotopically distinct in small New Zealand streams (Rounick et al. 1982), and
subsequent work based on stable carbon isotope tracing suggested the coexistence of very
different food chains, as well as the existence of hidden carbon pathways (Winterbourn
and Rounick 1985). Similarly, despite high variation in isotopic signatures, Zah et al.
(2001) found that a site-specific approach allowed discrimination between allochthonous
and autochthonous food sources in a glacier stream of the Swiss Alps. The use of stable
isotope analysis in this stream confirmed previous knowledge of macroinvertebrate
functional feeding groups – both grazers and shredders fed predominantly on algae, while gatherer-collectors appeared to be omnivorous (Zah et al. 2001).

Carbon isotope analysis is an effective method by which ultimate carbon sources may be identified. It can be useful in distinguishing among many sources which ones are actually assimilated by consumers, and which may be simply acting as habitat or accidentally ingested. In doing so, $\delta^{13}C$ analysis can assist in understanding which carbon sources may be of higher quality for consumers and hence provide focus for research and sustainable management of ecosystems and their food webs.

7.1.3 Assumptions

Jackson and Harkness (1987) succinctly state five major assumptions of stable carbon isotope analysis. Firstly, interpretation assumes that the food source(s) of interest can be distinguished from all other potential food sources on the basis of $\delta^{13}C$ values. Secondly, it is assumed that $\delta^{13}C$ values do not change substantially over time, or as a result of external environmental factors. Thirdly, within any given area, $\delta^{13}C$ values obtained for each species are considered as representative. Fourthly, the $^{12}C/^{13}C$ ratio of animal tissues is assumed to reflect accurately the mean ratio of the carbon assimilated from all food sources. Finally, it is assumed that animal diets do not change more rapidly than can be reflected by analysis of their carbon isotope ratios. These assumptions may prove to be either true or false depending on individual situations, as discussed below.

7.1.4 Potential problems

The biggest issue currently confronting researchers using isotope ratios is natural variability in $\delta^{13}C$ values – variability over both space and time, and among and within both sources and consumers. The usefulness of the stable carbon isotope technique depends upon clear separation in the $\delta^{13}C$ values of organic food sources. This does not always occur, and overlapping values among sources obscure and confound relationships between source materials and consumers. Frequently, overlapping stable isotope values
permit only broad knowledge of which primary producer is supplying carbon to a food web, e.g. allochthonous vs. autochthonous carbon, or C_3 vs. C_4 plants.

Variation in plant $\delta^{13}C$ values can stem from the incorporation of isotopically ‘light’ respiration CO_2 derived from decomposing litter ($\delta^{13}C$ of ~15.5/00), or from temperature or moisture levels. In humic freshwaters with elevated levels of dissolved organic carbon (DOC), respired CO_2 from heterotrophic microbial activity can produce low $\delta^{13}C$ values in autotrophs such as benthic algae (France 2000). Additionally, anaerobic decomposition and associated chemoautotrophy may alter the $\delta^{13}C$ value of detritus so that it no longer reflects the values of living source material (Rounick and Winterbourn 1986). In aquatic systems, current velocity, water temperature and the availability of dissolved CO_2 have been suggested as causes of variation in carbon isotope ratios in primary sources (such as algae) and consumers (Muller and Voss 1998; Zah et al. 2001). However findings are contradictory, due to both the erratic nature of the variability and a lack of understanding as to the mechanisms influencing carbon isotope ratios in autochthonous material (Zah et al. 2001).

Stable isotope signatures of energy sources and consumers can change continuously throughout the year (O'Reilly et al. 2002). Significant spatial and temporal variations in the $\delta^{13}C$ and $\delta^{15}N$ values of macrophytes have been recorded in small lentic waterbodies in south-eastern Australia (Boon and Bunn 1994). In this case the values of individual taxa could each vary by up to 10 delta units, according to site and season (Boon and Bunn 1994). Such variation has the potential to confound the results of carbon isotope studies that lack spatial and temporal replication. If changes in the signatures of consumers match these fluctuations, it can be presumed that the energy base is relatively constant (Zah et al. 2001). Conversely, where $\delta^{13}C$ values of food sources remain relatively constant throughout the year, a change in the $\delta^{13}C$ values of consumers can indicate a change in the relative availability of different food sources ((Huryn et al. 2001).

For consumers, it is important to understand how long assimilated carbon is held in isotopic ‘memory’ (Rounick and Winterbourn 1986). Diet-switching experiments have
found that tissues of both terrestrial locusts and aquatic snails in an Australian wetland began to reflect new carbon sources within the first ten days of a diet switch, but that the rate of response could vary (Nias 1999). Similar experiments have been conducted for caddisfly larvae (Rau and Anderson 1981), gerbils (Tiesezen et al. 1983), crabs (Haines and Montague 1979), marine molluscs (Jackson and Harkness 1987) and shrimp (Fry and Arnold 1982). Where carbon sources can change in quality and quantity over time, it is important to realise that the δ^{13}C signatures of consumers will take varying amounts of time to reflect changes in assimilation (O'Reilly et al. 2002).

Consumers can also discriminate between components of particular carbon sources, thereby changing their δ^{13}C value even though they may be consuming the same size fraction or source as other consumers (Hamilton et al. 1992; Wallace et al. 1997; Thorp et al. 1998)). Suspension-feeding invertebrates in particular have been shown to selectively assimilate a specific component of the seston (Hamilton et al. 1992; Wallace et al. 1997; Thorp et al. 1998). Thorp et al. (1998, p.560) suggested that ‘invertebrate consumers would preferentially assimilate the autochthonous component of the seston as either living phytoplankton or as detritus.'

An additional source of variability of carbon isotope signatures occurs within different tissues of both producers and consumers (Jackson and Harkness 1987). It is recommended to use muscle tissue in larger animals for stable isotope analysis because amino acids from muscle may show a closer animal-diet link than the whole animal (Fry and Sherr 1984). Overall, ‘isotopic variability decreases in relation to organism size…such that organisms of high trophic position are the best suited for estimating energy utilisation in aquatic food webs’ (France 2000, p.446). In aquatic systems, algae, diatoms and other micro-organisms often have δ^{13}C values intermediate to those of C_{3} and C_{4} plants, and consequently can make interpretation of results difficult (Jackson and Harkness 1987). Micro-organisms associated with vegetation also have the potential to introduce confusion, as it can be difficult to distinguish which is the actual food source for consumers such as macroinvertebrates (Jackson and Harkness 1987), however the isotopic signatures of epiphytic material are usually very similar to those of their hosts.
7.1.5 **Aquatic carbon isotope signatures**

**Dissolved inorganic carbon**

The dissolved inorganic carbon fixed by freshwater plants can vary considerably in $\delta^{13}$C value, from $-27^{0}/o$ to $+1^{0}/o$ (Osmond et al. 1981; Rounick and Winterbourn 1986; Palmer et al. 2001). This contrasts markedly with the isotopic consistency of atmospheric CO$_2$ used by land plants (~$-7^{0}/o$; Rounick and Winterbourn 1986).

Inorganic carbon ($\text{HCO}_3^-$, $\text{CO}_3^{2-}$, free CO$_2$) in streams may be derived from several sources, including 1) dissolution of carbonate and weathering of silicate minerals in soils and underlying bedrock, 2) in-stream respiration by aquatic plants and heterotrophic respiration of allochthonous and autochthonous organic matter, 3) shallow groundwater inputs from elevated levels of soil CO$_2$, and 4) atmospheric draw-down’ (Palmer et al. 2001, p.322, citing Wetzel 1983, 1992). Signatures for specific DIC sources range from ‘about $+1^{0}/o$ for HCO$_3^-$ derived from limestone, to about $-6^{0}/o$ for seawater HCO$_3^-$, and from $-7^{0}/o$ for dissolved CO$_2$ in equilibrium with air, to about $-27^{0}/o$ for dissolved CO$_2$ derived from respiration of decomposing C$_3$ material’ (Osmond et al. 1981). Carbon derived from mud respiration is also assimilated by plants (Osmond et al. 1981).

This variation is strong both spatially and seasonally (Hellings et al. 1999), and can stem from ‘i) the extent to which atmospheric CO$_2$ is in equilibrium with the water mass, although the contribution of atmospheric CO$_2$ to DIC in rivers is negligibly small….; ii) groundwater discharge; iii) respiration on particulate organic carbon of natural terrestrial and domestic sewage origin; and iv) in situ photosynthesis’ (Hellings et al. 1999, p.176).

The proportion of HCO$_3^-$ used by macrophytes in addition to CO$_2$ depends on several factors (Osmond et al. 1981 citing Allen and Spence 1981). ‘The proportion of total carbon available as CO$_2$ will range from approximately 80% at pH 5.5 to less than 1% at pH 8.4 and the concentration of carbon species in natural waters may range from 0.2 mg/L to 50 mg/L over the same pH range. There is also evidence for nocturnal CO$_2$ fixation via acid accumulation in some macrophytes (Osmond et al. 1981).
Dissolved organic carbon

The majority of dissolved organic carbon in stream and groundwater has $\delta^{13}C$ values close to those of litter and topsoil (Kaiser et al. 2001; Palmer et al. 2001). The $\delta^{13}C$ of dissolved organic carbon in soils generally increases with increasing depth, and is often accompanied by a decrease in the concentration of DOC. This suggests that microbial decomposition contributes to the loss of DOC, because aerobic metabolic processes preserve $\delta^{13}C$ and release $^{12}C$ via the evolution of CO$_2$ (Kaiser et al. 2001: Blair et al. 1985). However, when DOC comes into contact with mineral material, the $\delta^{13}C$ of that remaining in solution increases due to preferential sorption of $^{13}C$-depleted hydrophobic fractions (Kaiser et al. 2001). Soils also release hydrophilic organic carbon with large $\delta^{13}C$ values, increasing the $\delta^{12}C$ of organic carbon in effluents from soil compared with inflow (Kaiser et al. 2001). Thus, Kaiser et al. (2001, p.585) concluded that ‘selective sorption of organic C fractions changes $\delta^{13}C$ in a way that mimics metabolic transformation and decomposition.’

Dissolved organic carbon can be taken up by micro- and macro-invertebrates via a number of methods. Carbon isotope ratios have been used to prove this uptake, via diet-switching experiments, however the actual uptake of dissolved organic carbon can depend upon its original source (for example tree vs. grass) and the preferences of the consumer (Rau and Anderson 1981). DOC can also be made available to consumers by flocculation, adsorption to particles, microbial uptake, and the eventual ingestion of either bacteria, bacteria consumers, or biofilm (Thorp et al. 1998 and refs. therein).

Thorp et al. (1998) emphasise the need for ‘a more complete assessment’ of the role of dissolved organic matter (DOM) in large rivers. Their findings suggested ‘a linkage between primary consumers and DOM at both the floodplain and constricted-channel sites’. Thorp et al. (1998) went on to suggest that ‘whatever the method of uptake, DOM originating from autochthonous organic matter would be expected to have a higher
nutritional value (especially with regard to carbohydrates and proteins) than DOM originating from allochthonous organic matter.’

**Suspended particulate organic matter**

Carbon isotope values of suspended matter samples in turbid rivers and estuaries tend to reflect the dominant carbon isotope values of their source areas (Zhang *et al.* 1997). However the relationship is rarely simple. For example, in the Schelde Estuary, terrestrial organic matter is important for the sedimentary pool, but suspended matter is dominated by marine, riverine and estuarine components (Middelburg and Nieuwenhuize 1998). Sedimentary and suspended matter can differ significantly in terms of their C:N and isotope ratios. C:N ratios typically increase during the decomposition of organic matter, and autochthonous forms of organic matter tend to have a C:N mass ratio of approximately 12:1, whereas allochthonous forms of organic matter often range from 45:1 to 50:1 (Thorpe *et al.* 1998 citing Wetzel 1983). Suspended matter size fractions can also vary systematically in their signatures. For example, small particles were found to have low C:N ratios, depleted $\delta^{13}$C and enriched $\delta^{15}$N values relative to large particles in the upper Schelde Estuary, however in the lower estuary these differences were not apparent (Middelburg and Nieuwenhuize 1998).

Particulate organic carbon $\delta^{13}$C values can show considerable spatial and temporal variability (Hellings *et al.* 1999). As such, they can also assist in determining the main sources of carbon in an ecosystem. For example, Hellings *et al.* (1999) showed that during autumn and winter in the Schelde River, ‘almost all riverine particulate organic carbon is derived from allochthonous terrestrial matter either of anthropogenic or natural origin’ (Hellings *et al.* 1999, p.184). Very negative $\delta^{13}$C values for suspended particulate organic matter in the Schelde River were accompanied by high chlorophyll $a$ concentrations and low C:N ratios, suggesting that phytoplankton accounted for a significant fraction of particulate organic matter (Hellings *et al.* 1999).
In the lower Ohio River, USA, comparison of $\delta^{13}$C and $\delta^{15}$N of possible organic matter sources and invertebrate consumers in the floodplain area strongly indicated an association with UTOM, DOM and possibly FTOM (Thorp et al. 1998). Working from the premise of Thorp et al. (1998) that fine suspended particulate organic matter (FSPOM) is the most important form of carbon for riverine food webs, Olley (2002) used C isotope ratios to demonstrate that in an Australian lowland river, the carbon sources in this fraction change between flood and non-flood periods. During non-flood periods in the Murrumbidgee River, the proportion of carbon derived from autotrophic sources increases with distance downstream, and dominates the lower reaches. In contrast, catchment soil sources dominated the FSPOM fraction during a 1 in 10 year flood (Olley 2002).

**Algae**

Isotopic signatures of algae can vary widely among sampling sites and dates (Zah et al. 2001). For example, where phytoplankton productivity increases due to nutrient enrichment, discrimination against the heavier carbon isotope eventually decreases, giving the phytoplankton an enriched carbon signal (Farquhar et al. 1989). The $\delta^{13}$C ratios of algae can range from $12-47^{0/00}$, depending on the source of the carbon. The more negative values <30 are associated with algae which are accessing carbon derived from the breakdown of terrestrial organic matter (Olley 2002).

In many cases, stable carbon isotope analyses have revealed the importance of algae, rather than the more obvious vascular plants. For example, quantitative analyses of carbon sources and fish production in the Amazon Basin yielded results that appeared to clash significantly with the results of stable carbon isotope studies (Bayley 1989; Hamilton et al. 1992). Quantitatively, the trophic roles of phytoplankton and periphyton appeared to be minor – indeed, Bayley (1989, p.405) stated that: ‘unless the various phytoplankton productivity estimates cited are all grossly underestimated, it is difficult for this source to account for the entire productivity of this group [of fish species] in addition to that of pelagic…and young stages of fish’. However $\delta^{13}$C isotope ratios
indicated that the fish families concerned derived most of their assimilated carbon from phytoplankton-based food chains. Hamilton et al. (1992) confirmed this further for other consumers – their results showed that both phytoplankton and attached algae were important sources of energy for many aquatic animals, contradicting traditional interpretations of floodplain food webs. Indeed, Hamilton et al. (1992) go on to suggest that vascular plants may be more important as shelter from predators and substrata for epiphytic algae, than as a source of organic carbon (Hamilton et al. 1992).

Chlorophyll a concentrations in the water column of billabongs can exceed 1 mg L$^{-1}$, and the presence of dense stands of macrophytes does not necessarily make them the most important food source (Bunn and Boon 1993). Phytoplankton density can control the $\delta^{13}$C values of both dissolved and particulate carbon pools. Thorp et al. (1998) quoted Wehr et al. (1997) as suggesting that in the floodplain section of the Ohio River, total phytoplankton densities and flow conditions are the two most important factors regulating dissolved organic matter.

**Macrophytes**

Freshwater macrophyte $\delta^{13}$C values are highly variable. Besides variation due to the different $\delta^{13}$C values of CO$_2$ sources (France 2000), signatures appear to be affected by events immediately before CO$_2$ fixation. These include HCO$_3^-$CO$_2$ diffusion across the leaf-water interface, membrane transport of HCO$_3^-$CO$_2$, and the dehydration of HCO$_3^-$ to CO$_2$ inside the cell (Osmond et al. 1981; Rounick and Winterbourn 1986). Hydrology can significantly influence carbon uptake and hence $\delta^{13}$C values in freshwater plants (Osmond et al. 1981). Carbon isotope analysis has been used to determine the importance of riverine wetland macrophyte production to secondary production in Lake Victoria, Kenya (Gichuki et al. 2001).

The variation in $\delta^{13}$C values found in freshwater macrophytes is such that discrimination between sources can be virtually impossible. For example, Bunn and Boon (1993) found that for three floodplain billabongs in south-eastern Australia, stable carbon isotope
analysis could not be used to discriminate among the conspicuous potential sources of fringing, emergent or floating vegetation or benthic detritus. Results indicated that littoral and fringing vegetation could contribute to metazoan food webs in these billabongs only if an additional highly $\delta^{13}$C depleted source was consumed simultaneously. Bunn and Boon (1993) suggested that either methane from billabong sediments or an unknown source, such as phytoplankton, may constitute this $\delta^{13}$C depleted source. They go on to say that ‘if planktonic Chlorophyta [phytoplankton] in billabongs were heavily grazed, or secreted much of their fixed carbon as dissolved organic matter which was then assimilated by bacteria and incorporated into planktonic food webs via a microbial loop, they would support metazoan assemblages with the appropriate stable-carbon isotope ratios but never be apparent visually’ (Bunn and Boon 1993).

Occasionally it can also be difficult to differentiate between terrestrial signatures and aquatic plant signatures. Few submerged macrophytes in the floodplain billabongs studied by Bunn and Boon (1993) had distinctly higher stable carbon isotope ratios than terrestrial C$_3$ plants, as has been found for European floodplain lakes. Macrophytes appeared to contribute little to the billabong food webs, with the only consumer that clearly derived its biomass carbon from this source being the yabbie (freshwater crayfish) *Cherax destructor*, through consumption of detritus (Bunn and Boon 1993).

### 7.1.6 Summary

Several carbon isotope studies have suggested that autotrophic production plays a much more important role in aquatic food webs than previously assumed by conceptual models (Hamilton *et al.* 1992; Loneragan *et al.* 1997; Middelburg and Nieuwenhuize 1998; Thorp *et al.* 1998; Zah *et al.* 2001). Isotope tracing work in a glacier stream of the Swiss Alps led Zah *et al.* (2001, p.880) to ‘support the contention of Minshall (1978) that the importance of autotrophy in stream ecosystems is often underestimated.’ Even in the contrasting tropical Orinoco Floodplain River of Venezuela, stable carbon and nitrogen isotope ratios showed that microalgae, including both phytoplankton and epiphytes, were
primary energy sources for many aquatic animals, even though aquatic macrophytes were much more abundant (Hamilton et al. 1992).

The few stable isotope studies in floodplain systems emphasise the role of algal and other carbon sources, as well as the usefulness of the carbon isotope technique in drawing attention to previously unknown carbon sources. Australian carbon isotope studies suggest that the relatively large pool of allochthonous carbon supplied to riverine and estuarine systems is of small importance compared to the autochthonous (and especially algal) carbon pool (Loneragan et al. 1997; Bunn et al. 2003). In waterholes of the Cooper Creek system in central Australia, carbon isotope analysis showed that a relatively narrow band of attached algae on littoral sediments was the major source of energy for aquatic consumers, ultimately supporting large populations of crustaceans and fish (Bunn et al. 2003). In floodplain sections of the River Danube downstream of Vienna (Austria), plankton derived carbon (indicated by C:N ratios less than eight and \( \delta^{13}C \) values lower than –25\(^{0}/00\)), dominated the particulate organic carbon pool. Phytoplankton was the major component, emphasising the role of local autotrophic production (Hein et al. 2003).

In contrast to their expectations, Zah et al. (2001, p.879) found ‘no evidence….that the diet of primary consumers shifted from autochthonous towards an allochthonous diet, as potential terrestrial food sources increased across sites.’ Rather, autotrophic sources dominated across all sites and throughout the year. Their explanation for this was that where high stream velocities and high bed mobility exist (such as in upland or glacial streams), there is little storage of allochthonous organic matter. Consequently, the isotopic signatures of consumers in such streams reflect their consumption and incorporation of algae and autochthonous detritus (Zah et al. 2001). The only site where allochthonous organic matter had some influence was characterised by its proximity to trees and slow currents, which favoured the input and retention of terrestrial organic matter.
7.2 **WHY USE STABLE CARBON ISOTOPE ANALYSIS FOR THIS STUDY?**

Carbon isotope analysis provides valuable additional information regarding the *quality* of the major carbon sources that have been quantified in anabranche channels, the main channel and the floodplain. It will identify the carbon sources actually being assimilated by consumers, rather than those that are not utilised at all or simply ingested. In this way the work will clarify the importance of the different landscape patches – those that carry the largest *quantities* of carbon, and that therefore appear to be the most important, may actually be of less value to the ecosystem in terms of the *quality* of the carbon. Carbon isotope analysis will also help to distinguish the relative importance of allochthonous vs. autochthonous carbon sources to consumers during the disconnection phase, and may also provide more specific information that will elucidate the potential ecological effects of hydrological connection between anabranche channels and the main channel.

7.3 **AIMS, HYPOTHESES AND RATIONALE**

The aims of this chapter are to:

1. Determine which of the major available carbon sources the organisms in anabranche billabongs of the Macintyre River are assimilating
2. Determine which of the major available carbon sources the organisms in the littoral zone of the main channel of the Macintyre River adjacent to anabranches are assimilating

The hypotheses are that:

- Organisms in anabranche billabongs of the Macintyre River are dependent upon a mixture of allochthonous and autochthonous carbon sources during the winter disconnection phase
- Organisms in the littoral zone of the main channel of the Macintyre River are dependent upon predominantly autochthonous carbon sources during the winter disconnection phase
During the disconnection phase, aquatic consumers in anabranch billabongs have a mixture of allochthonous and autochthonous carbon sources available to them. The anabranch billabongs collect large amounts of terrestrial leaf litter (particularly \textit{Eucalyptus} spp.) throughout the year. This litter has the potential to support heterotrophic production as well as supply abundant nutrients for intense algal production. Anabranches also have significantly higher concentrations of carbon in their sediments compared to main channel sediments, and this carbon may be important to anabranchn consumers when made available by wetting. Anabranchn billabongs also appear to support more macrophytes compared to the main river channel. Thus, the apparent quantitative dominance of allochthonous sources (e.g. leaf litter) combined with the relative lability of autotrophic sources (e.g. algae) suggests that with time integration the tissues of consumers in anabranchn billabongs would reflect a mixed diet.

In contrast, the width and far greater volume of water in the main river channel may reduce the quantitative importance of direct litter inputs from the banks, and increase the potential for a quantitatively dominant role of labile phytoplankton and other suspended (pelagic) carbon sources in consumer diets. However it is important to note that most riverine consumers tend to aggregate close to the sheltered bank areas, where vegetation and large woody debris provide shelter, and also more varied potential food sources.

The predominance (and consumption) of autochthonous vs. allochthonous sources is also likely to change during partial connection, complete connection and draining phases between anabranches and the main river channel. In order to test this, one would have to a) run diet-switching experiments with representatives of the study area animals to determine the integration times for the tissue of each species; and then b) take consumer samples continuously throughout an entire flood cycle, including for some time after the connection event (according to the results of the integration experiments). This work was unfortunately not possible within the constraints of this project in terms of logistics, time and funding, however it would form a very interesting basis for further research in terms of anabranchn channels as well as the role of floodplain connection in general.
7.4 METHODS

The study area was sampled during June (winter) 2002. Winter is the dry season in this part of the catchment, and sampling also corresponded with the beginning of an El Nino event.

Carbon sources – sampling and preparation

Random samples of every major carbon source were collected throughout the reach, at least 50 m apart, on river banks, anabranch banks and within anabranch channels and billabongs. Six anabranch billabongs were selected, each from a separate anabranch channel (Chapter 4). Vegetation was collected by hand, where possible including the entire plant, placed in A4-size zip-lock plastic bags and sealed. Trees and shrubs were sampled only for leaves, and effort was made to collect separate samples of both fresh and desiccated litter material. Sources were frozen whole, transported to laboratory, and oven-dried at 60°C for 48 hours. Filamentous algae samples were rinsed in tap water before drying. Large samples were crushed to a fine powder in a Rocklab automated crushing machine; small samples and algae were pulverised to a fine powder using a mortar and pestle.

The only major potential carbon sources not sampled separately were phytoplankton and dissolved organic carbon. The $\delta^{13}C$ value of phytoplankton is difficult to assess (particularly in these highly turbid systems) because of the difficulty separating it from other suspended matter components (Hellings et al. 1999). Sampling of suspended matter was hoped to provide an estimate of phytoplankton signatures, however considering the time of year (winter), phytoplankton populations would have been depressed and their signatures difficult to detect. Suspended matter samples were collected by centrifuging several litres of river and anabranch billabong water in 250ml batches (5000 rpm for 20 mins), siphoning off the water, and freeze-drying the remaining slurry.
Forty-two source samples were analysed. These included sediments; suspended particulate matter; riparian tree leaves; riparian grasses, rushes and sedges and one shrub; benthic and epiphytic algae (where present); macrophytes and mud colonising plants (where present); cattle dung; surface biofilms; and floating organic matter (including pollen and seed).

Consumers – sampling and preparation

Anabranch billabongs were sampled for consumers using a seine net in pelagic and benthic zones and 250µm dip nets in littoral zones. Consumers were hand-picked and sorted in the field, held alive for 6 hours to void guts, then frozen. Large fish were filleted for white muscle tissue, and large crustaceans (>15mm) and molluscs were filleted for muscle tissue following removal of exoskeleton and gut. Large specimens were analysed individually and whole. Invertebrates, small fish and small crustaceans (<15mm) were left whole, sorted by site, and individuals of the same taxa were combined. All consumer samples were freeze-dried for 48 hours, then crushed to a fine powder and homogenised using a mortar and pestle. Half of each consumer sample was reserved, and half taken to the laboratory for analysis. Many more taxa were collected from anabranch billabongs than the main river channel (Table 7.1).

A total of 43 consumer samples were analysed. These included freshwater shrimp, dragonfly nymphs, yabbies, mussels, tadpoles, corixids, notonectids, cladocerans, mixed fish larvae, and various species of small and juvenile fish including gudgeons, goldfish, bony herring, spangled perch and Australian smelt.

Laboratory procedure

Carbon and nitrogen concentrations and stable isotope values (δ¹³C and δ¹⁵N) were determined using a Europa 20-20 isotope ratio mass spectrometer with an ANCA preparation system. Reference samples were run after every eight samples. The carbon isotope ratios are expressed as parts per mille (‰) deviation from world recognised standards (PDB), and analytical uncertainties are +/- 0.3. (Olley 2002).
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<tr>
<td>Gudgeon</td>
<td><em>H. hypseleotris spp.</em></td>
<td></td>
<td>√</td>
<td>√</td>
<td>√</td>
<td>√</td>
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<tr>
<td>Freshwater shrimp</td>
<td><em>M. macrobrachium australiense</em></td>
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<td></td>
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<tr>
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<td><em>A. alathyria jacksoni</em></td>
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<td>Backswimmers</td>
<td><em>N. notonecidae</em></td>
<td></td>
<td>√</td>
<td>√</td>
<td>√</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Dragonfly nymphs</td>
<td><em>O. odonata</em></td>
<td></td>
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<td>√</td>
<td>√</td>
<td>√</td>
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<td>Spangled perch</td>
<td><em>L. leiopotherapon unicolor</em></td>
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<td></td>
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<td></td>
</tr>
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<td>Tadpoles</td>
<td><em>L. litoria alboguttata</em></td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>√</td>
</tr>
<tr>
<td>Yabbie</td>
<td><em>C. cherax destructor</em></td>
<td></td>
<td>√</td>
<td>√</td>
<td>√</td>
<td>√</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mixed fish larvae</td>
<td><em>V. various spp.</em></td>
<td></td>
<td></td>
<td></td>
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7.5 **RESULTS**

**Carbon sources**

Carbon isotope ratios ($\delta^{13}$C values) for the sources varied widely (Table 7.2 and Table 7.3), ranging from –11.4‰ (Cyperus spp.) to –31.2‰ (Parkeriaceae). There was clear separation between four groups:

1. grasses and the Cyperus sedge (-11.4 to –14.4‰; indicating C4 metabolism);
2. cattle dung (-19.4‰);
3. filamentous algae and surface water biofilms (-23.8 to –26.4‰); and
4. tree and shrub leaves, rushes, mud-colonising plants, and the floating organic matter (OM, including pollen and seed; -26.8 to –31.2‰).

Delta $^{15}$N values for the source samples ranged from –2.4‰ (River suspended matter) to 16.2‰ (a mud fern).

**Consumers**

Carbon isotope ratios ($\delta^{13}$C values) for the consumers ranged from –23.6‰ (large yabbies) to –33.6‰ (Odonata). Delta $^{15}$N values for consumers ranged from 7.5‰ (Corixidae) to 14.5‰ (Gudgeons; Table 7.2 and Table 7.4).

**Table 7.2  Summary statistics for $\delta^{13}$C and $\delta^{15}$N values of all consumer and source samples**

<table>
<thead>
<tr>
<th>Sources</th>
<th>Maximum</th>
<th>Minimum</th>
<th>Mean</th>
<th>Median</th>
<th>Standard deviation</th>
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<td>-31</td>
<td>-23</td>
<td>-25</td>
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</tr>
<tr>
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<td>-34</td>
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<td>-29</td>
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<td>Delta PDB</td>
<td>Site</td>
<td>Source type</td>
<td>Name</td>
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<td>------</td>
<td>-------------</td>
<td>------</td>
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<td>Grass</td>
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<td></td>
</tr>
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<td>Grass</td>
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</tr>
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</tr>
<tr>
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<td>-13.9</td>
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</tr>
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<td>-14.4</td>
<td>A6XR</td>
<td>Grass</td>
<td>Graminae, Paspalidium spp.</td>
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<td>Epiphytic algae on rush</td>
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<td>Benthic algae, submerged</td>
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<td>Anabranch sediment</td>
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<td></td>
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<td>A1RBX1</td>
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</tr>
<tr>
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<td>A2M</td>
<td>Benthic plant</td>
<td>Haloragaceae, Myriophyllum spp.</td>
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</tr>
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<td>A1XF1</td>
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<td>Anabranch sediment</td>
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<td>Benthic algae, dry</td>
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<td></td>
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</tr>
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<td>A2ER</td>
<td>Rush</td>
<td>Juncaceae, Juncus usitatus</td>
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<td>-27.2</td>
<td>A2X</td>
<td>Floating OM/pollen/seed</td>
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<td>Rush</td>
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<td></td>
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<td>-28.0</td>
<td>A2E</td>
<td>Tree leaf, litter</td>
<td>Eucalyptus camaldulensis</td>
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<tr>
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<td>A2E</td>
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<td>Eucalyptus microtheca</td>
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<td>A3M</td>
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<td>Fern</td>
<td>Parkeriaceae, Ceratopteris thalictroides?</td>
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Table 7.4  Consumer samples, locations, and δ¹³C and δ¹⁵N values

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<th>Site code</th>
<th>Sample type</th>
<th>Tissue type</th>
<th>Number of individuals</th>
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<td>-23.6</td>
<td>A6</td>
<td>Big (&gt;5cm) yabbies</td>
<td>Muscle</td>
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</tr>
<tr>
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<td>A6</td>
<td>Small (&lt;5cm) yabbies</td>
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<td>2</td>
</tr>
<tr>
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<td>A5</td>
<td>Small mussell</td>
<td>Muscle</td>
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<tr>
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Linking potential food sources and consumers

Bivariate $\delta^{13}$C and $\delta^{15}$N plots are a common method for presenting stable isotope values. They provide an instant visual representation of the spread of the data, with individual data points representing the mean values. A dual plot of the mean values for both sources and consumers from anabranch billabongs and the river channel reveals considerable gaps between the signatures (Figure 7.1). Immediately apparent is the need to adjust consumer values for trophic level enrichment. There is wide variation in mean source signatures compared to consumers, indicating overall assimilation of only a portion of the range of sources sampled. There are distinct groupings:

Sources:
- Algae, billabong suspended matter, and anabranch sediments group together
- Tree leaves (mean, harvested, litter), rushes and the herb polygonum group together
- Grasses, floodplain sediment, river sediment and river suspended matter are clearly distinguishable from the remainder of the sample set and from each other.

Consumers:
- *Litoria alboguttata* tadpoles, *Cherax destructor* (yabbies) and *Macrobrachium* (shrimp) group together
- *Odonata* (dragonfly nymphs), and *Carrassius auratus* (goldfish) group together
- *Alathyria* (mussels), and *Notonectidae* (backswimmers) group together
- *Nematolosa erebi* (bony herring), *Retropinna semoni* (Australian smelt) and mixed fish larvae group together
- *Corixidae* (water boatmen), *Cladocera* (water fleas) and *Hypseleotris spp.* (gudgeons) are clearly distinguishable from each other and from the remainder of the sample set
Figure 7.1 Dual $\delta^{13}$C and $\delta^{15}$N plot for sources and consumers from anabranch billabongs and the river channel. Green indicates sources, red indicates consumers. Consumer values require correction for trophic enrichment before matching of signatures with sources.
Signature ranges

Matching of consumers to potential carbon sources proved difficult, due to a) the large amount of variation within taxonomic groups; b) the large amount of variation between sites; and c) the dominance of secondary consumers rather than primary consumers in the sample. To compensate for trophic enrichment (in the absence of specific knowledge of fractionation from diet to consumers), potential dietary sources for a primary consumer were considered to be those with a mean delta C ($\delta^{13}C$) value within the range of 2 less than or 1 greater than the mean consumer signature, and with a mean delta N ($\delta^{15}N$) value within the range of 1-5 less than the consumer signature (after Bunn and Boon 1993). For secondary consumers in the present study, this range was doubled (Table 7.5 and Table 7.2). Using this method, potentially important variability in consumer signatures may be overlooked (Nias 1999). Each source has potentially more consumers if the range of consumer values is considered instead of just the mean, and vice versa. This is less important where consumer signatures are less variable. In such a situation using the mean value is valid because there is less room for misinterpretation (Nias 1999).

Table 7.5  Trophic levels assumed in matching analysis.

<table>
<thead>
<tr>
<th>Consumer</th>
<th>Trophic level</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cladocera (water fleas)</td>
<td>1</td>
</tr>
<tr>
<td>Litoria (tadpoles)</td>
<td>1</td>
</tr>
<tr>
<td>Cherax (yabbies)</td>
<td>1</td>
</tr>
<tr>
<td>Macrobrachium (shrimp)</td>
<td>1</td>
</tr>
<tr>
<td>Alathyria (mussels)</td>
<td>1</td>
</tr>
<tr>
<td>Mixed fish larvae</td>
<td>1</td>
</tr>
<tr>
<td>Corixidae (water boatmen)</td>
<td>2</td>
</tr>
<tr>
<td>Hypseleotris (gudgeons)</td>
<td>2</td>
</tr>
<tr>
<td>Notonectidae (backswimmers)</td>
<td>2</td>
</tr>
<tr>
<td>Odonata (dragonfly nymphs)</td>
<td>2</td>
</tr>
<tr>
<td>Retropinna (Australian smelt)</td>
<td>2</td>
</tr>
<tr>
<td>Carrassius (goldfish)</td>
<td>2</td>
</tr>
<tr>
<td>Nematolosa (bony herring)</td>
<td>2</td>
</tr>
<tr>
<td>All fish</td>
<td>2</td>
</tr>
<tr>
<td>Leiopotherapon (spangled perch)</td>
<td>2</td>
</tr>
</tbody>
</table>
**By consumer**

The majority of consumers had signatures that matched with more than one source signature, indicating that they assimilate carbon and nitrogen from several different sources (Table 7.6). Those that matched with the greatest number of carbon sources included gudgeons (8) and spangled perch (8), while those that matched with only one source included mussels, macrobrachium and yabbies. Sources that did not appear to support any of the consumer samples included a) river suspended matter; b) grasses; c) floodplain sediment, d) cattle dung; e) ferns; and f) sedges. River sediment only appeared to have the potential to support corixids. The sources that appeared to account for the signatures of the most consumers sampled were floating organic matter including pollen and seed (11), leaf litter (9), rushes (8), harvested fresh leaves (8), and polygonum (7; Table 7.7). The average signatures of these sources matched with those of the fish (gudgeons, goldfish, bony herring, spangled perch, and sometimes smelt), notonectids, odonates and corixids. The floating organic matter (including pollen and seed) signature was the only source that matched the signatures of macrobrachium and yabbies, and one of the only three that matched with tadpoles. The only source that appeared to match signatures with mussels was the herb polygonum.

Anabranch billabong carbon sources such as algae, suspended matter and sediment displayed signatures matching those of tadpoles, corixids, gudgeons and spangled perch. In contrast, sources solely found in the river (river suspended matter and river sediment) and the floodplain (grasses, floodplain sediment, cattle dung) did not appear to support consumers at all (although river sediment only just matched with corixids). This is partially confounded by the fact that many more consumers were collected from anabranch billabongs compared to the river and the floodplain. However assuming that isotope ratios are a reflection of long-term diets, there would be some strength in the argument that anabranch consumers at least derive no support from river and floodplain carbon sources. Since most trees and shrubs are concentrated in and around anabranch channels, it is reasonable to assume that anabranch consumers assimilate only carbon sources that may be found within the anabranch channels themselves.
Table 7.6 Matching of sources and consumers. Potential dietary sources for a primary consumer were considered to be those with a mean delta C value within the range of 2 less than or 1 greater than the mean consumer signature, AND with a mean delta N value within the range of 1-5 less than the consumer signature. For secondary consumers in the present study, this range was doubled.

<table>
<thead>
<tr>
<th>Source</th>
<th>Consumers</th>
</tr>
</thead>
<tbody>
<tr>
<td>Floating OM/pollen/seed</td>
<td>Macrobrachium</td>
</tr>
<tr>
<td>Tree leaf, litter</td>
<td>Smelt</td>
</tr>
<tr>
<td>Rush</td>
<td>Smelt</td>
</tr>
<tr>
<td>Tree leaf, mean</td>
<td>Smelt</td>
</tr>
<tr>
<td>Tree leaf, harvested</td>
<td>Smelt</td>
</tr>
<tr>
<td>Herb (polygonum)</td>
<td>Mussel</td>
</tr>
<tr>
<td>Algae</td>
<td>Smelt</td>
</tr>
<tr>
<td>Billabong susp. matter</td>
<td>Tadpoles</td>
</tr>
<tr>
<td>Anabranch sediment</td>
<td>Tadpoles</td>
</tr>
<tr>
<td>River sediment</td>
<td>Corixids</td>
</tr>
<tr>
<td>River susp. matter</td>
<td>NONE</td>
</tr>
<tr>
<td>Grass</td>
<td>NONE</td>
</tr>
<tr>
<td>Floodplain sediment</td>
<td>NONE</td>
</tr>
<tr>
<td>Cattle dung</td>
<td>NONE</td>
</tr>
<tr>
<td>Fern</td>
<td>NONE</td>
</tr>
<tr>
<td>Sedge</td>
<td>NONE</td>
</tr>
</tbody>
</table>
Table 7.7 Number of consumers per source and number of sources per consumer.

<table>
<thead>
<tr>
<th>Source</th>
<th>No. consumers</th>
<th>Consumer</th>
<th>No. sources</th>
</tr>
</thead>
<tbody>
<tr>
<td>Floating OM/pollen/seed</td>
<td>11</td>
<td>Gudgeons</td>
<td>8</td>
</tr>
<tr>
<td>Tree leaf, litter</td>
<td>9</td>
<td>Spangled perch</td>
<td>8</td>
</tr>
<tr>
<td>Rush</td>
<td>8</td>
<td>Notonectids</td>
<td>6</td>
</tr>
<tr>
<td>Tree leaf, mean</td>
<td>8</td>
<td>Odonates</td>
<td>6</td>
</tr>
<tr>
<td>Tree leaf, harvested</td>
<td>8</td>
<td>Goldfish</td>
<td>6</td>
</tr>
<tr>
<td>Herb (polygonum)</td>
<td>7</td>
<td>Herring</td>
<td>6</td>
</tr>
<tr>
<td>Algae</td>
<td>4</td>
<td>All fish</td>
<td>6</td>
</tr>
<tr>
<td>Billabong suspended matter</td>
<td>3</td>
<td>Corixids</td>
<td>6</td>
</tr>
<tr>
<td>Anabranch sediment</td>
<td>3</td>
<td>Smelt</td>
<td>4</td>
</tr>
<tr>
<td>River sediment</td>
<td>1</td>
<td>Tadpoles</td>
<td>3</td>
</tr>
<tr>
<td>River suspended matter</td>
<td>0</td>
<td>Mussel</td>
<td>1</td>
</tr>
<tr>
<td>Grass</td>
<td>0</td>
<td>Macrobrachium</td>
<td>1</td>
</tr>
<tr>
<td>Floodplain sediment</td>
<td>0</td>
<td>Yabbies</td>
<td>1</td>
</tr>
<tr>
<td>Cattle dung</td>
<td>0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fern</td>
<td>0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sedge</td>
<td>0</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

By location

Where source signatures matched those of consumers, they did so at between four and six of the locations sampled (Table 7.8). Tree leaves, rushes and floating organic matter (including pollen and seed) were consumed at the greatest number of sites (6 sites), with algae, anabranch sediment, and polygonum being assimilated at five sites, and billabong suspended matter at four of the sites.

Overall, the number of sources assimilated (Table 7.9) was greatest at anabranch two and anabranch six billabongs (9 sources), closely followed by anabranch five (8), the river (8), anabranch one (7), anabranch four (6) and anabranch three (3 sources).
Table 7.8 Assimilation of sources by location.

<table>
<thead>
<tr>
<th>Source</th>
<th>Sites at which consumed</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tree leaf, mean</td>
<td>A1 A2 A3 A4 A5 A6 RIVER</td>
</tr>
<tr>
<td>Tree leaf, harvested</td>
<td>A2 A3 A4 A5 A6 RIVER</td>
</tr>
<tr>
<td>Tree leaf, litter</td>
<td>A1 A2 A3 A4 A5 A6 RIVER</td>
</tr>
<tr>
<td>Rush</td>
<td>A1 A2 A4 A5 A6 RIVER</td>
</tr>
<tr>
<td>Floating OM/pollen/seed</td>
<td>A1 A2 A4 A5 A6 RIVER</td>
</tr>
<tr>
<td>Herb</td>
<td>A1 A2 A3 A4 A5 A6</td>
</tr>
<tr>
<td>Algae</td>
<td>A1 A2 A5 A6 RIVER</td>
</tr>
<tr>
<td>Anabrandic sediment</td>
<td>A1 A2 A5 A6 RIVER</td>
</tr>
<tr>
<td>Billabong suspended matter</td>
<td>A1 A2 A5 A6 RIVER</td>
</tr>
<tr>
<td>River suspended matter</td>
<td>NONE</td>
</tr>
<tr>
<td>Grass</td>
<td>NONE</td>
</tr>
<tr>
<td>River sediment</td>
<td>NONE</td>
</tr>
<tr>
<td>Floodplain sediment</td>
<td>NONE</td>
</tr>
<tr>
<td>Cattle dung</td>
<td>NONE</td>
</tr>
<tr>
<td>Fern</td>
<td>NONE</td>
</tr>
<tr>
<td>Sedge</td>
<td>NONE</td>
</tr>
</tbody>
</table>
Table 7.9  Sources consumed at each location

<table>
<thead>
<tr>
<th>Location</th>
<th>A1</th>
<th>A2</th>
<th>A3</th>
<th>A4</th>
<th>A5</th>
<th>A6</th>
<th>RIVER</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Tree leaf, mean</td>
<td>Tree leaf, mean</td>
<td>Tree leaf, mean</td>
<td>Tree leaf, mean</td>
<td>Tree leaf, mean</td>
<td>Tree leaf, mean</td>
<td>Tree leaf, mean</td>
</tr>
<tr>
<td></td>
<td>Tree leaf, litter</td>
<td>Tree leaf, harvested</td>
<td>Tree leaf, harvested</td>
<td>Tree leaf, harvested</td>
<td>Tree leaf, harvested</td>
<td>Tree leaf, harvested</td>
<td>Tree leaf, harvested</td>
</tr>
<tr>
<td></td>
<td>Rush</td>
<td>Tree leaf, litter</td>
<td>Tree leaf, harvested</td>
<td>Tree leaf, litter</td>
<td>Tree leaf, litter</td>
<td>Tree leaf, litter</td>
<td>Tree leaf, litter</td>
</tr>
<tr>
<td></td>
<td>Floating</td>
<td>Rush</td>
<td>Tree leaf, litter</td>
<td>Rush</td>
<td>Rush</td>
<td>Rush</td>
<td>Rush</td>
</tr>
<tr>
<td></td>
<td>OM/pollen/seed</td>
<td>Floating</td>
<td>Tree leaf, litter</td>
<td>Floating</td>
<td>Floating</td>
<td>Floating</td>
<td>Floating</td>
</tr>
<tr>
<td>Algae</td>
<td>Herb</td>
<td>OM/pollen/seed</td>
<td>Tree leaf, litter</td>
<td>OM/pollen/seed</td>
<td>OM/pollen/seed</td>
<td>OM/pollen/seed</td>
<td>Algae</td>
</tr>
<tr>
<td>Anabranch sediment</td>
<td>Herb</td>
<td>Algae</td>
<td>Anabranch sediment</td>
<td>Algae</td>
<td>Algae</td>
<td>Anabranch sediment</td>
<td>Anabranch sediment</td>
</tr>
<tr>
<td>Billabong suspended matter</td>
<td>Anabranch sediment</td>
<td>Anabranch sediment</td>
<td>Billabong suspended matter</td>
<td>Anabranch sediment</td>
<td>Billabong suspended matter</td>
<td>Billabong suspended matter</td>
<td>Billabong suspended matter</td>
</tr>
</tbody>
</table>
7.6 DISCUSSION

Organisms in the main river channel and from the anabranch billabongs of the Macintyre River share many of the same carbon sources during the winter disconnection phase; however organisms in the main river channel appear to assimilate carbon from fewer sources overall than those in the anabranch billabongs. Organisms in anabranch billabongs are assimilating carbon from a mixture of sources. These sources include floating organic matter (including pollen and seed), leaf litter, rushes, harvested leaves, polygonum, billabong algae, billabong suspended sediments and sediment carbon. Overall, both allochthonous and autochthonous carbon sources support organisms in anabranch billabongs of the Macintyre River during the winter disconnection phase.

Organisms in the main river channel adjacent to anabranches are also assimilating carbon from a variety of sources, including tree leaves, rushes, floating organic matter (including pollen and seed), algae, anabranch sediment carbon and billabong suspended matter. Overall, allochthonous carbon sources appear to be relatively more important than autochthonous sources in this reach of the river channel during the winter disconnection phase.

Importantly, all the sources assimilated by river organisms are found in anabranch channels and billabongs. Sources with the closest delta C values to the mean river organism values include tree and shrub leaves, floating OM (including pollen and seed) and rushes. Leaf litter is apparently more important than initially thought – although feeding trials in the Murray River have suggested that the contribution of tree leaves to benthic invertebrate production in some Australian rivers can be significant (Schulze and Walker 1997). Tree leaves, rushes, floating organic matter and algae may contribute directly to the river from river banks, but the majority of these sources are concentrated in anabranches and their billabongs. River banks in this system, and other Australian dryland rivers, are relatively bare of vegetation. Assimilation of both anabranch sediment sources and billabong suspended matter by river organisms indicates that interaction between the river channel and the anabranches is of some importance. However
Polygonum, which is assimilated by a large number of consumers in anabranch billabongs, does not appear to be of importance to river organisms. This also suggests that organisms that consume polygonum in anabranch billabongs may not play an important role in the trophic structure of the river community itself. This plant is concentrated in anabranch channels in dense stands, and is rarely found on river banks. It is likely that its habit as a fast-growing, shallow and still water specialist, combined with a limited interaction with the main river channel (disconnection phase), has simply restricted its availability to river organisms.

Organisms in the main channel of the Macintyre River are not totally dependent upon predominantly autochthonous carbon sources during the winter disconnection phase. There are several potential explanations for this. During winter, low temperatures and shorter days mean that algal production is significantly reduced (see phytoplankton data), and may not sustain levels sufficient for the main river consumers. Also, the consumer signatures represent integrated diet values over time, and if tissue ‘memory’ is long, signatures will reflect sources consumed during either connection phases or warmer months. The influence of anabranch channels over time appears to stretch through all connection phases. It is possible that injections of anabranch carbon sources during connection events continue to sustain the main river organisms through disconnection periods.

These results indicate that there are substantial differences between patch types in the quality of their major carbon sources. Anabranch sources are the preferred choice. There is some potential for consumption of sources from the main river channel, but only those sources that are also found in anabranch channels (e.g. leaf litter). In contrast, the wider floodplain does not appear to contribute to the diets of aquatic consumers at all during this phase. This is of significant interest, as quantitative spatial analysis of the distribution of total carbon in surface sediments across all three patch types (Chapter 5) indicates that the highest concentration of carbon are found in the floodplain. Thus quantitatively, the floodplain appears to be of greatest relative importance; however the
stable isotope analysis shows that it is actually of little real value during the most
dominant phase in this system - disconnection.

Landscape heterogeneity is an integral part of the functioning of this floodplain river
system. Without the spatial complexity of anabranche channels and their temporal
interactions with the main river channel, carbon sources for riverine consumers are
limited in both quantity and quality. Artificial fragmentation leads to a reduction in
connectivity between anabranche channels and the main river channel. Stable isotope analyses
indicate that such a reduction would result in decreased diversity and quality of carbon
sources available. However natural fragmentation allows carbon sources in anabranche
channels to build up, including higher quality sources like polygonum and algae, and
allows for reproduction of organisms and carbon sources that would not survive in a lotic
environment, but which are high-quality food sources for riverine organisms. It also
allows for initial processing and degradation of ‘tougher’ more refractory sources such as
eucalypt leaf litter, before re-connection flushes the products into the river. Hence
natural fragmentation and connection patterns should be preserved.

7.7 SUMMARY

All of the major carbon sources in the selected anabranche channels of the Macintyre
River system are assimilated by consumers. Despite the large quantities of carbon found
in floodplain sediments, consumers are preferentially assimilating carbon sources found
in anabranche channels. Hydrological connection between anabranche channels and the
parent river channel appears to influence the carbon pools of the parent river channel,
insofar as it either supplies or allows access to carbon sources preferentially assimilated
by riverine consumers. Thus the role of anabranche channels in the floodplain-river
ecosystem is clarified, with stable isotope analysis demonstrating that during the winter
disconnection phase in the Macintyre River system, carbon sources predominantly found
in anabranche channels support both anabranche and river organisms, and that other carbon
sources found in the main river channel and the wider floodplain play a minimal role in
comparison.
Stable isotope studies have been used in food web debates about the relative roles of autotrophic and heterotrophic production, or autochthonous and allochthonous carbon sources in both constricted and large floodplain rivers (Hamilton et al. 1992; Bunn and Boon 1993; Boon and Bunn 1994; Thorp and Delong 1994; Thorp et al. 1998; Thorp and Delong 2002; Bunn et al. 2003). Thorp and Delong (2002, p.546) stated that in the context of whole floodplain river systems, a ‘critical question is the relative importance to metazoan production from autochthonous and allochthonous carbon in seasonally flooded habitat compared to autotrophic production in river channels and slackwater habitats’.

The results for the Macintyre River system indicate that ‘allochthonous’ carbon sources (from anabranches) support consumers in the river channel during the winter disconnection phase in this system, however seasonal changes in temperature, production, and hydrology may increase the importance of autochthonous sources at other times.

More extensive and detailed sampling through space and time, and of more sources and consumers, would provide better resolution of the relative importance of autotrophic and heterotrophic production, or autochthonous vs. allochthonous carbon sources for the Macintyre River as a whole. Rather, this chapter emphasises the importance of landscape heterogeneity and hydrological connectivity in floodplain river systems, and highlights the role of anabranche channels and the value of anabranche carbon sources (both autochthonous and allochthonous) compared to the floodplain and the river channel as landscape patches.
Key messages:
During the winter disconnection phase in the Macintyre River system:

- Carbon sources that are predominantly found in anabranch channels support both anabranch and river organisms.
  - These include tree leaves, rushes, floating organic matter (including pollen and seed), epiphytic and benthic algae, anabranch sediment carbon and billabong suspended matter
- Other carbon sources found in the main river channel and the wider floodplain appear to play a minimal role in comparison
  - These include grasses, floodplain sediment, river sediment and river suspended matter.
- Hydrological connection between anabranch channels and the parent river channel appears to either supply or allow access to anabranch carbon sources preferentially assimilated by riverine consumers
CHAPTER EIGHT: FRAGMENTATION BY WATER RESOURCE DEVELOPMENT

8.1 INTRODUCTION ................................................................................................ 291

8.2 METHOD .......................................................................................................... 297

8.2.1 Calculation of anabranch commence to flow discharges...................... 297

8.2.2 Modelling flow change ........................................................................... 299

8.2.3 Modelling changes in carbon availability .............................................. 299

8.3 RESULTS: MODELLED REGIMES........................................................................ 301

8.3.1 Natural vs. developed flow ..................................................................... 301

8.3.2 Natural vs. developed carbon availability............................................. 302

8.4 DISCUSSION ..................................................................................................... 305

  Reductions in event frequency ........................................................................ 306
  Reductions in event duration ........................................................................... 307
  Reductions to inundation extent ...................................................................... 308
  Reductions in landscape complexity ............................................................... 309

8.5 SUMMARY ........................................................................................................ 311
CHAPTER EIGHT: FRAGMENTATION BY WATER
RESOURCE DEVELOPMENT

8.1 INTRODUCTION

Landscape ecology theory suggests that fragmentation of the landscape is responsible for a great deal of the loss of biodiversity witnessed across the globe (Dynesius and Nilsson 1994; Debinski and Holt 2000; Haila 2002). Artificial or human-induced habitat fragmentation of ecosystems in its basic sense negates all the benefits of connectivity, as well as many of the benefits of ‘natural’ fragmentation. Fragmentation not only prevents the physical dispersal of flora and fauna through the landscape, as emphasised by landscape ecology literature – it also often prevents the transport, cycling and exchange of vital basic chemical elements and nutrients (Dynesius and Nilsson 1994; Fahrig and Merriam 1994; Debinski and Holt 2000; Jackson et al. 2001; Woodward and Hildrew 2002). In a system such as a floodplain river, where the exchange of carbon and nutrients via flooding or hydrological connection is fundamental to its continued productivity and survival, reductions in connectivity have far-reaching implications for the ecosystem (Power et al. 1995).

Water resource development includes a variety of activities such as dam or reservoir and weir building and operation (regulation for irrigation, human consumption and power generation). Other more indirect forms of water resource development include abstraction and diversion of water from the river channel for irrigation and human consumption, the building of levees to contain floods in the main channel or to contain water on the floodplain for agricultural use, and inter-basin transfers, which transfer water across catchment boundaries to supplement perceived deficiencies (Davies et al. 1994). Dynesius and Nisson (1994) found that seventy-seven percent of the total water discharge of the 139 largest river systems in North America north of Mexico, in Europe and in the republics of the former Soviet Union was strongly or moderately affected by fragmentation of the river channels by dams and by water regulation resulting from reservoir operation, inter-basin transfers and irrigation. They deduced from these results
that many types of river ecosystems had been lost and that the populations of many riverine species had become highly fragmented (Dynesius and Nilsson 1994).

Despite being part of the driest inhabited continent in the world, the semi-arid floodplain rivers of Australia are under constantly increasing pressure from water resource developments, which proceed based on methods and expectations derived from much wetter climates. In an environment of extreme climatic variability and unpredictability, dams, weirs and inter basin water transfers provide controlled and constant water supply for a growing agricultural industry and for residential use (Davies et al. 1994; Boulton et al. 2000; Kingsford 2000). In addition, floodplain development in the form of large on-farm water storages and levees has had major effects on the flow regime of inland rivers (Johnson et al. 1995; Kingsford 2000). Irrigated agriculture is the dominant influence over water resource development in Australia, is growing very rapidly, and is most prominent in dominantly dryland regions like the Murray-Darling Basin (CRBIA 1992; Kingsford 1999; 2000), of which the Macintyre River catchment forms a part (Walker 1985). Irrigated agriculture, while only taking up about 1% of the land area of the Murray-Darling Basin, accounts for about 90% of the abstracted water in the catchment (Maheshwari et al. 1995). Significant environmental problems have been attributed to these changes (Walker 1985). Yet development of semi-arid floodplain rivers in Australia continues to escalate (A.S.L. 2000; Thoms and Sheldon 2000b; 2000a). Agricultural practices and urban and rural communities in these areas demand ever-increasing quantities of water from river systems that are allogenic (derive their water from upstream mountainous areas and flow through relatively dry landscapes) and that under natural conditions frequently stop flowing altogether. This demand changes the natural character of connectivity and fragmentation in dryland floodplain river systems, with important consequences for their ecology.

The effects of water resource development on river systems have been well documented for some time (Petts 1980; 1984; Walker 1985; Close 1990). Water resource development can change the hydrological regime of a floodplain river system in a number of ways, all of which can greatly alter the level of connectivity between the parent river and its
floodplain features (Walker et al. 1992; Walker and Thoms 1993; Maheshwari et al. 1995; Walker et al. 1997; Kingsford and Porter 1999; Kingsford et al. 1999; Kingsford 2000; Thoms and Sheldon 2000b; McGinness and Thoms 2002; McGinness et al. 2002; Thoms et al. 2005). These changes can occur at a number of spatial and temporal scales, and effects also vary between locations. Irrigation storages or dams can generate short-term variable flows during peak demand and constant flows at other times, while other developments may also cause long-term reductions in flow through diversions and evaporation (Walker 1985). The character of individual flow events and floods (e.g. size and duration) is also often heavily affected. For example, Maheshwari et al. (1995) found that average annual floods had decreased in size by 50% on the Murray River since water resource development in 1920, while larger floods were not affected. Similarly, in the Barwon-Darling, Thoms and Sheldon (2000) reported reductions of between 35 and 70% for floods with an average recurrence interval of <2 years, while larger flooding events (1 in 25-year events) were reduced by between 9 and 36%. Water resource development has also affected the duration of individual flooding events. This change can be seen most clearly in the receding limb of a flood, with a steepening of the limb and hence faster recession time (Thoms and Sheldon 2000b).

Median river flows are also often reduced by water resource development. A reduction of 73% in median daily flows has been found in both the Barwon-Darling and Murray Rivers, over a 70 year period (Thoms and Sheldon 2000b). Low flow levels have in general become more stable (Boulton et al. 2000; Thoms and Sheldon 2000b). In addition, relative variation from one season to the next (seasonality) of flooding is frequently heavily affected by water resource development (Petts 1984). In the Barwon-Darling, seasonality has been dampened with summer monthly flows being reduced by up to 56% compared to 36% in winter (Thoms and Sheldon 2000b). The upper section of the Murray has also experienced a dampening of seasonality, as well as a shift in the seasonal distribution of flows with high flows now occurring in late summer and autumn instead of late winter and early spring as they did under natural conditions (Walker 1985; Maheshwari et al. 1995).
While irrigated agriculture heavily influences the natural flow regime of lowland floodplain rivers, the associated infrastructure also changes the connectivity of the floodplain with the river. The development of on-farm storages, channel systems, and levee banks to protect crops from flooding, and the damming of natural floodplain channels has lead to segregation of the floodplain both in a spatial and flow related sense. Research on the rehabilitation of degraded river ecosystems has recognised that ‘conventional exploitative development acts to isolate a river from its watershed, primarily by inactivating the biotic connections between a river system and the riparian component of the watershed’ (Regier et al. 1989, p.88). Flow regulation disrupts both hydrological and ecological connectivity, as well as natural fragmentation processes (Ward and Stanford 1995). Disruption or prevention of the hydrological connection between floodplain features and their parent river eliminates many of the advantages that human societies have come to depend upon from these systems. For example, levees prevent the natural nutrient replenishment once provided by floodwater to floodplains (and used for centuries to support crops), simultaneously removing the buffering effect that floodplains provide in terms of reducing nutrient loads in the river (Sparks 1995). They also interrupt lateral sediment transport, with serious consequences for sediment loads in the river channel, the morphology of the river channel and the floodplain, and associated nutrient transport and deposition (Sparks 1995). Channelisation and flow regulation often confine the river to a single channel and deny it access to floodplain features, decoupling the linked systems and causing degradation (Regier et al. 1989). In Australia, with no controls of the harvesting of local runoff or ‘overland flow’ during high flow periods, the amount of water that returns to the system after flowing out onto the floodplain has been greatly reduced (Kingsford 1999; 2000; Thoms and Sheldon 2000b). The development of levee banks around agricultural fields has resulted in vast areas of the floodplain now being cut off from the river floodplain system. Therefore there has been a reduction in the area of floodplain that is available for the release and deposition of sediment, carbon and nutrients, and for use by aquatic fauna (Johnson et al. 1995; Kingsford and Porter 1999; Kingsford et al. 1999).
Many floodplain wetland and riparian communities have evolved to be reliant on the timing, magnitude and frequency of flooding. A change to this regime causes a change in community composition and a reduction of diversity within these environments (Kingsford 2000). Regulation can reduce the duration and frequency of floods that partially inundate floodplain forests (Bren and Gibbs 1986; Bren 1987; Bren et al. 1987), and alter the seasonal pattern of flooding (Close 1990). These changes can reduce the area suitable for waterbird breeding in floodplain forests (Bren 1987), and erratic or rapid changes in water levels can cause waterbirds to desert their young, trees to die, and aquatic plant and invertebrate populations to collapse (Management guideline no. 6; Briggs and Thornton 1999). Flooding also determines vegetation abundance, patterns, composition and vigour in these environments (Bren and Gibbs 1986; Chesterfield 1986). These changes in vegetation structure and composition caused by a change in connection regimes potentially influence the quality and quantity of carbon exchanged between patches in this river floodplain system, with repercussions for the functioning of the entire ecosystem.

In the Macintyre River system demand for water has resulted in massive abstractions of water from rivers for irrigation and storage on the floodplain, as well as the installation of numerous dams and weirs on both the parent river and anabranch channels. Many anabranch channels have artificially constructed levees and weirs at their entrances, exits or other locations along their length, in order to prevent, control or contain water entering them during high flows. Temporal changes may occur due to factors such as upstream abstraction of water from the parent river, pumping into the anabranch, or the dictation of flow volume, frequency or duration by the control of an upstream dam.

Changes to the hydrology of floodplain rivers alter hydrological connectivity within these systems (Sheldon et al. 2002). These changes affect the frequency, size, duration and timing of individual connection events. Ultimately, all impacts integrate to change the temporal nature of flow connection, from preventing it altogether to permanent connection. The results of such alteration to anabranch channels can range from ‘permanent’ inundation of the anabranch channel to ‘permanent’ isolation of the
anabranch channel from its parent river. Either type of change has the potential to significantly alter the carbon quantities and composition found in the anabranch, compared to those found in anabranch channels that alternate between disconnection (drying) and reconnection (wetting) to the parent river (different phases of connection). However the specific dynamics of these alterations are not well understood. The change and the result are easily observed, but what of the mechanisms between them? How do the changes that occur due to water resource development uniquely function in semi-arid systems? How do these changes influence hydrological connectivity with specific floodplain features such as anabranch channels? How might anabranch channels play a special role in increasing or maintaining connectivity in artificially fragmented systems? And how might carbon pools change in these unique systems as a result of artificial fragmentation from water resource development?

This chapter aims to evaluate the influence of water resource development upon hydrological connectivity and carbon pools in the anabranch channels and river channel of the lower Macintyre River.

The objectives are to:

1. Model the spatial and temporal hydrological fragmentation of anabranch channels and their parent river channels during two different flow scenarios; and
2. Model the effect of spatial and temporal fragmentation upon carbon across the landscape for the two different flow scenarios

After initial broad-scale analysis of potential carbon loads pre- and post-development, the influence of changing flow regimes will be discussed with respect to the occurrence and duration of flow connection phases described in the conceptual model; and the implications of changes to flow connection phases in terms of carbon pools in anabranches, the main river channel, and the ecosystem as a whole.
8.2 Method

8.2.1 Calculation of anabranch commence to flow discharges

Cross-sectional data were collected at every anabranch outlet in the study area and in the river channel directly above or below each outlet, depending on riparian vegetation density and the ability to get a clear line of sight required for accurate surveying. The exact location of each anabranch outlet ‘sill level’ was surveyed in relation to the river cross-sections. All surveying was carried out using a TOPCON electronic total station (GTS - 210) and reflector staff. In areas too deep to survey, survey points were established on either side of the pool and then a portable depth sounder was used with distances from the total station estimated. These were later transformed to give a full profile of the channel. Channel cross sections were then entered into the 'Channel' computer program (Thoms and Ranson 2000) where channel shape parameters such as wetted perimeter, cross sectional area, and hydraulic radius were calculated (Chapter 4).

The commence to flow (CTF) discharge of individual anabranches was determined using the Manning equation (Equation 1), widely used for determining open channel flow (Gordon et al. 1992). The Manning equation used for 'commence to flow' calculations is represented by:

\[ Q = \frac{1}{n} AR^{2/3}S^{1/2} \]  \hspace{1cm} (Equation 1)

Where:
- \( Q \) is the discharge (m\(^3\)/s)
- \( n \) is a coefficient referred to as 'Manning n'
- \( A \) is the cross sectional area of the channel (m\(^2\))
- \( S \) is the slope of the reach, and
- \( R \) is the hydraulic radius (m)

Area and hydraulic radius values were calculated from each individual anabranch cross-section. Slope values were calculated from cross-sections surveyed at intervals down the reach. These sections were surveyed to Australian Height Datum (AHD) and were supplied by the New South Wales Department of Land and Water Conservation (NSW DLWC), Connell Wagner Pty Ltd. and SMK irrigation consultants. The Manning ‘n’
value generally increases as the effects of turbulence and flow retardance increase
(Gordon et al. 1992). There are several methods for selecting the appropriate n value. For
this chapter the Manning n value was estimated using the method recommended by
Cowan (1956) and verified against specific gaugings in the study reach.

Commence to flow (CTF) values were calculated for the entry and exit (if present) of
each anabranch channel in the study reach. At this point it should be stressed that the CTF
value of a channel is the discharge required to initiate inundation of that channel, it does
not imply full connection. For anabranches in this reach, complete connection discharges
are calculated for levels approximately one metre higher than their commence to flow
stage height, as recommended by Thoms et al. (1996).

All commence to flow discharges stated in this chapter are relative to the Goondiwindi
town gauge, because this gauging station is the main reference for river flows used by
managers and property owners in the study area. Main channel dimensions of the
Macintyre River decrease down the study reach. For this reason, raw CTF discharges
calculated for channels in the lower reaches of the study area were re-calculated using
conversion equations to correspond with the Goondiwindi gauge readings. These
conversion equations were formulated by plotting discharges from the Terrewah and
Boomi gauging stations against discharge values from the Goondiwindi gauge. Equations
for the line of best fit were calculated for different sections of these graphs. Anabranches
were grouped according to their proximity to the gauging stations and the relevant
equation was applied depending on the raw CTF discharge of these channels (Table 8.1).

<table>
<thead>
<tr>
<th>Gauge (discharge)</th>
<th>Equation</th>
<th>R² Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Terrewah</td>
<td></td>
<td></td>
</tr>
<tr>
<td>&lt;8500 MLD @ Terrewah</td>
<td>( y = 2^{-0.08}x^3 - 0.0002x^2 + 1.3118x - \frac{0.111}{0.111} )</td>
<td>0.9937</td>
</tr>
<tr>
<td>8500 – 9500 MLD @ Terrewah</td>
<td>( y = 2.676x - 14503 )</td>
<td>0.9325</td>
</tr>
<tr>
<td>&gt;9500 MLD @ Terrewah</td>
<td>( y = 4^{-20}x^{5.8801} )</td>
<td>0.9897</td>
</tr>
</tbody>
</table>

Table 8.1 Conversion equations used to calibrate discharge values for changes in channel dimensions downstream. ‘y’ is the projected Goondiwindi gauge value and ‘x’ is the raw commence to flow discharge.
8.2.2 Modelling flow change

The rapid rate of water resource development in the Macintyre River catchment and the natural variability of flows preclude the use of historical hydrological data. Therefore, fragmentation of anabranch channels from the parent river was modelled using simulated ‘natural’ and ‘current’ hydrological data. Simulated daily discharge data was obtained from the New South Wales Department of Land and Water Conservation (NSW DLWC) Integrated Quantity Quality Model (IQQM; (Black et al. 1997)). A full description of the model, its processes in relation to the Border Rivers, and its reliability, is provided by DNR (1999) and Black et al. (1997). Simulated ‘natural’ flows were compared with simulated ‘developed’ flows for the period 1900-1998 for the Goondiwindi gauging station. The ‘natural’ flow was simulated with a zero setting for flow regulating structures, abstractions of water and catchment development, utilising long-term climatic conditions. The ‘developed’ simulated flow used water and catchment development conditions present in 1997-98 combined with long-term climatic conditions.

Periods of connection and disconnection for the individual anabranch channels were determined from ‘SPELL’ analysis (Gordon et al. 1992). This analysis allows the operator to set a determined threshold value. This threshold is then passed over a dataset and an output is provided detailing the number of individual flow events above this threshold and the duration of each flow event or ‘spell’. Further descriptive statistics, such as total days wet and dry, and the mean, minimum and maximum duration of flows were then calculated for both ‘natural’ and ‘current’ flow scenarios.

8.2.3 Modelling changes in carbon availability

The potential availability of dissolved organic carbon (DOC) from the various anabranch channels of the Macintyre River was also calculated for each of the ‘natural’ and ‘developed’ flow scenarios. Potential dissolved organic carbon release during each of the two scenarios was calculated using data from the laboratory experiment described in
Chapter 6. Daily carbon concentrations were therefore available for a 6-day inundation event, equivalent to the median duration of natural connection events. Since these data are derived from sediments from a single anabranch (anabranch 3) and applied to all six anabranches, there are inherent assumptions that a) DOC release is the same spatially and temporally for all anabranches; and b) DOC release follows the same spatial within-anabranch pattern across sites. This method yields an estimate of potential carbon loads available that is useful as an indicator of potential change.

The surface area of each anabranch was estimated by multiplying average wetted perimeter (derived from surveys) with channel length. The surface area of each of the sites (entry, middle, and exit) was also estimated by multiplying the wetted perimeter of each of the three specific sites with a third of the total channel length. Dissolved organic carbon concentrations (mg L\(^{-1}\)) were transformed to mass units by multiplying by two litres of floodwater (surface water depth ~20 mm; Chapter 6), yielding mass (mg) per unit area (m\(^2\)). The potential loads of dissolved organic carbon available from entire individual anabranch channels during inundation were estimated by multiplying dissolved organic carbon loads per unit area by the total surface area of each anabranch channel. Potential loads were also estimated for individual sites/transects.

Comparisons of the potential dissolved organic carbon loads available from each anabranch over the entire modelled period were made by multiplying the total anabranch carbon loads made available during a 6-day event by the number of events that occurred during each scenario for each anabranch. Comparisons of the potential dissolved organic carbon loads available from each anabranch during individual flow events were made by noting the ‘median days wet’ for events in each modelled scenario, and calculating DOC loads for the corresponding number of days inundated (from the experimental data). This accounted for the changes in the median duration of events between the two scenarios.
8.3 RESULTS: MODELLLED REGIMES

8.3.1 Natural vs. developed flow

A total of fourteen anabranch channels were selected for flow modelling, including the six that form the focus of preceding chapters of this dissertation, as described in McGinness et al. (2002) and Thoms et al. (2005). The commence to flow (CTF) discharges of these fourteen anabranch channels were calculated to range from 1,195 to 47,367 Ml day\(^{-1}\). Analysis of the CTF values suggested that there were groups of anabranches in terms of hydrological connection, where relatively small increases in discharge resulted in a relatively large increase in the number of anabranches connected to the main river channel (Table 8.2; (Southwell 2002). Most of the six anabranches focused on in this dissertation fit into group 1 (CTF < 5000 Ml day\(^{-1}\)), except anabranches 4 and 6, which fit into group 4.

<table>
<thead>
<tr>
<th>Group</th>
<th>CTF (Ml day(^{-1}))</th>
<th>Anabranch</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0 - 5,000</td>
<td>1,2,3,5</td>
</tr>
<tr>
<td>2</td>
<td>5 – 10,000</td>
<td>N/A</td>
</tr>
<tr>
<td>3</td>
<td>10 – 20,000</td>
<td>N/A</td>
</tr>
<tr>
<td>4</td>
<td>20 – 50,000</td>
<td>4, 6</td>
</tr>
</tbody>
</table>

Using the simulated natural daily flow data the anabranch channels were calculated to have experienced between 107 and 468 wetting events for the period 1900-1998, depending upon the CTF discharge for each anabranch. Lower discharge anabranch channels (Group 1) experienced the greatest number of wetting events (n=468), with a median duration of 6 days under natural flows. Higher discharge channels (Group 4), experienced 81 wetting events with a median duration of 3 days. The character of hydrological connectivity changed with water resource development. All anabranches experienced a reduction in the frequency and duration of wetting with water resource development, but this differed between anabranch groups (Table 8.3). There was a 21 % reduction in the number of times Group 4 anabranches experienced wetting compared to a 13 % reduction for Group 1 anabranches.
Table 8.3  The wetting of anabranch groups under simulated natural (N) conditions and current (C) levels of water resource development and the percent difference (% Δ).

<table>
<thead>
<tr>
<th>Group</th>
<th>Flow scenario</th>
<th>N°. of events</th>
<th>Total days wet</th>
<th>Median days wet</th>
<th>Total days dry</th>
<th>Median days dry</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>N</td>
<td>468</td>
<td>3555</td>
<td>6</td>
<td>32512</td>
<td>25</td>
</tr>
<tr>
<td></td>
<td>C</td>
<td>407</td>
<td>2835</td>
<td>5</td>
<td>33232</td>
<td>33</td>
</tr>
<tr>
<td></td>
<td>% Δ</td>
<td>-13.3</td>
<td>-20.3</td>
<td>-16.7</td>
<td>2.3</td>
<td>29.4</td>
</tr>
<tr>
<td>2</td>
<td>N</td>
<td>322</td>
<td>1831</td>
<td>4</td>
<td>34236</td>
<td>46</td>
</tr>
<tr>
<td></td>
<td>C</td>
<td>287</td>
<td>1460</td>
<td>4</td>
<td>34607</td>
<td>45</td>
</tr>
<tr>
<td></td>
<td>% Δ</td>
<td>-10.9</td>
<td>-20.3</td>
<td>0.0</td>
<td>1.1</td>
<td>-2.2</td>
</tr>
<tr>
<td>3</td>
<td>N</td>
<td>192</td>
<td>850</td>
<td>4</td>
<td>35217</td>
<td>72</td>
</tr>
<tr>
<td></td>
<td>C</td>
<td>161</td>
<td>692</td>
<td>3</td>
<td>35375</td>
<td>95</td>
</tr>
<tr>
<td></td>
<td>% Δ</td>
<td>-16.1</td>
<td>-18.6</td>
<td>-25.0</td>
<td>0.4</td>
<td>31.0</td>
</tr>
<tr>
<td>4</td>
<td>N</td>
<td>81</td>
<td>249</td>
<td>3</td>
<td>35818</td>
<td>193</td>
</tr>
<tr>
<td></td>
<td>C</td>
<td>64</td>
<td>201</td>
<td>3</td>
<td>35866</td>
<td>226</td>
</tr>
<tr>
<td></td>
<td>% Δ</td>
<td>-21.0</td>
<td>-19.3</td>
<td>0.0</td>
<td>0.1</td>
<td>17.1</td>
</tr>
</tbody>
</table>

8.3.2  Natural vs. developed carbon availability

Approximately 1517 tonnes of dissolved organic carbon would have been made available from the six anabranch channels under ‘natural’ conditions compared to 1317 tonnes under ‘developed’ conditions, for the period 1900-1998. Differences within anabranches ranged from 2 tonnes reduction (anabranch 4) to 121 tonnes reduction (anabranch 2). Hydrological changes had a relatively greater impact on the Group 4 anabranches (study anabranches 4 and 6) where there was an approximately 21 % reduction in potential dissolved organic carbon supply (Table 8.4; Figure 8.1).

Table 8.4  The influence of hydrological change on potential DOC availability from anabranches over the entire modelled period.

<table>
<thead>
<tr>
<th>Anabranch</th>
<th>NATURAL</th>
<th>DEVELOPED</th>
<th>Difference</th>
<th>% Reduction</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>93</td>
<td>81</td>
<td>12</td>
<td>13</td>
</tr>
<tr>
<td>2</td>
<td>929</td>
<td>808</td>
<td>121</td>
<td>13</td>
</tr>
<tr>
<td>3</td>
<td>278</td>
<td>242</td>
<td>36</td>
<td>13</td>
</tr>
<tr>
<td>4</td>
<td>9</td>
<td>7</td>
<td>2</td>
<td>21</td>
</tr>
<tr>
<td>5</td>
<td>195</td>
<td>169</td>
<td>25</td>
<td>13</td>
</tr>
<tr>
<td>6</td>
<td>14</td>
<td>11</td>
<td>3</td>
<td>21</td>
</tr>
<tr>
<td>TOTAL</td>
<td>1517</td>
<td>1317</td>
<td>200</td>
<td>13</td>
</tr>
</tbody>
</table>
The influence of development was even greater in terms of dissolved organic carbon supply from individual flow events. Reductions in flow duration for Group 1 anabranches (study anabranches 1, 2, 3 and 5) resulted in a 28% loss of potential dissolved organic carbon loads (Table 8.5; Figure 8.2).

Table 8.5  The influence of hydrological change on potential DOC availability from anabranches during individual flow events.

<table>
<thead>
<tr>
<th>Anabranch</th>
<th>NATURAL</th>
<th>DEVELOPED</th>
<th>Difference</th>
<th>% Reduction</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>198</td>
<td>143</td>
<td>56</td>
<td>28</td>
</tr>
<tr>
<td>2</td>
<td>1984</td>
<td>1425</td>
<td>559</td>
<td>28</td>
</tr>
<tr>
<td>3</td>
<td>594</td>
<td>427</td>
<td>167</td>
<td>28</td>
</tr>
<tr>
<td>4</td>
<td>82</td>
<td>82</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>5</td>
<td>416</td>
<td>299</td>
<td>117</td>
<td>28</td>
</tr>
<tr>
<td>6</td>
<td>133</td>
<td>133</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>TOTAL</td>
<td>3407</td>
<td>2508</td>
<td>899</td>
<td>26</td>
</tr>
</tbody>
</table>
Figure 8.1 Potential DOC release over entire modelled period from each anabranch for each flow scenario (natural vs. developed).

Figure 8.2 Potential DOC release during individual flow events from each anabranch for each flow scenario (natural vs. developed).
8.4 Discussion

Water resource development changes have been documented in several large dryland rivers, with emphasis placed upon the critical implications for the ecology of these systems (Davies et al. 1994; Maheshwari et al. 1995; Thoms and Sheldon 2000b; 2000a). Of particular importance is the complex and long term nature of the changes that take place, and the need for interdisciplinary acknowledgement that both river and floodplain environments are changed (Davies et al. 1994). These environments are altered primarily through changes to hydrological connectivity, which can be naturally highly variable, creating natural fragmentation of floodplain river landscape patches over time and space. These patterns and processes of natural connection and fragmentation can significantly influence the quantity and quality of materials and their transformations in floodplain river ecosystems (Chapter 6). However water resource development creates artificial levels of fragmentation, by altering connectivity through anthropogenic change. This chapter illustrates the nature of some of these changes in a typical Australian dryland floodplain river system.

The flow regime of the Macintyre River has changed significantly because of water resource development. Consequently, hydrological connection and fragmentation of anabranche channels has also changed (Table 8.3), with associated reductions in the availability of a significant carbon source (dissolved organic carbon; Table 8.4). The significance of these changes is emphasised by the physical dominance of anabranches as patches in this landscape, where they comprise 62 percent of the total channel length of the lower Macintyre River (Southwell 2002). In addition, anabranche channels occupy intermediate positions between the main river channel and the adjacent floodplain, both spatially and temporally, and form important connections between the more traditionally recognised patches in floodplain river systems. Previous chapters have also demonstrated their intermediate position in terms of carbon pools, and their consequent importance in terms of carbon dynamics, over both space and time. Thus anabranche channels have a pivotal role, geomorphologically, hydrologically, and ecologically, and changes imposed upon them have implications for the functioning and rehabilitation of entire dryland...
floodplain river systems. Yet there has been limited study of the influence of water resource development on anabranhcing systems and their functioning.

The availability of the various carbon sources within anabranh channels is dependent upon the presence or absence of the four connection phases described in the conceptual model (Chapter 3). The occurrence of these phases has changed in the lower Macintyre River system because of reductions in the frequency and magnitude of flow events, reducing connectivity with anabranh channels in three primary ways:

1. by reducing the frequency of connection (because flows no longer reach the commence-to-flow (CTF) or sill level of the anabranh channels);
2. by reducing the duration of inundation; and
3. by reducing the extent of inundation (e.g. anabranh channels become only partially connected rather than completely connected).

All of these changes have specific impacts upon connection phases, and potential impacts upon the carbon dynamics of the system, as described below.

**Reductions in event frequency**

In the Macintyre River system, flow events sufficient to connect anabranh channels with the main river channel have been reduced in frequency by between 10% and 21%. Subsequently, the dominance and duration of the disconnection phase has been increased. As described for drought in rivers (Lake 2003), this has direct effects in terms of the loss of inundation, and indirect effects generated by the loss of water volume in billabongs, that affect water quality and resource availability that in turn affect the biota. For example, in the side channels of the Danube river, long periods of disconnection increased grazing impacts on phytoplankton concentrations (Hein *et al.* 1999), reducing the concentration of that resource and potentially changing overall energy pathways in the water column. Isolated floodplain waterbodies such as billabongs can be temporary hotspots (Lake 2003), as seen for dissolved organic carbon and phytoplankton in the Macintyre River system (Chapters 5 and 6). However during extended periods of disconnection such as those induced by anthropogenic flow change, anabranh billabongs are more likely to dry out completely before re-connection occurs with the main river.
channel. Consequently, the relatively more labile food energy materials held and produced by billabongs will not be immediately available when connection takes place, forcing organisms of the main river channel ecosystem to rely on other sources. As for other stream channels in drought, anabranch channels during the disconnection phase can also retain large amounts of various refractory carbon sources, that are available for export downstream during inundation (Lake 2003). However less frequent inundation isolates these sources from the system over time, and their quality when finally inundated is also potentially lower. Hence the loss of hydrological connection entails the loss of both labile and refractory carbon sources from the system over time. Increases in the duration of the disconnection phase in these systems therefore both increase fragmentation and reduce hydrological connectivity, creating ‘artificial’ fragmentation, and anthropogenic drought (Lake 2003).

**Reductions in event duration**

Water resource development in this system has also reduced the duration of connection events between anabranch channels and the river (anabranch CTF groups 1 & 4). In effect, these changes reduce inundation time for partial connection, complete connection and the draining phase. Ecological processes associated with inundation of the dry channel and flushing of the billabongs must therefore be unnaturally compressed in terms of time, making them limited or not viable. For example, benthic metabolism responds to changes in duration of inundation. The biological breakdown of organic matter by microbiota depends largely on contact time with water (Pusch et al. 1998), which is reduced by decreased duration of inundation. Microbial biofilms are key organizers and controllers of food webs in these systems; hence significant changes to their function have repercussions for the entire system (Sparling and Ross 1988; Qui and McComb 1995; Findlay and Sinsabaugh 1999; Robertson et al. 1999; Strauss and Lamberti 2002; Woodward and Hildrew 2002).
Reductions to inundation extent

The spatial extent of inundation of anabranch channels is dependent upon both the magnitude and duration of flow events sufficient to cross the commence-to-flow thresholds and continue to traverse the channels. When both magnitude and duration are reduced, complete connection of entire anabranch channels will be less frequent. Under natural conditions, partial connection is usually followed by complete connection; however it may also be followed immediately by the draining phase, depending upon the geomorphology of the anabranch channel and the character of the flow hydrograph. Changes to flows in the Macintyre River system due to water resource development increase the likelihood of a direct partial connection – draining phase path over time (shaded arrows). More flow events will achieve only partial connection, and revert to draining immediately afterward (Figure 8.3).

Figure 8.3 Phases of connection between anabranch channels and the parent river channel.

As a result, less inundated sediment area is available to release dissolved organic carbon, and other carbon sources in sections of the anabranch channels not connected are isolated from the river channel and its consumers. Replenishment of billabongs at middle sites would be less frequent. Moreover, previous chapters (5 and 6) have demonstrated high concentrations of carbon sources toward the ‘middle’ sites of anabranches – those sites most distant from the entry and exit points. These ‘middle’ sites are generally not
reached by floodwater during partial connection, and their relative importance in terms of both quantity and quality of carbon sources makes the loss of the complete connection phase and their subsequent isolation significant. Thus this chapter reveals potentially important influences of water resource development upon not only hydrological connections, but also on the processes and exchanges that they facilitate between patches in this flood plain-river landscape.

**Reductions in landscape complexity**

Water resource development usually results in flow regulation, and related reductions in channel forming flows (Kellerhals and Church 1989). Hydrological change has the potential to alter the physical structure of floodplain-river landscapes (Gurnell and Petts 2002) as well as the distribution and availability of biological resources (Gurnell *et al.* 2002). Flow regulation usually reduces ‘channel forming flows’ by elimination of flood peaks, while also altering sediment transport by installing dams and other barriers, and changing water velocities, depth, and pulse frequency (Kellerhals and Church 1989). Together with interruption of sediment transport by dams and weirs, this changes not only the hydrology, geomorphology and hence ecology of the main river channel, but also the development and maintenance of anabranch channels and other floodplain features. Thus landscape complexity is reduced, with concomitant reductions in productivity and biodiversity.

A similar loss of landscape complexity and functionality over time is apparent in the reach of the Macintyre River examined by this study. Floodplain river geomorphic patches such as anabranch channels physically influence the impacts of increasing or decreasing discharge and connection events, and therefore also control the surficial exchange of carbon between the floodplain, its features, and the river channel. Although hydrological connection moves particulate carbon sources such as wood, leaves and fine organic matter, including bacteria, within and between landscape patches, the physical nature of the landscape patches themselves also influences the quantity and quality of carbon deposited or released. This interaction between hydrology, geomorphology and ecology increases complexity and variability in the system at multiple scales, thereby
increasing the functionality and resilience of these systems (Amoros and Bornette 2002). Reductions in hydrological connectivity (such as those demonstrated in this chapter) reduce this complexity and variability by effectively removing anabranch channels from the landscape, both spatially and temporally, with potentially negative implications for system sustainability.

‘Environmental flows’ are a relatively recent innovation that attempts to restore hydrological connectivity (and hence natural dynamics) in rivers influenced by water resource development. They comprise water that is left in a river system or released into it to manage the health of the channel, banks, wetlands, floodplains and estuaries. In Australia and New Zealand, the goal of environmental flows is to sustain and where necessary restore ecological processes and biodiversity of water dependent ecosystems (ARMCANZ & ANZECC 1996 cited by Arthington and Zalucki 1998). Debate has occurred regarding exactly how much water is needed, and when and for how long it should be supplied. A comparative evaluation of environmental flow assessment techniques (Arthington and Zalucki 1998) reviewed techniques for assessing environmental flow requirements ranging from ‘simplistic use of the hydrological record to establish minimum and flushing flows to sophisticated modelling procedures linking changes in river discharge with geomorphological and ecological response’ (Arthington and Zalucki 1998). ‘Environmental flows’ are now key components of floodplain river management strategies (Burgess and Thoms 1997; Thoms and Cullen 1998; Thoms and Swirepik 1998; Kingsford 1999), yet their exact benefits are still being evaluated (Mitchell et al. 1999; Thoms et al. 2000). Knowledge of the role of anabranches and the influence of water resource development would aid in evaluation and targeting of environmental flows. The effective management and rehabilitation of ecosystems affected by water resource development requires recognition of both the spatial and temporal dimensions of fragmentation. While it may not be possible to re-establish pre-development connectivity regimes in this system (because of the reliance of so many stakeholders on water abstraction), this information produced by this study may be useful to provide some direction. The importance of landscape complexity and especially the presence and contribution of anabranch channels for long-term sustainability of the
A diversity of anabranch channel types as part of the landscape mosaic could be preserved through management of land development and also of flow regimes.

Anabranch channels are important patches in the landscape, in that they contain large amounts of high-quality carbon that are potentially available to the main river channel ecosystem during connection phases. There are complex spatial and temporal factors determining actual availability of anabranch carbon for the river when connection occurs. The modelled data presented in this chapter indicates that changes in the character of hydrological connection may have resulted in changes to the relative quantities of particular types of carbon (food energy) available over time, with subsequent implications for the transfer of energy through the food web and hence also for the functioning of the ecosystem as a whole. While water resource development provides significant benefits to human users of this ecosystem in the short term, the long-term integrity of the landscape is being eroded. Re-connection of anabranch channels via environmental flows should be considered as an option that may provide significant benefits to the system at relatively low cost, compared to attempting to reconnect the entire floodplain surface or other rehabilitation works.

8.5 **Summary**

This chapter builds on information produced by previous sections regarding the potential roles of hydrological connectivity, fragmentation and anabranch channels, in order to model the potential influences of water resource development upon a semi-arid floodplain river ecosystem. It shows that changes to phases of connection and fragmentation following water resource development change carbon availability and hence have the potential to change ecosystem function. The results demonstrate that the availability of the various carbon sources accumulated within anabranch channels during the disconnection phase, and released during inundation, is dependent upon the character of hydrological connection at multiple temporal scales. The frequency and duration of each phase will influence both the quantity and quality of carbon made available. These
characteristics have changed in the lower Macintyre River system because of water resource development.

The impact and sustainability of water resource development is a worldwide issue, particularly in arid and semi-arid areas where water is scarce and its quality unreliable. Semi-arid anabranching floodplain rivers are found worldwide, and are particularly common in inland Australia. Their productive and hydrologically variable nature makes them primary objects for water resource development. However insufficient knowledge regarding the ecological functioning of anabranching river systems is a problem for managers of these systems. Rapid water resource development changes hydrological connectivity and fragmentation of anabranches in semi-arid floodplain river systems, but without ecological understanding there is no way of accurately modelling potential impacts. Degradation of river and floodplain linkages and health, in addition to escalating rates of water resource development, endanger the sustainability of these systems as resources and in their own right. Further knowledge of how these systems function and the potential influence of developments will inform more effective amelioration, restoration and rehabilitation measures and enable better management decisions.
Key messages:

- Water resource development changes hydrological connectivity in the riverine landscape
- These changes included reductions in the frequency and duration of connection between anabranch channels and the main river channel.
- Reduced connectivity with anabranch channels over time decreases the influence of landscape complexity
- Loss of landscape complexity via loss of connectivity with anabranches has the potential to reduce the total availability of carbon sources to the ecosystem.
- Modelled data demonstrate a 13% reduction in potential dissolved organic carbon release from anabranch sediments
CHAPTER NINE: SYNTHESIS........................................................................................................ 315

9.1 INTRODUCTION .................................................................................................................. 315

9.2 MAJOR FINDINGS............................................................................................................. 316

9.3 THE CONCEPTUAL MODEL – IMPROVING UNDERSTANDING........................................ 323

9.4 THE LANDSCAPE ECOLOGY PERSPECTIVE .................................................................. 325

9.5 THE IMPORTANCE OF SCALE......................................................................................... 326

9.6 RECOMMENDATIONS FOR MANAGEMENT AND FOR FUTURE RESEARCH .......... 327
CHAPTER NINE: SYNTHESIS

9.1 INTRODUCTION

This thesis has demonstrated an association between riverine landscape complexity (the presence of anabranch channels), hydrological connectivity (of anabranches with the river channel), and the quantity and quality of carbon sources available in a dryland floodplain river system. In addition, it has taken steps to use this information in modelling the potential effects of water resource development upon hydrological connection, fragmentation, and the availability of carbon to the food web. This information is significant for several reasons. The widespread nature and economic importance of semi-arid anabranching floodplain rivers makes understanding their patterns and processes essential in both theoretical and practical senses. This is especially the case because of the changing influence of past, present and future water resource development. Sustainable management of these systems demands better knowledge. Limited understanding of the ecological importance of physical heterogeneity and hydrological connectivity reduces the effectiveness of the efforts of researchers and managers to model and ameliorate the potential impacts of rapid water resource development.

This thesis began with a review of the scientific literature regarding hydrological connectivity and anabranch channels in semi-arid floodplain river systems (Chapter 2). It then proposed a conceptual model of the influence of physical heterogeneity and four primary phases of hydrological connection upon the distribution and availability of major carbon sources across a dryland, anabranching floodplain river landscape (Chapter 3). The spatial configuration of the lowland Macintyre River landscape, in terms of geomorphology and hydrology, was measured and described, highlighting anabranch channels as important patches (Chapter 4). The distribution of the major carbon sources in this landscape was then measured spatially, at multiple scales (Chapter 5), and temporally, in terms of phases of hydrological connection and ‘natural’ fragmentation during flow pulses (Chapter 6). The potential value of these carbon sources to the
ecosystem during the dominant phase (disconnection) was evaluated using stable isotope analysis (Chapter 7). Modelled hydrological data were then used to describe how ‘artificial’ fragmentation due to water resource development alters connectivity between, and hence carbon availability within, anabranch channels and their parent river channel (Chapter 8). The present chapter highlights what has been learned, and suggests ways forward in understanding.

9.2 Major Findings

Primary outcomes of this thesis include recognition that:

- Physical heterogeneity in this riverine landscape significantly influences biological pattern. Carbon quantity and quality vary among major hydrogeomorphic patches in this landscape. Scale is important – patterns vary and are distinct at multiple scales. In particular, carbon pools are different in anabranch channels compared to other patches. Anabranch channels are particularly important patches in this dryland river landscape, not only in terms of their spatial and physical characteristics, but also in terms of their potential ecological role as carbon storages and sources.

- Hydrological connectivity interacts with physical heterogeneity to further affect biological pattern over both space and time. Different phases of hydrological connection between anabranch channels and the main river channel are associated with differences in the availability of carbon sources and with changes in trophic status in the aquatic components of the landscape. These differences and changes vary according to the landscape patch examined (parent river vs. anabranch channels).

- Anabranch channels act as both sinks and sources of carbon in this landscape. They are sinks for large quantities of sediment-associated carbon, facilitated by high rates of sediment deposition; and sources for dissolved organic carbon, particularly via inundation-stimulated release from surface sediments. This dual role influences pattern and process at multiple spatial and temporal scales (e.g. within-flow pulse phase differences and DOC-discharge hysteresis).

- During the winter disconnection phase in the Macintyre River system, carbon sources that are predominantly found in anabranch channels support both anabranch and river
organisms. Other carbon sources found in the main river channel and the wider
floodplain appear to play a minimal role in comparison. Hydrological connection
between anabranth channels and the parent river channel appears to either supply or
allow access to anabranth carbon sources preferentially assimilated by riverine
consumers.

- Water resource development changes hydrological connectivity in the riverine
landscape. Reduced connectivity with anabranth channels over time decreases the
influence of landscape complexity. Loss of landscape complexity via loss of
connectivity with anabranthes has the potential to reduce the total diversity and
availability of carbon sources in the ecosystem. Potential exists for more effective,
specifically targeted management of these systems in ecological terms.

Data collection for this thesis began with identification of the proportional importance
and distribution of individual features within a broad riverine landscape setting, using
anabranth channels as the primary feature of interest. The results provide data that
confirm that landscape heterogeneity together with hydrological connectivity is an
integral part of the functioning of this dryland floodplain river system. Without the
spatial complexity of anabranth channels and their temporal interactions with the main
river channel, carbon sources for riverine consumers would be limited in both quantity
and quality (Chapters 5 and 6). Artificial fragmentation via water resource development
leads to a reduction in hydrological connectivity between anabranthes and the main river
channel (Chapter 8). Stable isotope analyses and modelled data indicate that such a
reduction would result in decreased diversity and quality of carbon sources available to
the food web (Chapter 7). However natural fragmentation (via the disconnection phase)
allows carbon sources in anabranth channels to build up, and allows for production of
organisms and carbon sources that would not survive in a lotic environment, but which
are high-quality food sources for riverine organisms. It also allows for initial processing
and degradation of ‘tougher’ more refractory sources such as eucalypt leaf litter, before
re-connection makes them available to the river. Hence natural fragmentation and
connection patterns should be preserved in this system, and potentially also in similar
systems. These ideas have since been distilled amongst other concepts in the Riverine
Ecosystem Synthesis (RES; Thorp et al. 2006), which recently suggested that different types of hydrogeomorphic patches, at different scales, should differ in productivity, metabolism and carbon dynamics.

This thesis has demonstrated that the presence, geomorphic character and hydrological connectivity of individual anabranch channels can significantly influence carbon availability in a semi-arid floodplain river landscape, both spatially and temporally. The quantity of several major carbon sources is greater in anabranch channels compared to the adjacent river channel; and the quality and diversity of carbon sources is greater in anabranch channels than in the wider floodplain. Despite the overriding effects of the flow hydrograph, hydrological connection with anabranch channels in this dryland system has the ability to alter the relative concentrations of primary carbon sources in the river channel, during and after flow pulses. In addition, stable isotope analysis results revealed the relatively high importance of anabranch channels as sources of both autochthonous and allochthonous carbon in the aquatic food web, compared to other landscape patches (the river channel and the floodplain). High rates of production and consumption of carbon sources in floodplains and riparian zones are known to be important for ecosystem productivity in tropical and temperate systems (Spink et al. 1998; Hein et al. 2003), however until recently the situation has been less clear for semi-arid ecosystems (Davies et al. 1994; Walker et al. 1995; Robertson et al. 1999; Bunn et al. 2006). Several studies have emphasised the importance of autochthonous production for the food webs of dryland river systems, and discounted the role of allochthonous carbon sources from other parts of the landscape during both connection and disconnection (Bunn and Boon 1993; Thorp and Delong 2002; Bunn et al. 2003; Bunn et al. 2006). The results of this thesis imply that both autochthonous and allochthonous production are important in the aquatic food web of the lower Macintyre River system, when that system is viewed from the landscape scale as a composite of intimately linked patches. Tockner et al. (2000) suggested that spatial and temporal shifts in the relative importance of autochthonous and allochthonous carbon should correspond to the degree of hydrological expansion and contraction across riverine landscapes. Although an abundance of certain carbon sources (such as leaf litter) does not necessarily imply that
they are incorporated into the food web in greater proportions, those sources that are more refractory may still be incorporated over longer time scales, and are contributors to the ‘heterotrophy paradox’ described by Thorp and Delong (2002). A diversity of carbon sources in terms of both quantity and quality is required in floodplain river ecosystems to maintain their productivity and sustainability over both short and long time scales. River, anabranh and floodplain areas are distinguishable as separate patches from not only a physical, but a functional point of view, and this thesis has demonstrated that collectively, anabranh channels are relatively important compared to adjacent floodplain and river patches in terms of carbon quality and availability across the riverine landscape. In addition, the importance of anabranh channels in terms of floodplain and channel area, and their prevalence throughout the semi-arid and arid river systems of Australia and worldwide, gives them a combined eco-geomorphic identity and function that cannot be ignored.

Anticlockwise hysteresis patterns indicate that connectivity with anabranh channels, and particularly DOC input during the draining phase, alters the timing of peak dissolved organic carbon transport downstream. In effect, carbon discharge in the river channel appears to be delayed relative to hydrological discharge, because of the influence of anabranh contributions to the river channel during the draining phase. The physical heterogeneity provided by anabranh channels in this riverine landscape increases the retention, volume and diversity of carbon sources in this landscape over both space and time, while simultaneously slowing the rate of transport downstream. Hence at a landscape scale, anabranh channels may be viewed as contributors to a shortening of the ‘carbon spiral’, reminiscent of the nutrient spiralling concept (Newbold et al. 1982; Elwood et al. 1983; Newbold 1992). According to the nutrient spiralling concept, as nutrients move downstream, they are alternately taken up, used, and released by various organisms and processes. This process may be visualised as a circular cycle stretched into the shape of a spiral, because of the longitudinal nature of transport via river flow. In the presence of physical and biological diversity, the spiral is compressed because of the greater number of opportunities for cycling within a given location. This shortening can in turn increase productivity and diversity further; hence spiral length has been used as an
integrative measure of ecosystem function (Pringle et al. 1988). Pringle et al. (1988) discussed the influence of patchiness within main river channels upon nutrient spiralling. They concluded that nutrient spiralling in the river channel is controlled by the shifting mosaic of patch-specific biotic and abiotic processes existing at various spatial scales, and emphasised the influence of organic matter upon the spiralling of nutrients. The general concept of nutrient spiralling has also been incorporated into several riverine ecosystem theories, including the river continuum concept (Vannote et al. 1980), serial discontinuity concept (Ward and Stanford 1983; 1995), flood pulse concept (Junk et al. 1989), and riverine productivity model (Thorp and Delong 1994). This thesis demonstrates that in the context of the wider floodplain river landscape, the hydrogeomorphic complexity introduced by anabranched channels and other features also has the potential to reduce spiral length.

Shortening of the carbon spiral by physical and hydrological diversity (spatial and temporal) may have positive implications for ecosystem resilience. Resilience is the capacity of a system to experience shocks while retaining essentially the same function, structure, feedbacks, and therefore identity, or the amount of disturbance a system can absorb without shifting into an alternate regime (Walker et al. 2006). Alternate regimes can have different implications, and from a human point of view, may be considered economically, ecologically, or socially desirable or undesirable. Diversity significantly influences the dynamics and stability of ecosystems, and in the context of resilience, can be described in terms of a) functional diversity, which influences system performance (e.g. productivity); and b) response diversity, which influences resilience (Walker et al. 2006). Functional diversity is usually discussed in terms of functional groups of species (e.g. grasses, shrubs and trees); but in the context of riverine landscapes, may also apply to hydrogeomorphic diversity. Similarly, response diversity has been described in terms of responses to disturbance among species contributing to the same function in the ecosystem, but is also relevant to the diversity of responses displayed by different landscape patches or features. Retention of physical heterogeneity and natural variability in hydrological connectivity is important for maintaining both productivity and resilience in dryland riverine landscapes, and minimising the risk posed by the effects of water
resource development of shifts into undesirable alternate regimes. By increasing the production and diversity of carbon or energy sources over both space and time, hydrogeomorphic diversity buffers the ecosystem against both natural and ‘artificial’ or anthropogenic disturbances. Consequently system stability is maintained, with positive effects on long-term resilience. This emphasises the perspective that dryland floodplain river landscapes are actually social-ecological systems, requiring recognition, understanding and management of the interlinked feedbacks between ecological condition, anthropogenic use, and system resilience (Gunderson et al. 2006).

Some authors have considered hydrological connectivity in riverine landscapes as a form of natural disturbance (Townsend et al. 1997; Ward 1998; Mathooko and Kariuki 2000; Boulton et al. 2006; Brock et al. 2006). Flow and flood pulses have been regarded as events that ‘reset’ parts of the riverine ecosystem, facilitating succession and interfering with competition in ways that ultimately determine the biodiversity of the landscape (Tockner et al. 2000; Ward and Tockner 2001; Ward et al. 2002). In this context, the applicability of the Intermediate Disturbance Hypothesis (IDH) in river systems has been discussed in the literature (Townsend et al. 1997; Tockner et al. 2000; Ward et al. 2002; Thorp et al. 2006). The IDH (Connell 1978) states that maximum biodiversity is achieved when disturbance is neither too rare nor too frequent. In frequently disturbed environments, tolerant or fugitive organisms dominate and few species survive, while in rarely disturbed areas, a few superior organisms outcompete all others. Ward et al. (2002) discuss several studies from riverine landscapes that seem to support the IDH in terms of varying levels of hydrological connectivity representing varying levels of disturbance, however they also emphasise that the IDH has rarely been tested explicitly in lotic systems. One of the RES model tenets suggests that biocomplexity peaks at intermediate levels of connectivity between the main channel and lateral aquatic habitats of the riverine landscape (Thorp et al. 2006), but the authors also highlighted the lack of targeted testing of the hypothesis in the riverine context.

The patterns observed by the present study in the lower Macintyre River landscape are also reminiscent of the IDH. Relative to anabranch channels, the river channel may be
viewed as ‘frequently disturbed’ and the wider floodplain as ‘rarely disturbed’.

Anabranch channels represent intermediate patches in terms of geomorphology and levels of hydrological connectivity (or disturbance), and are associated with the greatest diversity of carbon sources. The intermediate levels of connectivity experienced by anabranch channels produce a range of conditions for carbon production, consumption, deposition, and release over time, ranging from lotic to lentic to terrestrial. Although anabranches contain intermediate quantities of allochthonous carbon sources compared to the river channel and the surrounding floodplain, they are hotspots for maximum quantities of autochthonous carbon sources, and hence are of relatively high value to the ecosystem.

Other factors influence the diversity of carbon sources across a riverine landscape; Ward et al. (2002) make the point that the relationship between biodiversity and connectivity is controlled by interactions between many complex variables. However they also emphasise that a broad range of connectivity levels across heterogeneous riverine landscapes will be most likely to optimise diversity. The diversity of spatial features in this riverine landscape forms the template for diversity in carbon sources, in terms of type, quantity and quality. Frequent shifts in water level during flow pulses below bankfull have been suggested to maximise primary production, particularly in riverine landscapes with complex morphology (Tockner et al. 2000; Gurnell and Petts 2002). In addition, the importance of secondary channels and other landscape components with a diversity of aquatic refugia and exposed sediment components has been demonstrated for fish, molluscs, beetles, grasshoppers and plants (Townsend et al. 1997; Gurnell and Petts 2002 and references therein). Simplification or isolation of the river channel or the floodplain, conceptually or in practice, is therefore damaging to both the understanding and the long-term sustainability of floodplain river ecosystems.

The roles and conservation of heterogeneity and connectivity of multiple elements of riverine landscapes should be priorities for both research and management. Rapidly increasing water resource development is changing many roles and processes before they are properly understood in their natural state, producing a complex situation where
interactions between ‘natural’ and ‘artificial’ fragmentation processes dictate productivity over both the short and long term. Successful manipulation of flows for ecological restoration requires knowledge of potential target conditions, and it is in this context that anabranch channels may prove useful as carbon sources that are accessible during within-channel flow pulses. Establishing the magnitude and frequency of controlled flood pulses required to maintain appropriate connectivity with anabranch channels, may aid in decisions aimed at maintaining or improving habitat diversity and the availability of various carbon sources in order to sustain ecosystem dynamics and resilience. As most restoration initiatives are relatively local in scale, eco-geomorphological modelling can help to determine which rivers, and which patches within them, are most suited to conservation or restoration of natural channel dynamics (Richards et al., 2002).

9.3 THE CONCEPTUAL MODEL – IMPROVING UNDERSTANDING

‘Understanding’ has been described as ‘an objectively determined, empirical match between some set of confirmable, observable phenomena in the natural world and a conceptual construct’, in other words, ‘a match between what scientists observe and what they think’ (Pickett et al. 1994, p.28). The combination of field, laboratory and modelled data explored in each of the chapters of this thesis enabled examination of the conceptual model described in Chapter 3 in light of observed pattern and process. The specific differences between expected and observed patterns of carbon distribution over both space and time were discussed in Chapters 5 and 6. Such comparison of ‘theory’ (in this case derived from the literature and field observation) with empirical results emphasises the complexity and variability of ecological systems at multiple scales, deepening understanding of the links between pattern and process, and producing further questions (Pickett et al. 1994). The integrative approach taken in this thesis has drawn on aspects of the emerging philosophy of science (Pickett et al. 1994), by pursuing understanding, both admitting and embracing multiple causality, and downplaying the falsification approach that has been deplored by many authors (Johnson 1999; Pickett et al. 1999; Anderson et al. 2000; Holling and Allen 2002). The conceptual model described in Chapter 3 represents part of the modern view that recognises that ‘theories do, in reality,
incorporate factual information in various of their components, and that facts have a conceptual aspect’ (Pickett et al. 1994, p.20).

The process used in this thesis has contributed to all three components of ‘understanding’ as described by Pickett et al. (1994). It began with a conceptual construct (the model, Chapter 3), it compared this conceptual construct with observable phenomena (Chapters 4-7), and it used generalisation, causal explanation, and testing, as tools with which to make this comparison, within a specified ‘domain’. The domain is the ‘set of objects, relationships, and dynamics occurring on specified spatial and temporal scales that are the subject of scientific enquiry’ (Pickett et al. 1994, p.30), and was described in Chapters 1-4 of this thesis, and at the beginning of each results chapter (5-8). In this context, the tools used to compare the conceptual model and observed phenomena in this thesis included: generalisation via pattern generation - used to condense and compare carbon values between patches and connection phases; causal explanation - suggested for the observed pattern of carbon concentrations in the river channel during different hydrological connection phases with anabranche channels; and testing of patterns and explanations - by asking whether those observed matched with those expected (Pickett et al. 1994).

An important element of the contemporary scientific approach in ecology entails recognition that theories and conceptual models are constantly evolving entities, rather than inviolable laws or statements (Pickett et al. 1994). Conceptual models can also influence interpretation of results – for example, including draining as a distinct phase in this thesis assisted in distinguishing the effects that anabranch connection has upon dissolved organic carbon concentrations in the main river channel. In this context, more complete understanding of the role of hydrological connectivity in a riverine landscape in terms of carbon dynamics may require integration and adaptive adjustment of multiple conceptual models from multiple sub-disciplines, and certainly requires answers to many more questions than those posed in this thesis. In addition to the spatial and temporal patterns of hydrological connection and carbon distribution that have been described, thorough understanding would involve further detailed knowledge of transformations,
transport mechanisms, quality, uptake and release, competition for consumption, and the implications of terrestrial and hydrological development for all of these variables. As stated in Chapter 1, this thesis used carbon simply as a landscape-scale ‘indicator’ of the influences of hydrological connectivity and fragmentation upon ecological processes in these systems, because of the importance of carbon as an energy source, and the dependence of carbon dynamics in dryland river landscapes upon water and its movement.

9.4 THE LANDSCAPE ECOLOGY PERSPECTIVE

This thesis has used landscape ecology as a framework for investigation of the ecological role of hydrological connectivity and fragmentation of anabranch channels in semi-arid floodplain river systems. Five of the seven central themes that unify landscape ecology (Wiens 2002) are identifiable in this study, including 1) landscapes comprise a mosaic of patches – such as river, floodplain and anabranches; 2) patches may differ in quality – as anabranches differ from river and floodplain patches; 3) patch boundaries affect flows – these boundaries are dynamic in anabranching floodplain rivers because of the temporal dimension of hydrological connectivity; 4) connectivity between patches is critical – as demonstrated by the influence of anabranches on river carbon sources and vice versa; and 5) scale is important – exemplified by carbon availability patterns at both patch and site scales in this system.

The hierarchical patch dynamics model used in the RES (Thorp et al. 2006) views ecological systems as nested, discontinuous hierarchies of patch mosaics (Wu and Loucks 1995). Viewing the riverine landscape in this way allows analysis of the role of small patches within large patches (e.g. anabranches within the riverine landscape, or sites within anabranches). It also allows for temporal changes in the nature and role of patches, such as those observed for anabranch channels between hydrological connection phases. The model states that the dynamics of ecological systems are derived from a composite of intra- and inter-patch dynamics. In the Macintyre river system, the results of intra-patch dynamics are observable in the sediment texture and carbon distribution
patterns within anabranch channels, while inter-patch dynamics are evident in terms of the distribution of carbon sources between the anabranches, river channel and floodplain during each hydrological connection phase. As predicted by the model, pattern and process in terms of carbon sources are interlinked and scale-dependent in this riverine landscape. Consequently, the results of this thesis support several of the RES model tenets, including: the importance of the hierarchical habitat template determined by interaction between geomorphic features and flow characteristics; the necessity of naturally dynamic hydrological patterns to maintain the evolved biocomplexity in river networks; and peaking of ‘biocomplexity’ at intermediate levels of connectivity between the main channel and lateral aquatic habitats of the riverine landscape (i.e. in anabranch channels). Corroboration of the RES model by the observed data, re-emphasises the interplay between conceptual models, theory and empirical data that ultimately improves understanding.

9.5 THE IMPORTANCE OF SCALE

The scale at which observations are made significantly affects the conclusions which can be drawn (Turner et al. 2001). This applies to observations across time as well as space. Viewing the anabranch channels surveyed in this study as a collective patch type, their relative value and potential function in terms of carbon sources appears to be similar. However observations at the site-scale, within anabranches, reveal spatial complexity in carbon distribution and potential value, with implications for ecological function. These implications are further complicated by temporal scales of flow connection. The division of flow pulses into phases of hydrological connection and disconnection (effectively temporally downscaling from ‘pulse’ to ‘phase’), together with sampling observations made at daily or more frequent intervals, enabled the detection of the influence of anabranch channel carbon sources upon river carbon concentrations during the draining phase. This influence may not have been detected had observations been made at larger temporal scales.
Hydrological connectivity occurs at multiple temporal scales, both absolute and relative. Differences in connectivity between anabranches, the river channel, and the wider floodplain depend upon their separation by commence-to-flow levels that are in turn determined by the interaction between geomorphology and hydrology, over both space and time. At the anabranch scale and the within-anabranch or site scale, this interaction further influences patterns in carbon distribution and availability, introducing complexity at progressively finer spatial and temporal scales. The nature of this complexity does not necessarily correspond between scales. Hence, evaluation of the relative ecological roles or value of different landscape patches (e.g. anabranches as sinks or sources of carbon, or anabranches as having greater carbon availability over time and space) must be placed in context, in terms of both the spatial and temporal scales of interest and observation.

9.6 RECOMMENDATIONS FOR MANAGEMENT AND FOR FUTURE RESEARCH

This thesis has applied an interdisciplinary approach, comprising geomorphological, hydrological and ecological analyses. Interdisciplinary studies are by necessity multi-scalar in nature. They are also often complex with nested designs, and their extent is correspondingly large in terms of spatial and temporal scale, and the resources required to execute them. Thus they can be fraught with challenges (Pickett et al. 1994). However an interdisciplinary approach has the potential to bring about fresh solutions to the study and management of floodplain river ecosystems, because of the fundamental integration and interdependence of hydrology, geomorphology and ecology at all scales. Although driven by logistics and the need for simplicity, ‘Divide and conquer’ generally is not an effective method in either natural sciences or natural resource management. In recent years there has been a trend toward explicit acknowledgement of the relationships between physical, chemical and biological components of the environment, predominantly by highlighting the issue of scale. Pickett et al. (1994) identified three consequences of combining disciplines: 1) gaps in understanding appear at the interface between disciplines; 2) disciplines focus on specific scales or levels of organization; 3) as subdisciplines become rich in detail they develop their own view points, assumptions, definitions, lexicons and methods. Each of these consequences has its positive and
negative aspects. However integrative studies such as these are essential in order to understand how the systems of concern truly function, a process that is in itself vital in order to meet the scientific and management challenges of today and of the future.

New questions are often triggered by conceptual clarification (Pickett et al. 1994). Spatial and temporal patterns of hydrological connection and disconnection between anabranches and the river warrant further examination, especially in terms of their influence on the food web of the main river system. Variation in carbon distribution across the landscape has important implications for the effects and roles of connectivity in floodplain river systems over longer time scales than connection phases or flow pulses. Interactions between connection characteristics (e.g. frequency, duration, magnitude) and the spatial location, quantity and quality of carbon sources will determine the accessibility of carbon to riverine consumers, the internal cycling, turnover and transformation of carbon, and ultimately the quantities, forms and bioavailability of carbon sources made accessible by subsequent hydrological connections.

River-floodplain systems require hydrological connectivity via flood and flow pulses for ecological integrity and long-term sustainability (Bayley 1991; Jungwirth et al. 2002). In recognition of this fact, restoration strategies for heavily developed river floodplains along large lowland rivers in Europe and elsewhere attempt to reintroduce or improve hydrological connectivity with planned flood and flow pulses and physical alteration of floodplain structures (Burgess and Thoms 1997; Galat et al. 1998; Buijse et al. 2002). A similar avenue for rehabilitation in the Macintyre system and other anabranching systems may be the use of anabranch channels as targets for environmental flows. Current environmental flow management in the Macintyre River system focuses on the restoration of low and overbank flows, as well as protecting the surrounding floodplain. However the ecological role of in-channel flow pulses and their connection to anabranch channel functioning is ignored. This thesis has shown that flow pulses of varying magnitude connect different anabranch channels, and that different phases of connection have the potential to significantly influence carbon dynamics over both space and time. In view of the results of this study, strategic timing and distribution of flow events
released from upstream dams could improve ecological outcomes, especially when combined with identification of key patches or ‘hotspots’ (e.g. middle/apex sites within anabranches) for carbon storage and release. These patches could be given priority status for conservation or integrated management methods. At present, many management strategies do not recognise the parts of floodplain river systems that can or need to be managed, and often do not support their decisions with scientific knowledge at the appropriate scale (Wiens 2002). Recognition of the role of anabranch channels and the importance of within-channel flow pulses in connecting them to the river channel will produce more effective and targeted management solutions, with long-term benefits to the floodplain river ecosystem as a whole.
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345


351


Connectivity and fragmentation of flood plain–river exchanges in a semiarid, anabranching river system

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Abstract The ecological integrity of flood plain–river systems is dependent upon hydrological connections between the main river channel and adjacent flood plain. These connections facilitate the exchange of carbon and nutrients and influence productivity. This paper considers carbon dynamics during phases of connection and disconnection in a large lowland river in southeast Australia. Data are presented on carbon stores in a number of anabranch channels during the disconnection phase, and the potential availability of dissolved organic carbon from these channels during the connection phase. Anabranch channels are an important physical patch type in this flood plain–river system, containing significant quantities of various carbon sources. During flooding these channels are potentially important sources of dissolved organic carbon for the main river channel. However, water resource development has reduced this potential supply of carbon by reducing hydrological connectivity between the anabranches and the main river channel. These changes have implications for the transfer of energy through the food web and hence also for the functioning of the ecosystem as a whole.

Key words connectivity; fragmentation; flood plain; anabranch channels; carbon; water resource development; Macintyre River

INTRODUCTION

Flood plain–river ecosystems are dynamic spatial mosaics in which water plays an important role in connecting landscape patches. The temporal character of flooding or hydrological connectivity influences the exchange of materials between the main river channel and flood plain patches (Spink et al., 1998). During inundation, dissolved organic carbon and nutrients are released from flood plain sediments and plant matter and may be transported into the river channel. Carbon is an important food source for riverine organisms, and forms the base of the food web in flood plain river ecosystems (Robertson et al., 1998). Hence its exchange between river and flood plain patches is important for the productivity of these systems.

Fragmentation is the reduction or elimination of connections between patches in a landscape (Kotliar & Wiens, 1990). Hydrological fragmentation in flood plain rivers is facilitated by the “flood pulse” (sensu Junk et al., 1989), creating heterogeneous patterns of wetting and drying on adjacent flood plain surfaces. Changes to wetting and drying regimes can interfere with the release, availability and exchange of carbon between river channels and the flood plain (Baldwin & Mitchell, 2000).
Anabranch channels are a common feature of Australian lowland rivers and are important patches in flood plain–river landscapes (Thoms & Sheldon, 2000a). They become connected to the main river channel during flood pulses, and gradually dry out and disconnect during flood recession and low flow periods. During periods of disconnection, anabranch channels accumulate leaf litter and other organic matter and may hold ephemeral billabongs (water holes) containing other potential carbon sources. Both particulate and dissolved forms of carbon may enter the main channel from anabranches during connection phases. This paper presents data on carbon pools present in anabranch channels of the Macintyre River, Australia, during the disconnection phase, and then examines the implications of changing hydrological connectivity for the potential availability of carbon from anabranch channels for the main river channel ecosystem.

**Fig. 1** The Macintyre River and its catchment, at the border of Queensland and New South Wales, Australia.
STUDY AREA

The Macintyre River is one of the principal streams in the Border Rivers catchment (48 000 km²), forming the border of New South Wales and Queensland, Australia (Fig. 1). It is typical of the many lowland river systems in the Murray Darling basin, having a predominantly semiarid climate and variable flows. Annual discharges at Goondiwindi ranged from 61 000 to 4 488 000 Ml day⁻¹ for the period 1900–1990. Three large headwater dams regulate flows in the Macintyre, and the flood plain is subject to extensive irrigated agriculture. Similar water resource development has reduced the magnitude and frequency of a range of discharges in the rivers of the Murray Darling basin (Thoms & Sheldon, 2000b).

This study focuses on a 15.8 km reach of the lower Macintyre River between Goondiwindi and Boomi (Fig. 1). Downstream of Goondiwindi, the Macintyre is a low gradient, highly sinuous “wash load” channel, with cohesive boundary sediments and an extensive flood plain (up to 20 km wide). The flood plain is heavily dissected by anabranch channels of various sizes. These ephemeral channels are disconnected from the main channel for most of the year (though many retain pools of water for several months) and commence to flow at various discharges.

METHODS

All channels in the study reach were mapped from aerial photographs and surveyed in the field for calculation of length, width and surface area. The commence to flow (CTF) discharge for individual anabranch channels was determined by surveying the main channel at the entry and exit points of each anabranch channel and calculating the corresponding discharge of the various sill heights via the Manning equation. To ensure that these discharges represented complete flow connection through each anabranch, an extra metre was added to each sill height and the discharges recalculated (Thoms et al., 1996). Periods of connection and disconnection for the individual anabranch channels were determined from “SPELL” analysis (Gordon et al., 1992) of simulated daily discharge data obtained from the New South Wales Department of Land and Water Conservation (NSW DLWC) Integrated Quantity Quality Model (IQQM; Black et al., 1997). Simulated “natural” flows were compared with simulated “current” flows for the period 1900–1998 for the Goondiwindi gauging station. The “natural” flow is simulated with a zero setting for flow regulating structures, abstractions of water and catchment development, utilizing long-term climatic conditions. The “current” simulated flow used water and catchment development conditions present in 1997–1998 combined with long-term climatic conditions. The rapid rate of water resource development in the catchment and the natural variability of flows precluded the use of historical data.

Three anabranches, which were representative of those found in the study reach in terms of geomorphic character, were studied in detail during December 2000 and July 2001. Within each anabranch, transects were established at the entry, mid and exit points and at each transect three 0.5 m × 0.5 m quadrants were randomly located. The dry biomass of surface leaf litter and the total carbon content of surface sediment samples were measured via standard methods (APHA, 1998). Two replicate water
column samples were taken from the top 0.3 m of the littoral zone in each anabranch billabong and from the main river channel downstream of the entry and exit point of each anabranch. Water samples were analysed for dissolved organic carbon (DOC) and phytoplankton (chlorophyll $a$; APHA, 1998). All samples were collected during the dry or disconnection phase, while anabranches and their billabongs were hydrologically isolated from the main river channel.

**RESULTS**

Fourteen anabranch channels were identified in the study reach, with a combined length of 20.5 km or 56% of the total channel length within the reach. Individual anabranch channels range in length from 0.4 to 3.9 km, corresponding to surface areas between 1 and 10 ha (Table 1). Individual anabranch channels are therefore smaller in size than the main river channel, which has a surface area of 61 ha within the reach, but combined they are an important patch type (surface area 51 ha).

The CTF discharges of the anabranch channels were calculated to range from 1195 to 47 367 Ml day$^{-1}$, and four groups of anabranches were recognized on the basis of these discharges (Table 1). Using the simulated natural daily flow data anabranch channels in the study area were calculated to have experienced between 107 and 468 wetting events for the period 1900–1998 (Table 2), depending upon the CTF discharge for each anabranch. Lower discharge anabranch channels (Group 1) experienced the greatest number of wetting events ($n = 468$), with a median duration of 6 days under

<table>
<thead>
<tr>
<th>Anabranch group</th>
<th>CTF (Ml day$^{-1}$)</th>
<th>Channel length (km)</th>
<th>Surface area (ha)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0–5000</td>
<td>10.18</td>
<td>25.28</td>
</tr>
<tr>
<td>2</td>
<td>5–10 000</td>
<td>6.76</td>
<td>16.78</td>
</tr>
<tr>
<td>3</td>
<td>10–20 000</td>
<td>0.83</td>
<td>2.05</td>
</tr>
<tr>
<td>4</td>
<td>20–50 000</td>
<td>2.73</td>
<td>6.78</td>
</tr>
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</table>

<table>
<thead>
<tr>
<th>Group</th>
<th>Flow scenario</th>
<th>No. of events</th>
<th>Total days wet</th>
<th>Median days wet</th>
<th>Total days dry</th>
<th>Median days dry</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>N</td>
<td>468</td>
<td>3555</td>
<td>6</td>
<td>32 512</td>
<td>25</td>
</tr>
<tr>
<td></td>
<td>C</td>
<td>407</td>
<td>2835</td>
<td>5</td>
<td>33 232</td>
<td>33</td>
</tr>
<tr>
<td></td>
<td>% Δ</td>
<td>−13.3</td>
<td>−20.3</td>
<td>−16.7</td>
<td>2.3</td>
<td>29.4</td>
</tr>
<tr>
<td>2</td>
<td>N</td>
<td>322</td>
<td>1831</td>
<td>4</td>
<td>34 236</td>
<td>46</td>
</tr>
<tr>
<td></td>
<td>C</td>
<td>287</td>
<td>1460</td>
<td>4</td>
<td>34 607</td>
<td>45</td>
</tr>
<tr>
<td></td>
<td>% Δ</td>
<td>−10.9</td>
<td>−20.3</td>
<td>0.0</td>
<td>1.1</td>
<td>−2.2</td>
</tr>
<tr>
<td>3</td>
<td>N</td>
<td>192</td>
<td>850</td>
<td>4</td>
<td>35 217</td>
<td>72</td>
</tr>
<tr>
<td></td>
<td>C</td>
<td>161</td>
<td>692</td>
<td>3</td>
<td>35 375</td>
<td>95</td>
</tr>
<tr>
<td></td>
<td>% Δ</td>
<td>−16.1</td>
<td>−18.6</td>
<td>−25.0</td>
<td>0.4</td>
<td>31.0</td>
</tr>
<tr>
<td>4</td>
<td>N</td>
<td>81</td>
<td>249</td>
<td>3</td>
<td>35 818</td>
<td>193</td>
</tr>
<tr>
<td></td>
<td>C</td>
<td>64</td>
<td>201</td>
<td>3</td>
<td>3866</td>
<td>226</td>
</tr>
<tr>
<td></td>
<td>% Δ</td>
<td>−21.0</td>
<td>−19.3</td>
<td>0.0</td>
<td>0.1</td>
<td>17.1</td>
</tr>
</tbody>
</table>

Table 1 Commence to flow discharge groupings and physical character of anabranch channels in the study area.

Table 2 The wetting of anabranch groups under simulated natural (N) conditions and current (C) levels of water resource development and the percent difference (% Δ).
natural flows. By comparison, higher discharge channels (Group 4), experienced 81 wetting events with a median duration of 3 days. The character of hydrological connectivity changed with water resource development. All anabranches experienced a reduction in the frequency and duration of wetting with water resource development but this differed between anabranch groups (Table 2). There was a 21% reduction in the number of times Group 4 anabranches experienced wetting compared to a 13% reduction for Group 1 anabranches.

Surface leaf litter was abundant in the three anabranch channels sampled (mean 687 g m⁻²). Litter composition was highly variable, but overall the majority of the dry weight was attributable to “bark” (material other than leaves). Dry weights were spatially heterogeneous both within and between transects and anabranches (Table 3). Total mass is generally lower at the entry points and higher at the exits, and separation of the “leaves” and “bark” components clarifies this distinct pattern. The pattern of total carbon (TC) content in the surface sediments reflected that of ground surface litter, with lower levels near the entry of the anabranch channels increasing toward the exit point (Table 3).

Mean concentrations of dissolved organic carbon in the anabranch billabongs were approximately double those found in adjacent segments of the main river channel during all sampling periods (Table 4). For example, average DOC concentrations in anabranch billabongs during December 2000 were 9.58 ppm compared to 5.75 ppm in the main channel. Chlorophyll a analysis of water samples taken during July 2001 also revealed large populations of phytoplankton in the anabranch billabongs in comparison to the main channel (Table 4).

### DISCUSSION

There are four defined phases of hydrological connectivity between the main channel and anabranch system during a flood pulse. These are the dry phase or period of...
disconnection between intervening flow events; the partial connection phase when flood waters begin to enter anabranch channels and wet the surface; complete flow of water through the channel; and the draining phase during the recession of the flow pulse. Carbon dynamics are likely to differ during each phase, and changes to the character of each in terms of its frequency and duration may result in changes in ecological functioning of the river system as a whole.

The disconnection phase dominates the Macintyre River ecosystem in terms of total time. Accumulation and concentration of carbon sources such as litter and detritus, algae, and dissolved organic carbon (DOC) occur within each anabranch during this phase. Stores of carbon present vary spatially regarding both quantity and quality. In terms of quantity, a general lack of carbon is evident near the entry points of anabranches in terms of both surface leaf litter and sediment (Table 3). The distribution of leaf litter in these channels is inherently controlled by vegetation distribution and type, but also appears to be heavily influenced by flow dynamics. This is reflected in the distribution pattern found in this study, and the fact that large woody debris dams and leaf packs appear to increase in frequency and size with distance down anabranches in the study area, being absent at entry points and accumulating at exit points. The character of an individual flow pulse is important in determining:
(a) whether litter is moved or buried within anabranches;
(b) the type and size of litter moved;
(c) the distance litter is moved; and
(d) where litter is deposited.

Flow dynamics are also of fundamental importance in determining patterns in sediment carbon content, which may be attributed to several related factors, including the biomass of the overlying litter, flushing and deposition of leaf litter and other organic matter during high flows, and sediment grain-size patterns within the anabranches. Flow pulses through anabranches deposit coarse sandy sediment at the entry point, and progressively finer silts and clays toward the exit, which have much higher affinity for carbon due to their greater surface area.

In terms of quality, the most labile sources of carbon (immediately available to the riverine food web) in the anabranches include the DOC and phytoplankton found within ephemeral billabongs. Comparison of the different “patches” or channels in the lower Macintyre system reveals that these sources of labile carbon are highly concentrated within anabranch billabongs when compared to the main river channel (Table 4). Thus anabranch billabongs are potentially important patch types in terms of providing “immediately available” food energy to the main river ecosystem during connection phases. Surface leaf litter is a more refractory, relatively longer-term source of carbon, particularly considering the dominance of “bark” material—it takes longer to break down, and can be buried and stored in sediments for significant lengths of time. Quantity and quality of leaf litter within anabranches would depend upon season and flood frequency. The natural flood season in the Macintyre system coincides with that for leaf-fall of the dominant Eucalyptus species. Freshly dropped litter is of much higher quality for consumption by riverine organisms than desiccated, degraded leaves. Thus frequent connection events may result in smaller quantities being transported to the river channel, however these quantities are likely to be of higher quality, and vice versa.
The availability of the various carbon sources within anabranch channels is dependent upon the character of hydrological connection. This character has changed in the lower Macintyre system because of water resource development. For example, water resource development has resulted in the increased duration of the disconnection phase in this system (Table 2). Hence, anabranch billabongs are more likely to dry out before re-connection occurs with the main river channel. Consequently, the relatively more labile food energy materials held and produced by billabongs will not be immediately available when connection takes place, perhaps forcing organisms of the main river channel ecosystem to rely on locally produced and/or more refractory sources.

Wetting of sediments and leaf litter in anabranch channels also releases quantities of DOC that can be readily assimilated into aquatic food webs (Baldwin & Mitchell, 2000). The high total carbon content of surface sediments, and the large loads of litter present in anabranches of the Macintyre system indicate that release of dissolved organic carbon may be an important carbon source during connection phases. McGinness & Thoms (in press) found that for surface sediments of the lower Balonne flood plain, Australia, the average DOC release upon wetting (in the laboratory) was equivalent to 2.28 kg (0.002 t) per hectare per day. Applying these results to the hydrological and geomorphological data generated in this study, the potential availability of dissolved organic carbon from the surface sediments of the various anabranch channels of the Macintyre River can be calculated for each of the natural and current flow scenarios. Approximately 283 t of DOC would have been made available from anabranch channels under “natural” conditions compared to 225 t under “current” conditions, for the period 1900–1998. Hydrological changes appeared to have a relatively greater impact on the Group 1 and 2 anabranches where there was an approximately 20% reduction in potential dissolved organic carbon supply (Table 5). These estimates reveal the potential impact of water resource development upon hydrological connections and the exchanges that they facilitate between patches in this flood plain–river landscape.

<table>
<thead>
<tr>
<th>Anabranch group</th>
<th>Potential DOC release (t):</th>
<th></th>
<th>% Reduction</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Natural</td>
<td>Current</td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>205</td>
<td>164</td>
<td>20</td>
</tr>
<tr>
<td>2</td>
<td>70</td>
<td>56</td>
<td>20</td>
</tr>
<tr>
<td>3</td>
<td>4</td>
<td>3</td>
<td>19</td>
</tr>
<tr>
<td>4</td>
<td>4</td>
<td>3</td>
<td>19</td>
</tr>
</tbody>
</table>

In this reach of the Macintyre River, anabranch channels are important patches in the landscape in that they contain large pools of carbon that are potentially available to the main river channel ecosystem during connection phases. There are complex spatial and temporal factors determining actual availability of anabranch carbon for the river when connection occurs. Changes in the character of hydrological connection may result in changes to the relative quantities of particular types of food energy available over time, with subsequent implications for the transfer of energy through the food web and hence also for the functioning of the ecosystem as a whole.
Acknowledgements This project is supported by funding from Land and Water Australia, the Australian Research Council, the Co-operative Research Centre for Freshwater Ecology, and the W. J. Weedon family.

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Floodplain–river ecosystems: Fragmentation and water resources development

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Received 7 September 2004; received in revised form 29 October 2004; accepted 30 October 2004
Available online 18 April 2005

Abstract

Floodplain–river ecosystems are natural fragmented systems because of periodic hydrological connections. The integrity of these ecosystems is thought to be dependent, in part, upon exchanges of energy and matter between patches, such as the main river channel, adjacent floodplain surface and other morphological features, during periods of connection. Flow regulation and its associated infrastructure change the natural character of fragmentation in floodplain–river ecosystems, and have important consequences for their overall productivity. This paper considers the influence of water resources development on the character of fragmentation in a large lowland river in SE Australia. Large-scale water resources development in the Macintyre River, Australia, has significantly altered the spatial and temporal patterns of hydrological connections. The construction of weirs and other embankments on the lower Macintyre River floodplain prevents water movement through a series of anabranch channels thereby reducing the availability of these floodplain patches by 55%. In addition, because of flow regulation, hydrological connections to these channels occur up to 22% less often. Data are presented showing the impacts of these changes on the potential supply of dissolved organic carbon from the anabranch channels during periods of inundation over a 98-year period. Reductions of up to 98% of potential dissolved organic carbon supply from some anabranch channels were noted.

Keywords: Connectivity; Fragmentation; Flood plain; Anabranch channels; Dissolved organic carbon; Water resource development; Macintyre River, Australia

1. Introduction

Floodplain–river ecosystems are dynamic mosaics of patches. Water plays an important role in connect-

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size being a product of current and past geomorphic activity where as their quality can be measured in terms of associated plant biomass (Karrenberg et al., 2002), soil productivity (Ogden et al., 2002), or nutrient status (Thoms, 2003), among other things. Hydrological connectivity between the river channel and various floodplain patches is thought to be an important factor stimulating floodplain–river ecosystems (Tockner et al., 2000). Flooding facilitates exchanges of water, sediments, nutrients and biota between river channels and floodplain patches and these transfers are considered to be essential for the functioning and integrity of these systems (Amoros and Bornette, 2002).

Fragmentation is a term used for the reduction or elimination of patches and or connections between patches in a landscape (Kotliar and Wiens, 1990). Hydrological fragmentation in floodplain–river ecosystems is facilitated by ‘flood pulses’ (sensu Junk et al., 1989), which create variable but natural patterns of wetting and drying on adjacent flood plain surfaces. Fragmentation of floodplain–river ecosystems is exacerbated by human activities in two ways. First, the construction of levees, dykes and other engineering structures, commonly used as a flood control measures, isolates floodplain patches not only from the river channel but also from other floodplain patches. Reductions in reactive floodplain surface area and the different patches they contain may have significant implications for floodplain–river food webs (e.g., Power et al., 1995; Thoms, 2003). Second, water resources development changes the period of hydrological connection. The impact of water resource development on river systems is well documented (e.g., Petts, 1984) and hydrological change can occur at different scales (cf. Thoms and Sheldon, 2000a). Dams, weirs and water extractions have been reported to: (i) reduce mean annual flows, (ii) alter the magnitude, frequency and duration of floods, (iii) change the seasonality of flows and (iv) change the shape of individual flood events. Thus, fragmentation of floodplain–river ecosystems has both a spatial and temporal dimension but the significance of each dimension has rarely been studied in a collective manner. From cartographic sources, aerial photography and/or remotely sensed images, the disconnection of floodplain and wetland areas from rivers because of levee and dyke construction and drainage activities have been documented by Bird (1980), Bhownik and Adams (1986) and Kesel et al. (1992). Other researchers (e.g., Maheshwari et al., 1995; Thoms and Sheldon, 2000a) have used long-term flow data to describe flow regulation, and thereby have demonstrated changes in floodplain hydrology as a consequence. Many of the world’s large floodplain–rivers have been altered by human activity, and water resources development is blamed as a primary cause of decline in the biodiversity and ecological integrity of these systems (Welcomme, 1979). The management and rehabilitation of these altered ecosystems requires knowledge about the effects of activities such as water resources development on both the spatial and temporal dimensions of fragmentation.

Anabranch channels are a common feature of Australian lowland floodplain–rivers (Thoms and Sheldon, 2000a). In the Murray–Darling Basin, Australia’s largest catchment, with an area of 1.06 m km², anabranching rivers comprise approximately 87% of the total length of rivers in the basin. Characterized by extensive floodplains and small gradients, anabranch channels are only connected to the main river channel during episodic floods. During these periods of hydrological connectivity they have been demonstrated to be sources of dissolved organic carbon (Thoms, 2003). Inundation is thought to facilitate the release of dissolved organic carbon and nutrients from anabranch surface sediments, making the carbon and nutrients potentially available, along with plant matter, to be transported back into the main river channel. Carbon is an energy source for aquatic organisms and it is at the base of food webs in floodplain–river ecosystems. Robertson et al. (in press) demonstrate that the export of dissolved organic carbon from billabongs (another kind of floodplain patch) to the main channel of the Murrumbidgee River in Australia, during a single flood event, was sufficient to support in-channel respiration for approximately 20 days. It is during periods of disconnection that anabranch channels not only accumulate leaf litter and other organic matter but also contract to ephemeral water bodies (billabongs) that contain other potential carbon sources (McGinness et al., 2002).

Large-scale water resources development has occurred in most rivers in the Murray–Darling Basin.
since the 1960s (Thoms et al., 2004). In the Darling sub-catchment, for example, there are 12 large headwater dams with a combined storage capacity of 5048 gigalitres (GL), in excess of 5000 small weirs, and more than 300 water licenses. During 1997/1998, 2074 GL were diverted from the Darling catchment; by comparison, the long-term annual mean flow is 2370 GL in the lower reaches of the Darling River at Wilcannia (Thoms and Sheldon, 2000a). Large-scale developments have also occurred on the floodplains of many of these rivers with the construction of levees and water storages for the irrigation industry. In the Lower Balonne, for example, 179,750 ha of floodplain, or approximately 10% of reactive floodplain surface, is isolated within levees.

The aim of this study was to quantify the change in fragmentation of a large floodplain–river ecosystem that has been subject to water resource development. It considers both the spatial and the temporal effects of fragmentation on the potential exchange of dissolved organic carbon between a series of floodplain patches (anabranch channels) and the main river channel. The study has used a framework partly derived from landscape ecology, to advance our understanding of the structure and functioning of floodplain–river ecosystems.

2. Study area

The Macintyre River drains the highlands of southeastern Australia and forms part of the border between the states of Queensland and New South Wales (Fig. 1). Like many Australian inland systems the Macintyre is an allogenic river, originating in a well-watered area but flowing for most of its length across a dry flat landscape (Thoms and Sheldon, 2000a,b). Approximately 50% of the catchment is lower than 650 m above sea level. Rainfall within the catchment is variable, and droughts and floods occur periodically throughout the region. The long-term median annual rainfall (n = 68 years) decreases from east (1100 mm at Tenterfield) to west (480 mm at Mungindi) across the catchment. Most rainfall occurs in the summer months (November–April) and is associated with tropical monsoonal activity. Mean annual evaporation ranges from approximately 200 mm in the headwaters to 1900 mm in the lower catchment. Flows in the Macintyre are highly variable, with annual flows at Goondiwindi, in the lower catchment, ranging from 61,000 to 4,488,000 mega-litres per day (ML/d) (during years 1900–1990) with an annual median of 910,000 ML. In general, the Macintyre River has a summer-dominated annual flow pattern with flood events more common between November and April.

Three main rivers drain the upper sections of the catchment: namely, the Severn and Dumaresq Rivers and Macintyre Brook. These join together approximately 50 kilometres (km) upstream of Goondiwindi to form the Macintyre River. Of the five geomorphological river zones identified in the Macintyre catchment, the anabranch zone in the lower reaches of the river system, downstream of Goondiwindi, is the longest (Thoms et al., 1996). Extensive floodplains up to 20 km wide with a network of anabranch channels characterize this part of the catchment. These ephemeral channels, disconnected from the main channel for most of the year (though many retain pools of water for several months), commence-to-flow at a range of discharges in the main river. The four main anabranch channels which off-take from the main Macintyre channel are the Boomi River, Callandoon Creek, Dingo Creek and Whalan Creek, and they inundated sequentially when flow at Goondiwindi exceeds 650–5700 ML/d (Kingsford, 1999). The contemporary floodplain–river system has developed upon the surface of a series of Cainozoic alluvial fans described by Riley and Taylor (1978). The main channel of the Macintyre River, downstream of Goondiwindi, can be described as a wash-load channel (cf. Schumm, 1977) with low bed gradients (0.0002 to 0.0003), tortuous planforms (sinuositices exceed 2.3); highly cohesive boundary sediments and transporting predominantly fine sediments. Bankfull cross-sectional areas of the Macintyre River in this region of the catchment range from 38 to 65 m², and display not the typical increase in area with increasing catchment area but instead a pattern that varies with distance downstream. This downstream response in channel cross sectional area has been observed in other rivers of the Murray–Darling Basin and may result from inherited controls such as a variable degree of confinement afforded via palaeo channels.

There are three headwater dams in the catchment with a combined storage of 648,200 ML. Coolmunda
Dam regulates flow in Macintyre Brook, whilst Glen Lyon and Pindari Dams regulate flows in the Dumaresq and Severn Rivers respectively. The degree of flow regulation of these three dams, expressed as the ratio of storage capacity to the mean annual inflow, varies from 1.67 to 3.43. There are also 15 main channel weirs constructed to assist in providing water for irrigation, urban, stock and domestic purposes, as well as numerous small weirs on tributaries and anabranch channels. Boggabilla Weir, constructed in 1991 and located 20 km upstream of Goondiwindi, is the largest of the main channel weirs.
with a capacity of 5400 ML. This is the main regulating structure for the lower sections of the Macintyre River, controlling flows during the main irrigation season from October to March. Large quantities of water are stored in on-farm storages and these amounted to 423,500 ML in year 2000.

The flow regime of the Macintyre River has changed significantly because of water resource development. Preliminary assessments of hydrological change were made by Thoms et al. (1996) and Kingsford (1999). These studies note that mean annual volumes have decreased by up to 38.5% at Goondiwindi and the flow duration curves for most sites downstream of the major impoundments have changed in character. In general, flows that used to occur 80% of the time have increased, whilst those that used to occur 20% of the time have decreased. A comparison of pre- and post-flood frequencies indicates a reduction in the magnitude and frequency of floods up to and including those with an average return interval of 40 years.

This study focuses on a 380 km reach of the lower Macintyre River between Goondiwindi and Boomi (Fig. 1). The reach contains numerous anabranch channels and is typical of anabranching systems in the region (cf. Thoms and Sheldon, 2000b). Land use in the study area is dominated by irrigation, particularly for cotton farming, and grazing. Cotton development in the study reach has only occurred since the irrigated agriculture began in the 1960s. It has resulted in clearing of native floodplain vegetation, along with the construction of levees to protect crops and block banks, on the many anabranch channels.

3. Methods

A series of 15 digital aerial photographs (scale 1:20,000) were used to construct a single georeferenced photo mosaic of the study area. The photographs were rectified and stitched together using ER Mapper. All channels in the study reach were mapped from this photo mosaic, together with additional photography, topographic maps and Landsat TM images of the area. Each stream channel was then digitized using ARCVIEW, and the position of each channel was verified in the field. These data, combined with measurements made at three cross-sections per anabranch channel ($n = 207$ for all anabranches) and at 207 places along the main channel of the study reach, were used for calculating the length and surface area of individual anabranch channels and the main river channel. The locations of weirs, regulators or block banks that prevented natural flow through anabranch channels were recorded from the photo mosaic and during a field inspection of the study reach.

The commence-to-flow discharge (CTF) for individual anabranch channels was determined from cross-section surveys of the main channel at the entry and exit points of each anabranch channel combined with the elevations of sill heights for each anabranch channel. The actual discharge was calculated using the Manning equation. Manning’s $n$ was estimated using the method recommended by Cowan (1956) and verified against gaugings of the Macintyre River undertaken by staff from the local water resources department. All CTF estimates were checked against field observations made by local water agency personnel. To ensure that the discharges used in this study represented a complete flow connection through each anabranch, they were then recalculated as if each sill had been 1 m higher, as per the recommendation of Thoms et al. (1996). Calculated discharges for each anabranch channel were then calibrated against the river gauge at Goondiwindi, some 20 km upstream of the study reach, via a series of backwater curves provided by the local water authority.

Periods of connection and disconnection for the individual anabranch channels were determined from a SPELL analysis (Gordon et al., 1992) of simulated daily discharge data obtained from the New South Wales Department of Land and Water Conservation (NSW DLWC) Integrated Quantity Quality Model (IQQM; Black et al., 1997). The rapid rate of water resources development in the region, combined with the naturally variable flow, makes historical data inadequate for evaluating the impact of water resources development on the hydrological regime of the Macintyre River. Thus, simulated daily discharge data from the New South Wales Department of Land and Water Conservation Integrated Quantity Quality Model (IQQM) were used when evaluating hydrological change. Black et al. (1997) gives a full description of the model and its reliability. The ‘natural’ or ‘pre-development’ flows were simulated
from long-term mean climatic conditions, using a zero setting for flow regulating structures, abstractions of water and land-use development. The ‘current’ flows were simulated using water and land-use conditions present in 1999–2000 combined with long-term mean climatic conditions. Simulated ‘natural’ flows were compared with simulated ‘current’ flows for the period 1900–1998 for the Goondiwindi gauging station.

Fifteen anabranch channels were selected to represent the different anabranch types, and the various carbon stores within each were measured during a dry period when all the anabranch channels had been disconnected from the main river for at least 30 days. Transects were established at the entry, mid and exit points of each anabranch channel, and surface organic material was collected from three randomly placed 0.5 m × 0.5 m quadrats along each transect. The samples were air-dried and then weighed to determine the dry mass of surface organic matter. Three surface sediment samples were also collected from each transect and analyzed for the total carbon concentration, using standard methods (APHA, 1998). Intact sods of sediment were also collected from randomly chosen sites on each transect; their areas were measured and they were flooded in the laboratory under controlled conditions. The overlying water was sampled at hourly intervals for a period of 60 h and analyzed for dissolved organic carbon (DOC) content (see O.I. Analytical, 1996). Corresponding samples of surface organic matter, surface sediments and intact sediment sods were collected from the adjacent floodplain and banks from the main river channel, and treated in the same way.

To estimate the impact of water resources development on the Macintyre River, a simple budget for dissolved organic carbon was derived for the simulated ‘natural’ flow scenario and ‘current’ scenario, as discussed above. Individual dissolved organic carbon budgets were calculated in three steps. Step one incorporated data on the release of dissolved organic carbon from wetted surface sediment collected from the various anabranches. Then, the potential supply of dissolved organic carbon from individual anabranches during could be calculated. Step two used the simulated daily discharge data from the New South Wales Department of Land and Water Conversations IQQM. Both simulated ‘natural’ and ‘current’ flows at Goondiwindi were used for the period 1900–1998. From the daily flow data, the area of anabranch channel inundation in the flow scenarios were estimated. Step three estimated the daily dissolved organic carbon released from the wetted surface of each anabranch channel, and hence the potential supply of dissolved organic carbon from the collective of the anabranch channels calculated.

4. Results and discussion

4.1. The size and function of anabranch channels in the study area

Sixty-nine anabranch channels were identified and found to have a combined length of 236 km, which was 62% of the total channel length of the study reach. Individual anabranch channels ranged in length from 0.32 to 112.5 km and had a mean wetted perimeter of 24.81 m (S.D. = 10.65) compared to a mean of 46 m (S.D. = 7.65) for the main channel of the Macintyre River. Although individual anabranch channels are smaller in size than the main channel of the Macintyre River, which has a total surface area of 658 ha within the study reach, the anabranch channels altogether have a comparable surface area of 586 ha. Hence, they represent a significant patch-type in the study reach.

Four distinct anabranch channel planform types were identified in the study area. Anabranch channels of one type have one well-defined entry and exit point each, and are the most common type, making up 62% of the total length of anabranch channels there. They commence-to-flow once the stage height in the Macintyre River exceeds the sill height at the entry point of the anabranch. A second type of anabranch has a combined channel length and surface area of 24 km (10% of the total length of anabranch channels) and 59.6 ha, respectively. This group is characterized by having a single connection to the main channel, usually at the exit point, and they only convey flow during major inundation events. The third group has several entry points but only one exit point. All these anabranches commence-to-flow at similar river stages, and their flow is conveyed back into the main channel
through a common exit point. This group of anabranch channels is the second most abundant, with a combined surface area of 129.3 ha and channel length of 52 km (22% of the total anabranch channel length). The fourth group has a single entry point but multiple exit points. These channels have well developed sills at the entry point and only commence-to-flow once water levels in the main channel are exceeded. They are the least common anabranch channels; combined surface area is 33.27 ha, and total channel length is 13.4 km (6% of the total anabranch channel length).

Commence-to-flow discharges range from 1195 to 47,367 ML/d for the anabranches. Five distinct commence-to-flow phases or flow bands are recognised in the study reach from the cumulative frequency distribution of commence-to-flow discharges (Fig. 2). These flow bands were determined from changes in slope of the cumulative frequency curve. One group of anabranch channels commences to flow at between 200 and 7000 ML/d; a second group commences to flow at 8000–13,000 ML/d; a third begins at between 16,000 and 20,000 ML/d, a fourth group commences to flow at 24,000–31,000 ML/d, and the fifth group are inundated at discharges > 56,000 ML/d (Fig. 2).

Data on anabranch morphology were combined with the commence-to-flow values to establish a hydro-geomorphic classification of anabranch channels. Each hydro-geomorphic group is recognized as a functional patch group, similar in nature to the ‘functional floodplain water body patches’ described by Ward et al. (2002) for the Danube River floodplain. There is a diverse array of functional patch groups, with 15 of a potential 20 being present in the study reach (Table 1); that is, an observed-to-expected ratio of 0.75. Functional patch group 1 (single anabranch channels inundated at flows less than 7000 ML/d) has the most members (n = 20, or 29% of the total number of anabranch channels). However, this functional patch group contributes relatively little to the overall surface area of anabranch channels present in the study reach (47.6 ha or 8.1%) (Table 1). By comparison, there are only five channels in functional patch group 5 and they contribute 49% of the total anabranch surface area.

There were no real differences in the quantities of surface organic matter, and the total carbon content of surface sediments, between the riverbanks, anabranch channels and adjacent floodplain areas within the study reach. Although on average the anabranch channels contained 64% and 73% more surface organic matter than the riverbanks or floodplain respectively, the differences were not statistically significant. Mean total carbon content for floodplain surface sediments was 5.6% (coefficient of variation (Cv)= 44%); for anabranch channel sediments it was 3.3% (Cv=39%); and for riverbank sediments it was 2.9% (Cv=91%). Again, differences between the three areas were not significant statistically (ANOVA: F_{0.05(2),3,405}=2.13 for surface organic matter and 12.93 for total carbon content), because of large within-area variability in both parameters, as suggested by the relatively high coefficients of variation (Table 2).

In contrast, the quantity of dissolved organic carbon made available from the surface sediment

![Fig. 2. The cumulative frequency of commence-to-flow discharges for anabranch channels in the study reach of the Macintyre River, Australia. Flow groups were determined by the locations of changes in slope of the cumulative frequency curve.](image-url)
after 24 h of wetting was statistically different between the river banks, anabranches and floodplains (ANOVA: $F_{0.05(2),3,405} = 20.13$). Rates of dissolved organic carbon release from the surface sediments did not change after 24 h. Anabranch channel sediments produced, on average, 39.7% and 59.1% more dissolved organic carbon upon wetting than the riverbanks and adjacent floodplain, respectively. There were statistical differences between individual functional patch groups (i.e., different anabranches).

Thus, anabranch channels are a recognizable ‘functional patch type’ in this lowland floodplain–river system in terms of their potential supply of dissolved organic carbon during periods of hydrological connectivity.

### 4.2. Fragmentation of anabranch channels

Using the simulated ‘natural’ daily flow data, anabranch channels in the study area would have been inundated between 64 and 394 times between 1900 and 1998 (Table 3) depending upon their commence-to-flow discharge. For individual anabranches, this would have been equivalent to 181 to 2564 days of inundation over the 98-year period. Anabranch channels that commence-to-flow at lower discharges in the main river channel (i.e., functional patches 1 to 4—flow group 1) experienced the largest number of simulated wetting events ($n = 394$ and 290, respectively) and hence the longest flow durations (2564 and 1407 days, respectively). By comparison, functional patches 13 to 20 (i.e., flow groups 4 and 5) experienced 107 and 64 simulated wetting events and total flow durations of 348 and 181 days respectively.

When flow-regulating structures, abstractions of water and land-use development for 1999–2000 were included in the IQQM simulation, the frequency and duration of wetting in the study anabranches and floodplain were reduced, but by different amounts for

---

### Table 1

Classification, frequency and surface area of anabranch channels

<table>
<thead>
<tr>
<th>Flow group 1 (200–7000 ML/d)</th>
<th>Functional patch group 1</th>
<th>Functional patch group 2</th>
<th>Functional patch group 3</th>
<th>Functional patch group 4</th>
</tr>
</thead>
<tbody>
<tr>
<td>No. of channels</td>
<td>20</td>
<td>7</td>
<td>8</td>
<td>5</td>
</tr>
<tr>
<td>Surface area (ha)</td>
<td>47.6</td>
<td>32.3</td>
<td>99.5</td>
<td>33.3</td>
</tr>
<tr>
<td>Flow group 2 (8000–13,000 ML/d)</td>
<td>Functional patch group 5</td>
<td>Functional patch group 6</td>
<td>Functional patch group 7</td>
<td>Functional patch group 8</td>
</tr>
<tr>
<td>No. of channels</td>
<td>5</td>
<td>4</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Surface area (ha)</td>
<td>287</td>
<td>12.7</td>
<td>2.6</td>
<td>0</td>
</tr>
<tr>
<td>Flow group 3 (16000–20000 ML/d)</td>
<td>Functional patch group 9</td>
<td>Functional patch group 10</td>
<td>Functional patch group 11</td>
<td>Functional patch group 12</td>
</tr>
<tr>
<td>No. of channels</td>
<td>9</td>
<td>10</td>
<td>11</td>
<td>12</td>
</tr>
<tr>
<td>Surface area (ha)</td>
<td>4.7</td>
<td>1.8</td>
<td>6.3</td>
<td>0</td>
</tr>
<tr>
<td>Flow group 4 (24000–31000 ML/d)</td>
<td>Functional patch group 13</td>
<td>Functional patch group 14</td>
<td>Functional patch group 15</td>
<td>Functional patch group 16</td>
</tr>
<tr>
<td>No. of channels</td>
<td>13</td>
<td>14</td>
<td>15</td>
<td>16</td>
</tr>
<tr>
<td>Surface area (ha)</td>
<td>12.6</td>
<td>12.8</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Flow group 5 (&gt;56000 ML/d)</td>
<td>Functional patch group 17</td>
<td>Functional patch group 18</td>
<td>Functional patch group 19</td>
<td>Functional patch group 20</td>
</tr>
<tr>
<td>No. of channels</td>
<td>17</td>
<td>18</td>
<td>19</td>
<td>20</td>
</tr>
<tr>
<td>Surface area (ha)</td>
<td>11.8</td>
<td>0</td>
<td>21</td>
<td>0</td>
</tr>
</tbody>
</table>

The classification of the individual anabranch channels was determined according to their hydrology (commence-to-flow) and morphology (planform) and are noted as functional patch groups.

### Table 2

Summary statistics for the total mass of surface litter, total carbon (TC) content of the surface sediment and quantity of dissolved organic carbon (DoC) released from the surface sediment for the main river channel, anabranch channels and the adjacent floodplain surface

<table>
<thead>
<tr>
<th>Carbon pool</th>
<th>Main river channel</th>
<th>Anabranch channels</th>
<th>Floodplain surface</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total surface litter (g m$^{-2}$)</td>
<td>245.8</td>
<td>686.7</td>
<td>185.5</td>
</tr>
<tr>
<td>Bark (g m$^{-2}$)</td>
<td>98.5</td>
<td>586.5</td>
<td>85.5</td>
</tr>
<tr>
<td>Leaves (g m$^{-2}$)</td>
<td>147.3</td>
<td>100.2</td>
<td>100</td>
</tr>
<tr>
<td>Total carbon in surface sediment (TC %)</td>
<td>2.9</td>
<td>3.3</td>
<td>5.6</td>
</tr>
<tr>
<td>Dissolved organic carbon (DoC) released from surface sediment after 24 h (ppm)</td>
<td>9.71</td>
<td>16.10</td>
<td>6.54</td>
</tr>
<tr>
<td>Means and coefficients of variation (in italics) are given.</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

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the individual functional patches and flow groups (Table 3). Anabranch channels that commence-to-flow between 200 and 7000 ML/d (i.e., functional patches 1–4 or flow group 1) had 12% and 19% reductions in the frequency and duration of wetting. Those commencing to flow between 8000 and 13,000 ML/d had the greatest change in hydrology, with 17% and 22% reductions, respectively, in wetting frequency and duration. Differences in the frequency and duration of wetting for all functional patches between the simulated 'natural' and 'current' discharge scenarios were all statistically significant (Student’s t test, p < 0.01).

Four anabranch channels along the study reach had earthen banks and weirs constructed on their entry and exit points to prevent losses of irrigated water to wider floodplain environments. This is a common form of floodplain water resource development on Australian lowland rivers (Kingsford, 2000). In the study reach, this type of floodplain development resulted in 129.5 km or 321.6 ha of anabranch channels being disconnected from the main river, equating to a 55% loss in total area of functional patches. Functional patches 2 and 6 were respectively 69% and 97% smaller in surface area in the study reach because of this development.

The availability of the functional patches for a 98-year period was determined by combining the data for periods of hydrological connection and the data for surface areas of the different types of anabranch channels, for the two scenarios (Fig. 3). Overall, there was a 60% reduction in total patch connection with the river as a result of water resources development for the 98-year period; 996,329 hectare days (ha-days) of anabranch channels were available in a 'natural' scenario compared to 397,385 ha-days with 'current' water resources development. In addition, there was also a change in the dominant functional patch associated with water resources development (Fig. 3). Under a 'natural' scenario, functional patches 5, 3 and 1 provided 40.5%, 25.62% and 12.65% of the total available functional patch area over the 98 years. By comparison, functional patches 3, 1 and 4 provided 40%, 25% and 17% respectively of the total available functional patch area in the ‘current’ scenario.

### 4.3. Ecological Implications

The modeled data suggest that water resources development would have prevented the potential supply of 1400 tonnes of dissolved organic carbon from the functional patches (anabranch channels) in

![Fig. 3. The availability of different functional patch groups in the lower Macintyre River. Availability for the 98-year period were calculated as the number of days a hectare of anabranch channel was inundated.](image-url)
the Macintyre River during the simulated years 1900 to 1998 (Fig. 4). Approximately 2308 tonnes of organic carbon would have been dissolved in flood-water under ‘natural’ conditions, compared to 908 tonnes under ‘current’ conditions, during that period. Reductions in organic carbon that would potentially have dissolved into flood-waters covering individual functional patches range from 1 tonne to 900 tonnes for those years, or 12.5–98% (Fig. 4).

Water resources development has had a differential impact on the potential supply of dissolved organic carbon from the anabranch channels of the Macintyre River. In the simulated ‘natural’ flow scenario, anabranch channels belonging to functional patches 3 and 5 (which would be inundated when main river discharge was between 200 and 13,000 ML/d and have relatively simple planform types) would potentially have supplied 1502 tonnes of dissolved organic carbon or 65% of the total potential dissolved organic carbon supply between 1900 and 1998 (Fig. 4). In the simulated ‘current’ scenario, these functional patches would supply only 383 tonnes of dissolved organic carbon during the same period. Water resources development has increased the relative importance of anabranch channels represented by functional patches 1 and 3, from which potentially 587 tonnes of organic carbon would have dissolved during inundation in 1900–1998. That is 65% of the potential dissolvable organic carbon in the ‘current’ scenario, but 25% of the amount that could potentially have dissolved in the ‘natural’ scenario. The impact of these reductions in the potential supply of dissolved organic carbon from anabranch channels on riverine food webs is an emerging research area that is currently under investigation in the Macintyre River.

4.4. Floodplain–river landscapes

The present study has applied an interdisciplinary approach, linking hydrology, geomorphology and landscape-ecology, within a framework to investigate the consequences that changed hydrology and availability of functional floodplain patches (anabranch channels) can have on an ecological process—namely, the potential supply of dissolved organic carbon. Five of the seven central themes that unify landscape ecology (Weins, 2002) were used in this study: 1) landscapes comprise a mosaic of patches; 2) patches may differ in quality; 3) patch boundaries affect flows; 4) connectivity between patches is critical; and 5) scale is important.

Anabranch channels are a feature of Australian lowland rivers and represent important patches in these riverine landscapes (Thoms and Sheldon, 2000b).
They are the dominant physical patch in this dryland river system, accounting for 62% of the total channel length of the lower Macintyre River. There is also a relatively high diversity (observed to expected ratio of 0.75) of different physical patch types in the study area according to a classification of their hydro-geomorphology, in that 15 different functional patch groups were recorded there. As already mentioned, the functional patch groups contribute different proportions of total anabranch length and surface area. Thus, there is a dynamic mosaic of spatial functional patches (anabranch channels) in the lower Macintyre River. This floodplain–river mosaic is similar in nature to that described by Pringle et al. (1988), albeit at a different scale, for headwater lotic systems.

There have been limited studies of the impact of water resources development on anabranching floodplain–river systems despite the importance of anabranch channels to floodplain–river system functioning (e.g., Hein et al., 2003; Tockner et al., 2000). Most tend to focus on main channel (Petts, 1984) and or floodplain (Galat et al., 1998) environments. Anabranch channels occupy intermediate locations between the main river channel and adjacent floodplain and are important connectors between these traditionally recognized patches in floodplain–river ecosystems (Thoms, 2003). We have shown that blockages associated with water resources development have isolated some of the important functional patches in the study area, separating them from the main river and local source of inundation.

Recognizing differences in patch quality is important in linking a descriptive morphological map of a floodplain–river mosaic to something that can represent the spatial aspects of ecological processes (Weins, 2002). The effects of variations in patch quality have been illustrated on stream macroinvertebrate assemblages (Palmer et al., 2000), growth rates of fish (Hughes, 1998) and nutrient and carbon dynamics (Thoms, 2003). Those studies recognize that not all patches are equal. Whilst there was no statistical difference between individual anabranch channels in the study area on the Macintyre River, collectively these functional patches differ from the main river channel and adjacent floodplain surface, in the quantities of organic matter stored there, or the potential supply of organic carbon dissolved upon wetting. Thus, at a larger ‘landscape or riverscape’ scale these intermediate or riparian areas are relatively more important in terms of the potential supply of dissolved organic carbon. The Riverine Productivity Model of Thorp and Delong (1994) hypothesizes that riparian areas are important for biogeochemical cycles in river ecosystems, contributing to the structure of biotic communities and the overall ecological integrity of floodplain–river ecosystems. The results of the present study support the heuristic model of Thorp and Delong (1994) by indicating that the riparian zone can be an important potential source area for dissolved organic carbon. Therefore, if the model incorporates elements of the physical complexity of the riparian zone, such as different functional patches, its predictive ability may be improved.

Boundaries exist between floodplain–river patches, and the character of the boundaries will influence the exchange of energy and material between patches (Weins et al., 1985). In floodplain–river ecosystems, such as the Macintyre River, boundary character is governed, in part, by the timing of hydrological connections. Commence-to-flow values in the study area vary by an order of magnitude (Fig. 2) thereby adding to the fragmented nature of hydrological connectivity over time. Levees and weirs constructed within anabranch channels represent a physical barrier, resulting in a 55% reduction in [wettable] surface area of these functional patches in the study area; for some functional patch groups this has been reduced by 97%. Hydrological changes may further add to this spatial fragmentation, although this will depend upon the nature of changes associated with those that result in connecting the different anabranch channels. In the Macintyre River, water resources development has reduced the duration of hydrological connectivity of all functional patch groups, with reductions increasing in prominence for those connecting at higher flow levels.

Hydrological connectivity is a key element of floodplain–river ecosystem functioning (Pringle, 2003), and Ward (1989) recognizes four dimensions to hydrological connectivity in river systems: longitudinal, lateral, vertical connectivity and connectivity overtime. Water resources development and its associated floodplain infrastructure have led to functional patches being wetted less often and for less time, and have changed the patch mosaic associated with the Macintyre River. The simulation applied in this study
has demonstrated that large quantities of organic carbon potentially dissolve in flood-waters during periods of lateral connection, and that these are significantly reduced (by 61%) when water resources and floodplain development prevent flooding.

Landscape patterns and processes change with the scale of observation and all of the factors discussed above (patch size, quality, boundaries, connectivity) change with changes in scale; hence the need to consider ecosystems at a range of scales (Thoms and Parsons, 2002). Moreover, the scale on which river management is often applied differs from the scales on which data have been collected to inform such management (Weins, 2002). The current management focus in the Macintyre River is with flow restoration, especially low and overbank flows as well as protecting the greater floodplain. This ignores the importance of functional patch groups in maintaining the diversity of the lower Macintyre River floodplain and in particular the role of within-channel flow pulses that connect a range of anabranch channels. The differential role of flood pulses of varying magnitude connecting different anabranch channel types, and the influence on the potential supply of dissolved organic carbon to the Macintyre River, suggest there may be ‘hotspots’ of carbon supply in this floodplain-ecosystem that should be managed in terms of their spatial and temporal importance.

5. Conclusions

Little is known about the functioning of large floodplain–rivers as ecosystems and there is considerable debate about the roles of various landscape patches and periods of hydrological connectivity. Water resources development is one situation (another is drought) that prevents the main river channel from being connected with a host of floodplain patches (anabranch channels) in this study. Such fragmentation has both a spatial and a temporal context and these contexts must be considered individually and collectively when investigating the impact of water resources development of floodplain–river ecosystems. Moreover, for effective management of floodplain–river ecosystems, it is essential that the key interactions, both spatial and through time, be identified. At present, many management strategies do not adequately recognize the part(s) of floodplain–river systems that can or need to be managed, and often fail to provide scientific knowledge at the appropriate scale. An interdisciplinary approach has the potential to bring about fresh solutions to the study and management of floodplain–river ecosystems, because the hydrology, geomorphology and ecology of river systems interact at many geographic and time scales.

Acknowledgements

Thanks are given to Dr. Patty Beyer for organizing an excellent Binghamton and her patience in receiving the manuscript. Much of the research presented in the manuscript was supported by grants from Land and Water Australia and the Australian Research Council to MCT and scholarships from Land and Water Australia, Co-operative Research Centre for Freshwater Ecology (MS and HM), and the W.J. Weeden family (HM).

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