RESPONSES IN AQUATIC ECOSYSTEM METABOLISM TO MANAGED INUNDATION OF A REGULATED DRYLAND RIVER FLOODPLAIN

A thesis submitted in partial fulfilment
of the requirements for the degree of

Doctor of Philosophy

by

Sanjina Upadhyay

School of Biological Sciences
THE UNIVERSITY OF ADELAIDE

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CHAPTER

ABSTRACT

Environmental flows have emerged as major restoration tool in regulated rivers. When used correctly, they can restore hydrological connectivity to help improve the ecological condition of the floodplain rivers that have been impaired as a result of river regulation. However, in highly modified river systems, there are multiple constraints to providing adequate flows at large spatial scales. These constraints include conflicts between ecological requirements, social and economic expectations. As a result, management authorities are increasingly considering the use of floodplain environmental regulators to enable targeted delivery of environmental water to specific, high value floodplains. These infrastructures are intended to enable the managed inundation of larger areas of floodplains than would otherwise occur at a given discharge, and reinstate a flow regime closer to natural patterns in terms of frequency, duration and extent of flooding.

Throughout the Murray-Darling Basin in Australia, the goals of flooding the floodplain through the use of environmental flows have often focussed on maintaining and improving the conditions of floodplain vegetation and structuring of floodplain biotic communities reliant on inundated floodplains. However, environmental flows also have capacity to mobilise resources such as carbon and nutrients, and hence stimulate ecosystem productivity. Therefore, understanding how to deliver environmental flows in the best possible way to maximise ecosystem productivity that can support aquatic food webs, without leading to perverse outcomes such as hypoxic blackwater events and problematic algal blooms, is crucial.

Measurements of ecosystem metabolism are often used as indicators of ecosystem responses to flow variability, and to gain insights into relative health of rivers, based on a concept that they reflect energy sources and carbon fluxes in aquatic food webs. However, how information obtained from ecosystem metabolism measurements provide an understanding of the overall health of rivers is not well understood. Therefore, in this study, the utility of metabolism measurements as an indicator of riverine ecosystem health was also evaluated.

Ecosystem metabolism rates in an anabranch creek of the Chowilla Floodplain adjacent to the lower River Murray in South Australia, and in the main river channel upstream and downstream of the floodplain were compared prior to, during, and after a managed inundation event. The operation of a newly constructed environmental flow regulator facilitated the managed inundation of the floodplain. Additionally, the whole ecosystem metabolism was partitioned to assess the contribution of different biotic components, by estimating the production and respiration rates of each biotic component and scaling the rates to a reach over which the whole ecosystem metabolism was measured.

While there was substantial increase in ecosystem productivity rates in the anabranch sites during the managed inundation period, the responses were highly variable between sites. The results indicate substantial spatial variation in outcomes, even along a linear section of anabranch creek. Ecosystem productivity rates in the river channel also increased at sites located approximately 2 km and 40 km downstream of the return flows, indicating the potential of managed inundations to stimulate productivity at larger spatial scale. Partitioning of whole ecosystem metabolism indicated that a large part of the whole system production and respiration was accounted for by microorganisms, while the contribution by zooplankton, invertebrates and fish was less significant; indicating low carbon flux through higher order organisms.

Managed floodplain inundation events have the potential to positively influence riverine productivity, even during periods of low water availability. However, it is important to consider spatial variability across floodplains while assessing the ecosystem metabolism in response to inundation events. Greater understanding of how the mosaic of habitats present within a floodplain moderate ecological outcomes is required to enable managers to achieve desired ecological objectives at low inherent risk. Although ecosystem metabolism is a useful metric to complement monitoring of higher order organisms and to develop a reliable picture of river health, caution is required while interpreting the measurements of metabolism as an indicator of overall river health. This is because metabolism measurements may only reflect metabolic activity of phytoplankton and microbial communities, and not the ecosystem more broadly.

DECLARATION

I certify that this work contains no material which has been accepted for the award of any other degree or diploma in my name, in any university or other tertiary institution and, to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference has been made in the text. In addition, I certify that no part of this work will, in the future, be used in a submission in my name, for any other degree or diploma in any university or other tertiary institution without the prior approval of the University of Adelaide.

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Sanjina Upadhyay
Signed on, 25 May 2017

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STRUCTURE OF THE THESIS

This thesis consists of five chapters, and is presented in a combined conventional and publication format. The three data chapters have been prepared for submission to relevant journals for publication. As a result, some repetition of texts occur in the thesis.

Chapter 1 sets the background and motivation for the study, and introduces key ecological concepts and information pertinent to the investigations in three subsequent chapters. This chapter also introduces objectives and hypotheses, and provides a general overview of the study area.

Chapter 2 describes results from a study comparing ecosystem productivity at a reference site in the main river channel and two sites in an anabranch creek of the Chowilla Floodplain adjacent to lower River Murray, during managed inundation achieved from the operation of a newly constructed environmental flow regulator.

Chapter 3 describes results from a study that assesses the effectiveness of a managed inundation event in stimulating riverine productivity in the main channel of the River Murray.

Chapter 4 describes results from a study to estimate metabolic rates of various riverine organisms, and compares functional group specific metabolism estimates with whole ecosystem metabolism to partition their contributions to carbon flux in the system.

Chapter 5 provides a synthesis of the findings discussed in the thesis, and identifies important areas for future research.

CHAPTER 1

GENERAL INTRODUCTION

CONTEXT

The measurement of ecosystem metabolism in aquatic systems has been evolving for more than 75 years since the ground-breaking contributions of Lindeman (1942) and Odum (1956) that pioneered the concepts of trophic-dynamics in ecology. Aquatic ecosystem metabolism is governed by the processes of gross primary production (GPP) by in-stream autotrophs and community respiration (CR) by both autotrophs and heterotrophs. They are the major drivers of dissolved oxygen dynamics in the rivers, and tracking changes in the dissolved oxygen concentration can provide an effective measure of the ecosystem metabolism (Cole et al. 2000, Hanson et al. 2003, Staehr and Sand-Jensen 2007, Staehr et al. 2010, Staehr et al. 2012). In-stream primary production by autotrophs, such as algae and macrophytes, provides a source of energy to heterotrophs in the system (Odum and Barrett 1971), and therefore, estimates of GPP provide measures of the rate at which this energy is made available to the in-stream food web. CR, on the other hand, reflects the in-stream use of both internally and externally sourced energy by autotrophs and heterotrophs (Odum and Barrett 1971, Pomeroy 1974), and estimates the rate at which energy supplies are used by the system (Woodwell and Whittaker 1968, Pomeroy 1974). Net ecosystem production (NEP) is the difference between GPP and CR, and can be used to describe the metabolic status of an ecosystem (Odum 1956, Woodwell and Whittaker 1968, Howarth et al. 1996, Staehr and Sand-Jensen 2007, Staehr et al. 2012). These measurements of ecosystem metabolism have been widely used as indicators of ecosystem responses to flow variability, and to assess the overall health of river systems (Young and Huryn 1996, Mulholland et al. 2001, Fellows et al. 2006, Fellows et al. 2007). Despite the long history of study, the extent to which ecosystem metabolism measurements provide an understanding of the overall health of a riverine ecosystem, is not well understood.

It has been widely recognised that lateral hydrological connectivity is crucially important for a healthy functioning of river-floodplain ecosystems in many regions throughout the world (Junk et al. 1989, Robertson et al. 1999, Tockner and Ward

1999). In a natural, undisturbed state, hydrological connectivity enables the exchange of matter and energy between both the river and floodplain, providing synergistic ecological benefits for habitats across the mosaic of river-floodplain ecosystems (Junk et al. 1989). Such benefits include, among others, movement of river organisms between habitats (Lyon et al. 2010), growth of macrophytes and creation of new carbon pools in floodplains (Baldwin et al. 2012), and transport of carbon and nutrients from floodplain to the main river channel (MRC) through return flows (Sheldon et al. 2002, Lyon et al. 2010). Organic carbon transport from floodplains is an important energy source that provides basal food resources supporting aquatic biota in river-floodplain ecosystems (Thoms 2003).

While the importance of floodplain carbon subsidies in supporting healthy river ecosystems has been widely demonstrated, many large rivers are highly regulated to cater for various human needs, through the construction of storages dams, locks and weirs. River regulation alters the natural flow regime and causes hydrological fragmentation in river-floodplain ecosystems (Walker 1985, Maheshwari et al. 1995), creating a highly disturbed wetting and drying patterns across the adjacent floodplain (Thoms 2003). The resulting variability in wetting and drying of floodplain surfaces impedes the availability, release and transport of resources from floodplains to the river channels, which potentially result in energy limitation in the riverine ecosystems, stressing a host of biotic organisms in the aquatic food webs. In floodplain rivers particularly, the intensified flow regulations have altered the community composition of phytoplankton (Bowling and Baker 1996, Sherman et al. 1998), zooplankton (Nielsen et al. 2000), macroinvertebrates (Extence 1981, NECKLES et al. 1990, Nielsen et al. 1999), and fish (Leslie 1995, Humphries and Lake 2000), thereby impacting the food-web structure (Ruhí et al. 2016). These alterations affect the way different biotic organisms in an ecosystem contribute to the carbon and nutrient cycling in the system (Schindler et al. 1997).

Reinstating lateral connectivity between floodplain and MRC through the use of environmental flows has been advocated and practiced to help recover riverine ecosystems degraded as a result of intensive flow regulation (Ward and Stanford 1995, Jansson et al. 2007). Environmental flows aim to provide the quantity, timing and quality of water flow required to sustain and protect ecosystem and social values (Arthington et al. 2010). However, such attempts are often constrained by limited water availability for environmental flows, perceived risks, including black water and hypoxia in the river channels, and limited information for effectively planning the scale and timing of targeted flows to produce beneficial ecological outcomes (Wolfenden et al. 2017). Under such constraints and uncertainty, floodplain infrastructure known as environmental flow regulators, has emerged as a popular tool to control and manage timing and patterns of flooding by modifying natural, regulated, or environmental flows. Environmental flow regulators are managed to cause flows to the fragmented floodplain, and to harness the floodplain resources through return flows back to the river channel. Return flows potentially enrich nutrient levels in the river channel and stimulate primary productivity, in addition to providing external carbon subsidies for heterotrophic organisms.

Sources of Energy in Riverine Ecosystems

There are two primary sources of organic materials in riverine ecosystems: autochthonous materials, which are produced within the river by photosynthetic organisms and include primary producers such as phytoplankton, benthic algae and riparian vegetation (Thorp and Delong 1994, 2002, Bunn et al. 2003); and allochthonous materials, which are imported into the river from the surrounding floodplain, primarily through flooding (Thorp et al. 1998, Medeiros and Arthington 2011, Bartels et al. 2012). The input, transformation, and movement of the organic material through food webs are key processes for the functioning of river ecosystems (Lindeman 1942, Odum 1956). Different models of riverine ecosystems vary considerably in their predictions about the relative importance of these two sources in lowland rivers, in relation to varying patterns of connectivity to upstream reaches, riparian zones and floodplains (Vannote et al. 1980, Junk et al. 1989, Thorp and Delong 1994, 2002).

The river continuum concept (RCC) (Vannote et al. 1980) highlights the importance of upstream terrestrial organic matter as a major carbon source supporting the riverine food web downstream. This model, emphasizes the longitudinal exchanges of carbon and nutrients with less emphasis on investigating and understanding the role of floodplain dynamics on carbon and nutrient cycling in riverine systems. The flood pulse concept (FPC) (Junk et al. 1989) and its extension to arid and semi-arid zone rivers (Tockner et al. 2000) emphasizes lateral transfer of carbon and nutrients between the floodplain and the main river channel but focuses mainly on the period when the floodplain is inundated. In contrast to the RCC and FPC; the riverine productivity model (RPM) (Thorp and Delong 1994) highlights the importance of in-stream primary production and the direct input of organic material from the riparian zone as major drivers of riverine ecosystems. The RPM was originally proposed for highly regulated river systems but has since been broadened to unregulated floodplain rivers (Thorp and Delong 2002).

Evidence to enable validation of these models is sparse in lowland regulated rivers (Gawne et al. 2007). In such systems, the magnitude and duration of natural flooding regimes is highly altered due to the construction of weirs and levees to provide water for irrigation, industrial and household needs (Maheshwari et al. 1995, Burford et al. 2008, Watkins et al. 2010), disrupting the lateral exchange of organic material between the two habitats (Junk et al. 1989, Robertson et al. 1999, Oliver and Merrick 2006). Such anthropogenic regulation is known to have deleterious consequences on the lifecycles of fish and aquatic communities overall, which ultimately have significant impacts on riverine productivity (Tockner et al. 1999, Gawne et al. 2007, Kaminskas and Humphries 2009, King et al. 2009, Zampatti et al. 2010, Cook et al. 2015, Nielsen et al. 2015).

Many studies have demonstrated that autochthonous sources of carbon are a primary source of energy for aquatic food-webs (Thorp et al. 1998, Thorp and Delong 2002, Delong and Thorp 2006, Oliver and Merrick 2006, Gawne et al. 2007, Hadwen et al. 2010, Medeiros and Arthington 2011), supporting the prediction of the RPM that the algal carbon is the primary supporter of the aquatic food webs of large rivers. However, these studies were primarily conducted during low flow conditions or during periods where there was little or no connectivity between a river and its floodplain (Zeug and Winemiller 2008, Cook et al. 2015). In Australia the dryland rivers become fragmented for much of the year and occur as remnant creek-lines or isolated waterbodies as they are subjected to highly variable seasonal flows (Arthington et al. 2005). These disconnected waterbodies are exposed to little allochthonous carbon inputs at low water levels, and thus are dependant primarily on autochthonous carbon sources for supporting aquatic biota (Arthington et al. 2005, Burford et al. 2008). Additionally, rivers like the River Murray in southern Australia generally tend to exhibit light and nutrient limitations (Baker et al. 2000), thus resulting in low rates of primary production (Oliver et al. 1999). Consequently, additional inputs from allochthonous sources are important to sustain secondary productivity, by subsidising the carbon sources within the system (Polis et al. 1997, Dolbeth et al. 2012).

A plethora of studies have suggested that very frequent temporal sampling is needed to reveal periods where allochthonous carbon may be a major source of carbon fuelling aquatic consumers in food webs of lowland rivers (Findlay and Sinsabaugh 1999, Robertson et al. 1999, Huryn et al. 2001, Arthington et al. 2005, Zeug and Winemiller 2008, Hadwen et al. 2010, McGinness and Arthur 2011, Hladyz et al. 2012, Cook et al. 2015), especially in rivers with unpredictable variable discharge and rainfall pattern that may result in short duration of flood periods (McGinness and Arthur 2011). Overall, it is likely that the external and internal carbon sources are not exclusive of one another and that their relative importance may vary significantly over the year, emphasizing the need for adequate sampling frequency (Arthington et al. 2005).

Floodplains as an External Source of Energy for Riverine Ecosystems

Floodplains generally accumulate large quantities of carbon over time, primarily through leaf litters and detritus, which gets transported into the river channel through flooding, thereby providing a surge of energy to riverine food webs (Baldwin 1999, Burford et al. 2008, Cook et al. 2015). Thus, flooding has been shown to be an important process in floodplain rivers (Junk et al. 1989, Robertson et al. 1999, Humphries et al. 2014), in regard to liberation of terrestrially derived carbon and its effect on river metabolism and aquatic food webs (Humphries et al. 2014, Cook et al. 2015, Nielsen et al. 2015). However, despite the perceived importance, many lowland rivers have limited connectivity to their adjacent floodplain because of the effects of intensified flow regulation, disrupting the exchange of organic carbon and nutrients between the two habitats (Junk et al. 1989, Robertson et al. 1999, Tockner et al. 1999, Benke et al. 2000, Nilsson et al.

2005, Gawne et al. 2007, Nielsen et al. 2015). For such regulated rivers, environmental flows have become a major river restoration tool (Baldwin et al. 2016).

The goals of flooding the floodplain through the use of environmental flows have often focussed on maintaining and improving the conditions of floodplain vegetation and structuring of floodplain biotic communities that are reliant on inundated floodplains (Baldwin et al. 2016). Less attention has been given to the ecological benefits that could be gained in the MRC through return flows that provide terrestrial subsidies such as organic carbon, nutrients and plant propagules to the MRC consumers (Nielsen et al. 2015, Baldwin et al. 2016, Mitrovic and Baldwin 2016, Robertson et al. 2016). Understanding how to maximize ecological benefits by using environmental water regulation as a means to stimulate ecosystem productivity and aquatic food webs without leading to perverse outcomes such as hypoxic black water events and problematic algal blooms, is therefore a critical area of research. In this thesis, I investigated the influence of a managed inundation event using a flow regulator on the mobilisation of nutrients and DOC from the floodplain, and on aquatic metabolism.

River floodplains often have a high degree of heterogeneity (Junk et al. 1989, Tockner et al. 2000), characterized by the presence of multiple secondary channels, wetlands and lakes (Walker et al. 1995, Ward et al. 1999, Thoms 2003, Humphries et al. 2014). Floodplain anabranch channels are secondary channels that form a primary spatial component of the floodplain river landscape and are a potentially important source of energy for riverine ecosystems (McGinness and Arthur 2011). Anabranch channels break out from the MRC at the upstream section, traverses the floodplain for several kilometres before they re-join the MRC at a distance downstream (Nanson and Knighton 1996). Floodplain anabranches are comparatively easy to target for management, as they require relatively small amounts of water to maintain lateral hydrological connection (McGinness and Arthur 2011), and they provide suitable sites for constructing regulators. However, the ecological roles which anabranch channels play in improving the riverine productivity, have largely been ignored (Gurnell and Petts 2002). Anabranch channels are restricted in their area of direct influence during low flows, but during periods of higher flows, the channels become connected to low lying temporary creeks, wetlands, and lakes and eventually the extended floodplain habitats. The patterns of connections of anabranches to the river is expected to have a significant ecological impact, as the connectivity influence the flood residence times and the physico-chemical characteristics of the source water (Thomaz et al. 2007). This thesis also investigates the role anabranch habitats play in connecting various floodplain components with the river, and influencing riverine productivity, during the managed flood of a spatially heterogeneous floodplain.

Contribution of Biotic Components to the Measurements of Metabolism

Metabolism measurements have been based mainly on the fluxes in oxygen concentrations that are analysed to estimate the contribution of primary production of autotrophs and the respiration of autotrophs and heterotrophs to the whole system NEP (Cremona et al. 2014). The conceptual diagram (Figure 1-1) depicts the different contributors to the measurement of the aquatic ecosystem metabolism in a system.

The biotic components of an ecosystem make different contributions to the overall ecosystem metabolism, partly because of differing metabolic rates, which is controlled primarily by their body sizes and temperature (Gillooly et al. 2001) and partly by their relative abundances. Despite this, little consideration is given to estimating the contributions of higher order organisms to the whole ecosystem metabolism measurements. An important reason for this is the complexities involved with estimating the metabolic activity of higher order components of ecosystems. The analysis requires estimates of the metabolic activity of different biotic groups and also their biomasses (Oliver and Merrick 2006, Gawne et al. 2007, Cremona et al. 2014), an often-difficult task for the patchily distributed larger organisms. So, despite a long history of study, our understanding of the contributions that higher order organisms make to the measurements of ecosystem metabolism remains very limited (Cremona et al. 2014, Benjamin et al. 2016). This thesis investigates the contributions different biotic components make to the overall carbon dynamics in the system in order to better assess the utility of aquatic ecosystem metabolism as an indicator of riverine ecosystem health.

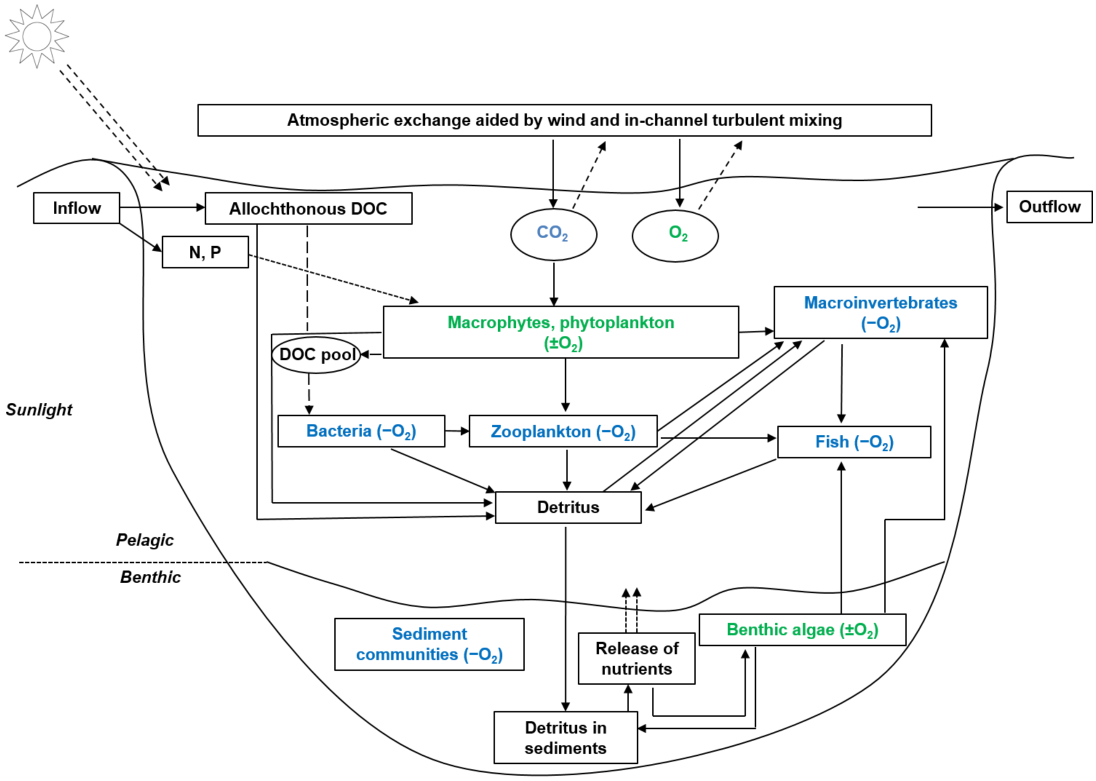

Figure 1-1: Conceptual diagram showing the contributors to the measurement of ecosystem metabolism in the ecosystem. Ecosystem components in green font represent autotrophs which produce oxygen during primary productivity (+O_2) and consume oxygen (–O_2) during respiration, while ecosystem components in blue font represent heterotrophs which only consume oxygen (–O_2) during respiration.

OBJECTIVES, HYPOTHESES AND APPROACH

The overall objectives of this study were to investigate the impacts of a managed floodplain inundation on ecosystem productivity in anabranch sites, and in the river channel downstream of an inundated floodplain. In addition, I also assessed the contribution of different biotic components to overall ecosystem productivity, by estimating metabolic rates of each functional group of organisms and comparing the results with the estimates of whole ecosystem metabolism.

The first step in this research was to examine the influence of the managed flood on the ecosystem metabolism in floodplain anabranch sites, which is discussed in detail in Chapter 2 of this thesis. The hypothesis was that managed floodplain inundation would lead to significantly elevated levels of nutrients and DOC concentrations at anabranch sites thus stimulating gross primary production (GPP) and community respiration (CR) during the period of increased connectivity with the peripheral floodplain habitats. Ecosystem metabolism was measured and compared at two sites in an anabranch creek of the inundated floodplain, and compared with a reference site in the main river channel above the influence of return water from the floodplain. Measurements were made during periods of lateral connection and disconnection of the anabranch creek to the adjacent floodplain, resulting from the operation of a newly constructed environmental flow regulator.

In Chapter 3 of this thesis, the influence of the return flows from the managed floodplain inundation events on ecosystem metabolism rates was assessed at two river channel sites, one immediately downstream of the inundated floodplain and the other approximately 40 km downstream, and compared the results with a reference site in the main river channel, located upstream of the influence of return water from the floodplain. The objective was to examine whether the return flows from the managed inundation have a larger spatial impact on riverine productivity, beyond the immediate vicinity of the inundated floodplain areas. The study focussed particularly on the effect of flooding on concentrations of nutrients (total and dissolved), DOC and changes in GPP, CR and NEP rates. The hypothesis was that the return flows from the managed inundation event would increase the concentrations of nutrients and DOC at two sites in the MRC downstream of the inundated floodplain that would then stimulate the GPP and CR rates.

The primary goal of Chapter 4 of this thesis was to partition the whole ecosystem measurement of metabolism, particularly CR, to assess the contribution of different biotic components in carbon cycling and processing, to better understand the utility of aquatic ecosystem metabolism measurements as an indicator of riverine ecosystem health. The prediction was that micro-plankton, mainly phytoplankton, small zooplankton and bacteria would contribute to the majority of the measured metabolism, owing to the higher metabolic rates per unit biomass as compared to other metazoans. In contrast, the contribution of higher order organisms to the metabolism were predicted to be very small, due to the overall low biomass and lower biomass specific respiration rates. A combination of field and laboratory experiments were performed to estimate the size specific respiration rates for a range of biotic components. Biomass of the biotic components were estimated using a combination of approaches in the field. The findings on biomass specific respiration were then used to partition the whole ecosystem measurements.

STUDY AREA

Murray-Darling Basin and the River Murray

The Murray-Darling Basin is Australia's largest and most iconic river system, with two sub-catchments comprised respectively of the Murray and Darling Rivers (Figure 1-2). The River Murray, as a principal contributor, rises in the Snowy Mountains and runs for 2,560 km in length and flows to the Southern Ocean in South Australia. The Darling River rises in the South East Queensland flows for 2,740 km and joins the River Murray at Wentworth, about 300 km from the sea (Walker 1985). The majority of the basin has an arid or semi-arid climate with highly variable flow (Maheshwari et al. 1995). There have been significant hydrological alternations made to the system by the construction of weirs to manage river channel flows and large storages dams to capture and secure water supplies for agricultural, industrial and domestic purposes. Altogether there are 13 regulating weirs with navigation locks distributed along the River Murray (Walker et al. 1995). These changes have led to a 56 % reduction in the long-term mean annual river discharge (Thomson 1994, Maheshwari et al. 1995).

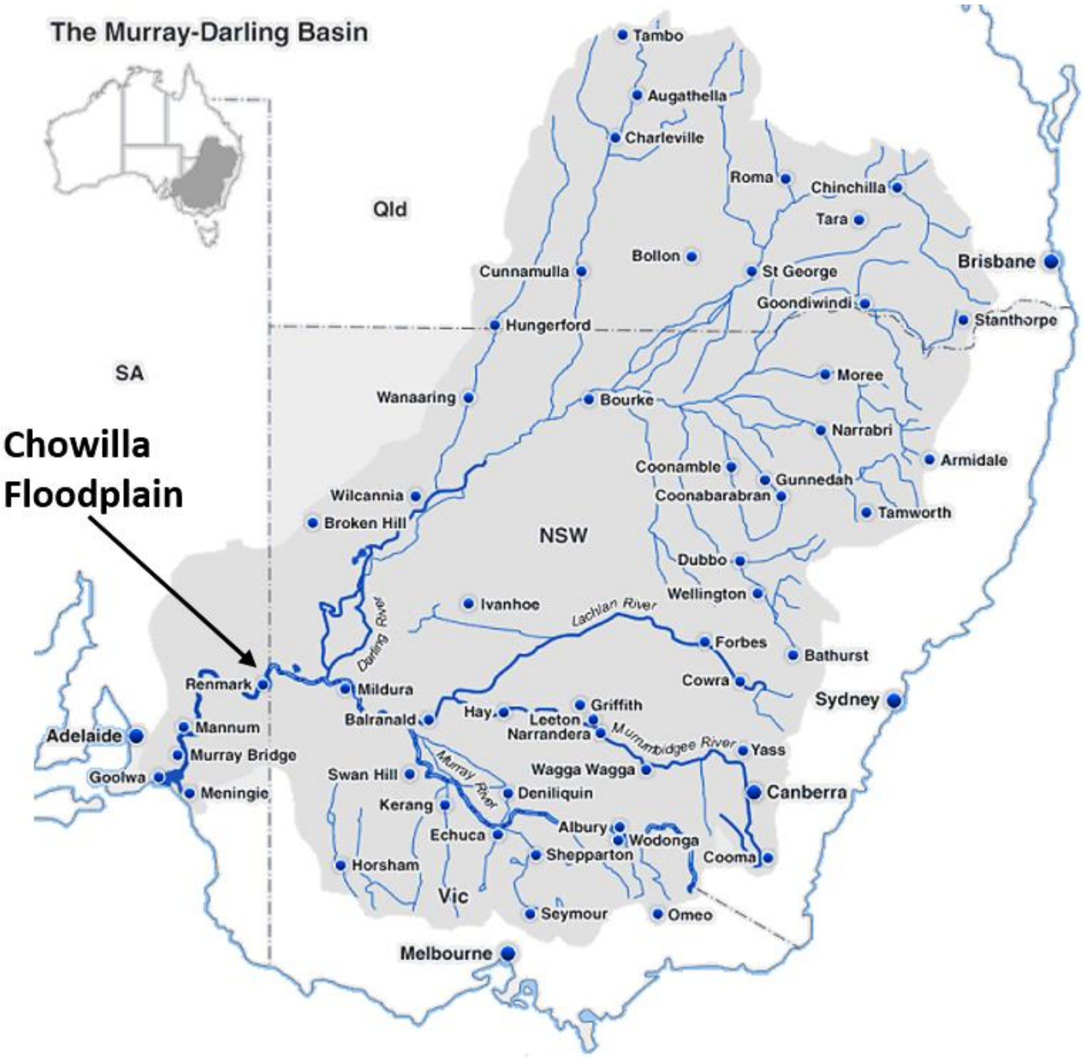

Figure 1-2: The Murray-Darling Basin. Inset- the map of the Australia, shows the location of the Murray-Darling Basin in Australia. Black arrow shows the location of the Chowilla Floodplain, which was the site chosen for this study. Blue thicker and thinner lines indicate larger and smaller tributaries, respectively (modified from Ben Spraggon (ABC 2013))

The Murray-Darling Basin experienced severe drought throughout the 2000's that further exacerbated the impacts of regulation on the river ecosystem. The rapid decline in ecosystem functions and increasing pressure for water prompted the development of various management strategies, leading to the Murray-Darling Basin Plan. The plan included the recovery of up to 2,800 GL yr^{-1} of water for environmental water provisions (MDBA 2014). To deliver environmental water in the most effective way, planning of major environmental structures such as regulators, levees channels and fish-ways began (MDBA 2012). There is a growing interest in the construction and operation of environmental flow regulators throughout the Murray-Darling Basin (Wallace and Furst 2016). It was the construction of a flow regulator at the Chowilla Floodplain that provided the impetus for the design of this research project and led to its selection as the study site.

The Chowilla Floodplain

Chowilla Floodplain (Figure 1-3), lies in the South part of the Murray-Darling Basin, and is one of the major floodplains adjoining the River Murray in its lower reaches. The floodplain straddles the South Australia- New South Wales border covering an area of 17,700 hectares. It has a semi-arid climate with an annual rainfall of 250 mm yr^{-1} (Kingsford 2000) . Because of its low rainfall, the floodplain relies on flows from upstream, largely from the upper Murray but also the Darling River (Maheshwari et al. 1995). It is one of the six Icon Sites in the Murray Darling Basin Authority's *The Living Murray Program* (MDBA 2012). It also forms part of the Riverland Ramsar site, recognised as a wetland of international importance under the Ramsar Convention (Taylor et al. 1996, MDBA 2012).

The Chowilla Floodplain contains a large diversity of habitat types as a result of its complex geomorphology and hydrological variability. It comprises a combination of lentic and lotic habitats, including lakes, wetlands, anabranches, and shallow depressions. Water diverted from the MRC upstream of Lock and Weir 6 (named Lock 6 hereafter), enters into a network of streams and passes into the main anabranch of the floodplain, Chowilla Creek, which passes back into the MRC approximately 8 km downstream of Lock 6 (Jolly et al. 1994). The hydraulics of the Chowilla anabranch system is controlled by Lock 6. Inflows to the Chowilla anabranch system are controlled by a combination of river discharge, water levels in the river, and the height of the Lock 6 (Sharley and Huggan 1995). Water levels at the lower reaches of the anabranch are controlled by a combination of river discharge, inflows through the anabranch and the height of the next downstream weir, Lock and Weir 5 (named Lock 5 hereafter), which lies about 40 kilometres downstream of Chowilla Creek confluence with the MRC of the River Murray (Sharley and Huggan 1995).

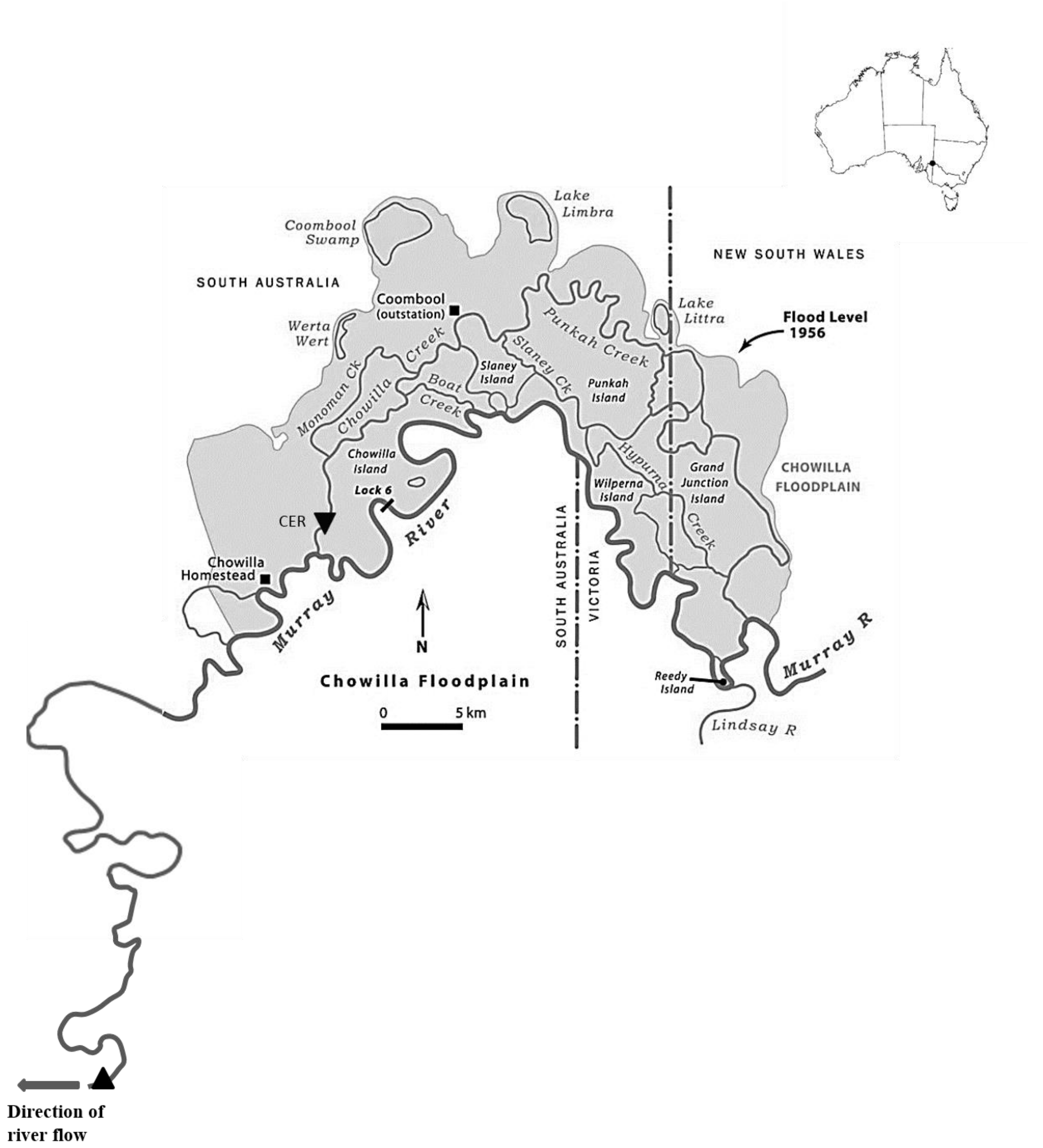

Figure 1-3: The Chowilla Floodplain and the adjacent River Murray (modified from (MDBA 2012)) showing the Chowilla Environmental Regulator (CER) (black inverted triangle) on the Chowilla Creek, Lock 5 (black triangle) on the MRC; and the direction of flow (arrow) on the MRC of the River Murray. The boundary of the floodplain (shaded grey) is defined by the extent of the historically significant 1956 flood.

There are numerous inlet creeks that feed from the River Murray into the permanent Chowilla Creek (Figure 1-3), which, during periods of high flow, becomes connected to a series of temporary creeks, wetlands and lakes. Once the flow breaches the banks of the MRC of the River Murray at approximately 33000 ML d^{-1}, a range of habitats in the Chowilla Floodplain including, fast and slow meandering creeks, ephemeral depressions, abandoned channels and swales and cut-off meanders become inundated (Mackay 1990). Discharge, measured as flow to South Australia (QSA) of 150,000 ML d^{-1} is required to completely inundate the Chowilla Floodplain. Under regulated low flow conditions, QSA is < 7000 ML d^{-1} (Sharley and Huggan 1995).

Due to the intensive regulation of the River Murray and the associated increasing diversions of flow, the floodplain has undergone severe decline in environmental condition (MDBA 2012). The effect of flow regulation and diversions on the Chowilla Floodplain has significantly reduced the flooding frequency, extent and duration of floods (Table 1-1). Small floods of the extent of about 40 000 ML d^{-1} that once occurred 91 of every 100 years now only occur 40 years in 100, and large floods of the extent 110 000 ML d^{-1} that once occurred 27 of every 100 years now only occur 5 years in 100 (Table 1-1) (MDBA 2012). The flow regulation and diversions significantly affected native fauna and flora. The health of the icon site's river red gum (*Eucalyptus camaldulensis*) and black box (*E. largiflorens*) woodlands rapidly declined. Chowilla Environmental Regulator (CER) was constructed through *The Living Murray* (TLM) Program that facilitates the use of environmental water to improve the ecological function of the floodplain by increasing the frequency, duration and extent of floodplain inundation (MDBA 2012).

CER was constructed in 2014 in Chowilla Creek, approximately 1.45 km upstream from where Chowilla Creek re-joins the River Murray in the South Australian section of the river (Figure 1-3). There are several other ancillary structures on the floodplain that control water levels and outflow on smaller flow paths. Used in combination with Lock 6, the CER together with other ancillary structures enabled water levels to be raised within the anabranch. This increase in the water level helped environmental water to be delivered to the floodplain and its associated wetlands and temporary creeks.

Table 1-1: Flooding extent, frequency, and duration under natural and current conditions: Chowilla Floodplain (obtained from (MDBA 2012))

River Murray flow (ML/day)	Area inundated (ha)	Return period ** (Number of times peak flows occur in 100 years)		Duration (Number of months flow is exceeded)	
		Natural	Current	Natural	Current
3,000	-	100	100	11.8	11.9
10,000	-	100	94	10.1	4.6
20,000	-	99	63	7.8	4.6
40,000	1,400	91	40	4.9	3.3
45,000	1,700	83	34	4.6	3.2
55,000	3,100	-	-	-	-
65,000	4,800	-	-	-	-
75,000	6,700	45	-	-	-
80,000	8,200	45	12	3.2	2.6
90,000	11,100	37	11	3.1	2.1
110,000	14,200	27	5	2.4	3.2
140,000	16,800	14	4	2.1	2.5
200,000	17,700	3	1	2.0	2.0
300,000	17,700	1	0	2.0	-

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

The water level at the CER is typically 16.3 m Australian Height Datum (AHD) under normal river operation conditions (Wallace and Furst 2016) and the maximum achievable operating height for the CER is 19.87 m AHD, but during the first managed inundation event, the maximum height of the regulator was set to 19.10 m AHD (Figure 1-4). Accordingly, water level at the CER was raised gradually from 16.90 m AHD to 19.10 m AHD between 10 September and 14 October 2014, which inundated a floodplain area of approximately 23 km^2. Water was then held at the level of about 19.10 m AHD for two weeks, between 15 October and 28

October 2014. Water level decreased from 29 October to 03 December 2014, and returned to the level prior to the inundation.

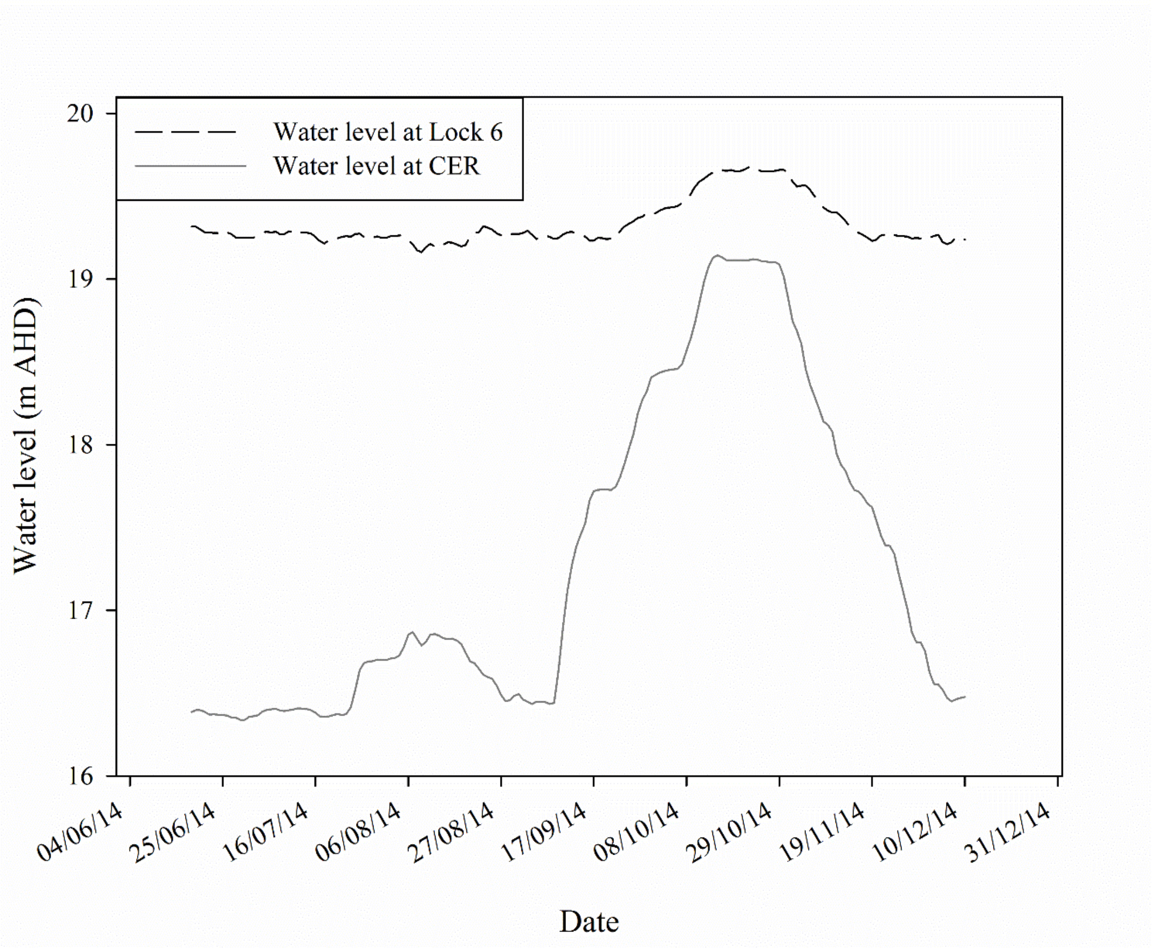

Figure 1-4: Water levels recorded at upstream of Lock 6 (black dotted line) and at the CER (grey solid line) during the 2014 managed inundation event.

The height of the Lock 6 was raised from normal pool level, which is 19.25 m AHD to 19.68 m AHD (Figure 1-4) to facilitate the managed inundation event in 2014. Flow to South Australia was regulated by releases from upstream storages during the event (Wallace and Furst 2016). About 50 days before the managed inundation commenced, there was a small rise in flow to South Australia, with discharge peaking at 18,000 ML d^{-1} for a short duration, compared to a pre-flow level of 4,500 ML d^{-1} (Figure 1-5). This inflow raised the water level in Lock 5, and the backwater curve created by Lock 5 raised water levels within Chowilla Anabranch, causing an unexpected increase in the water level prior to the planned managed inundation. Flow then declined again prior to the managed inundation. During the testing period of the CER, discharge in the River Murray upstream of the Chowilla Creek inlet was in the range of 5,000 to 10,000 ML day^{-1}.

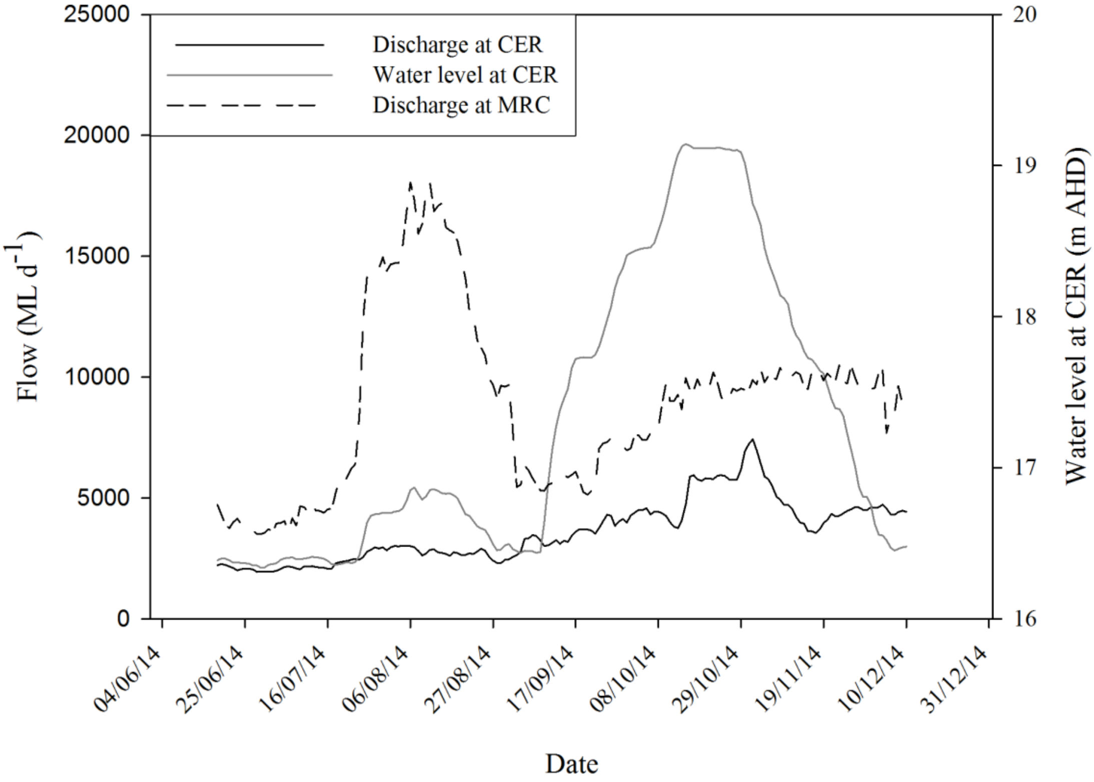

Figure 1-5: Hydrographs of flow (ML d^{-1}) at CER (black solid line) and in the MRC (black dotted line), and the water level (m AHD) at CER (grey solid line) throughout the study period.

REFERENCES

ABC. 2013. Murray-Darling Basin Plan.

Arthington, A. H., S. R. Balcombe, G. A. Wilson, M. C. Thoms, and J. Marshall. 2005. Spatial and temporal variation in fish-assemblage structure in isolated waterholes during the 2001 dry season of an arid-zone floodplain river, Cooper Creek, Australia. Marine and Freshwater Research **56**:25-35.

Arthington, Á. H., R. J. Naiman, M. E. McClain, and C. Nilsson. 2010. Preserving the biodiversity and ecological services of rivers: new challenges and research opportunities. Freshwater Biology **55**:1-16.

Baker, P. D., J. D. Brookes, M. D. Burch, H. R. Maier, and G. G. Ganf. 2000. Advection, growth and nutrient status of phytoplankton populations in the lower

River Murray, South Australia. Regulated Rivers: Research & Management **16**:327-344.

Baldwin, D. S. 1999. Dissolved organic matter and phosphorus leached from fresh and 'terrestrially'aged river red gum leaves: implications for assessing river–floodplain interactions. Freshwater Biology **41**:675-685.

Baldwin, D. S., M. J. Colloff, S. M. Mitrovic, N. R. Bond, and B. Wolfenden. 2016. Restoring dissolved organic carbon subsidies from floodplains to lowland river food webs: a role for environmental flows? Marine and Freshwater Research.

Baldwin, D. S., G. N. Rees, J. S. Wilson, M. J. Colloff, K. L. Whitworth, T. L. Pitman, and T. A. Wallace. 2012. Provisioning of bioavailable carbon between the wet and dry phases in a semi-arid floodplain. Oecologia:1-12.

Bartels, P., J. Cucherousset, C. Gudasz, M. Jansson, J. Karlsson, L. Persson, K. Premke, A. Rubach, K. Steger, and L. J. Tranvik. 2012. Terrestrial subsidies to lake food webs: an experimental approach. Oecologia **168**:807-818.

Benjamin, J. R., J. R. Bellmore, and G. A. Watson. 2016. Response of ecosystem metabolism to low densities of spawning Chinook Salmon. Freshwater Science **35**:810-825.

Benke, A. C., I. Chaubey, G. M. Ward, and E. L. Dunn. 2000. Flood pulse dynamics of an unregulated river floodplain in the southeastern US coastal plain. Ecology **81**:2730-2741.

Bowling, L. and P. Baker. 1996. Major cyanobacterial bloom in the Barwon-Darling River, Australia, in 1991, and underlying limnological conditions. Marine and Freshwater Research **47**:643-657.

Bunn, S. E., P. M. Davies, and M. Winning. 2003. Sources of organic carbon supporting the food web of an arid zone floodplain river. Freshwater Biology **48**:619-635.

Burford, M. A., A. J. Cook, C. S. Fellows, S. R. Balcombe, and S. E. Bunn. 2008. Sources of carbon fuelling production in an arid floodplain river. Marine and Freshwater Research **59**:224-234.

Cole, J. J., M. L. Pace, S. R. Carpenter, and J. F. Kitchell. 2000. Persistence of net heterotrophy in lakes during nutrient addition and food web manipulations. Limnology and Oceanography **45**:1718-1730.

Cook, R. A., B. Gawne, R. Petrie, D. S. Baldwin, G. N. Rees, D. L. Nielsen, and N. S. Ning. 2015. River metabolism and carbon dynamics in response to flooding in a lowland river. Marine and Freshwater Research.

Cremona, F., T. Kõiv, V. Kisand, A. Laas, P. Zingel, H. Agasild, T. Feldmann, A. Järvalt, P. Nõges, and T. Nõges. 2014. From bacteria to piscivorous fish: estimates of whole-lake and component-specific metabolism with an ecosystem approach. PloS One **9**:e101845.

Delong, M. D. and J. H. Thorp. 2006. Significance of instream autotrophs in trophic dynamics of the Upper Mississippi River. Oecologia **147**:76-85.

Dolbeth, M., M. Cusson, R. Sousa, and M. A. Pardal. 2012. Secondary production as a tool for better understanding of aquatic ecosystems. Canadian journal of fisheries and aquatic sciences **69**:1230-1253.

Extence, C. 1981. The effect of drought on benthic invertebrate communities in a lowland river. Hydrobiologia **83**:217-224.

Fellows, C. S., J. E. Clapcott, J. W. Udy, S. E. Bunn, B. D. Harch, M. J. Smith, and P. M. Davies. 2006. Benthic metabolism as an indicator of stream ecosystem health. Hydrobiologia **572**:71-87.

Fellows, C. S., M. L. Wos, P. Pollard, and S. Bunn. 2007. Ecosystem metabolism in a dryland river waterhole. Marine and Freshwater Research **58**:250-262.

Findlay, S. and R. L. Sinsabaugh. 1999. Unravelling the sources and bioavailability of dissolved organic matter in lotic aquatic ecosystems. Marine and Freshwater Research **50**:781-790.

Gawne, B., C. Merrick, D. G. Williams, G. Rees, R. Oliver, P. M. Bowen, S. Treadwell, G. Beattie, I. Ellis, and J. Frankenberg. 2007. Patterns of primary and heterotrophic productivity in an arid lowland river. River Research and Applications **23**:1070-1087.

Gillooly, J. F., J. H. Brown, G. B. West, V. M. Savage, and E. L. Charnov. 2001. Effects of size and temperature on metabolic rate. Science **293**:2248-2251.

Gurnell, A. M. and G. E. Petts. 2002. Island-dominated landscapes of large floodplain rivers, a European perspective. Freshwater Biology **47**:581-600.

Hadwen, W. L., C. S. Fellows, D. P. Westhorpe, G. N. Rees, S. M. Mitrovic, B. Taylor, D. S. Baldwin, E. Silvester, and R. Croome. 2010. Longitudinal trends in river functioning: patterns of nutrient and carbon processing in three Australian rivers. River Research and Applications **26**:1129-1152.

Hanson, P. C., D. L. Bade, S. R. Carpenter, and T. K. Kratz. 2003. Lake metabolism: Relationships with dissolved organic carbon and phosphorus. Limnology and Oceanography **48**:1112-1119.

Hladyz, S., D. Nielsen, P. Suter, and E. Krull. 2012. Temporal variations in organic carbon utilization by consumers in a lowland river. River Research and Applications **28**:513-528.

Howarth, R., R. Schneider, and D. Swaney. 1996. Metabolism and organic carbon fluxes in the tidal freshwater Hudson River. Estuaries and Coasts **19**:848-865.

Humphries, P., H. Keckeis, and B. Finlayson. 2014. The river wave concept: integrating river ecosystem models. BioScience:biu130.

Humphries, P. and P. Lake. 2000. Fish larvae and the management of regulated rivers. River Research and Applications **16**:421-432.

Huryn, A. D., R. H. Riley, R. G. Young, C. J. Arbuckle, K. Peacock, and G. Lyon. 2001. Temporal shift in contribution of terrestrial organic matter to consumer production in a grassland river. Freshwater Biology **46**:213-226.

Jansson, R., C. Nilsson, and B. Malmqvist. 2007. Restoring freshwater ecosystems in riverine landscapes: the roles of connectivity and recovery processes. Freshwater Biology **52**:589-596.

Jolly, I. D., G. R. Walker, and K. A. Narayan. 1994. Floodwater recharge processes in the Chowilla anabranch system, South Australia. Soil Research **32**:417-435.

Junk, W. J., P. B. Bayley, and R. E. Sparks. 1989. The flood pulse concept in river-floodplain systems. Canadian special publication of fisheries and aquatic sciences **106**:110-127.

Kaminskas, S. and P. Humphries. 2009. Diet of Murray cod (Maccullochella peelii peelii)(Mitchell) larvae in an Australian lowland river in low flow and high flow years. Hydrobiologia **636**:449-461.

King, A., Z. Tonkin, and J. Mahoney. 2009. Environmental flow enhances native fish spawning and recruitment in the Murray River, Australia. River Research and Applications **25**:1205-1218.

Kingsford, R. T. 2000. Ecological impacts of dams, water diversions and river management on floodplain wetlands in Australia. Austral Ecology **25**:109-127.

Leslie, D. 1995. Moira Lake: a case study of deterioration of a Murray River natural resource. Forestry Science.

Lindeman, R. L. 1942. The trophic-dynamic aspect of ecology. Ecology **23**:399-417.

Lyon, J., I. Stuart, D. Ramsey, and J. O'Mahony. 2010. The effect of water level on lateral movements of fish between river and off-channel habitats and implications for management. Marine and Freshwater Research **61**:271-278.

Mackay, N. 1990. Understanding the Murray. The Murray.

Maheshwari, B., K. F. Walker, and T. McMahon. 1995. Effects of regulation on the flow regime of the River Murray, Australia. Regulated Rivers: Research & Management **10**:15-38.

McGinness, H. M. and A. D. Arthur. 2011. Carbon dynamics during flood events in a lowland river: the importance of anabranches. Freshwater Biology **56**:1593-1605.

MDBA. 2012. Chowilla Floodplain Environmental Water Management Plan 2012. Australian Government: Canberra, ACT.

MDBA. 2014. Preliminary Overview of Constraints to Environmental Water Delivery in the Murray–Darling Basin. Retrieved 1/04/2014, 2014, from http://www.mdba. gov. au/what-we-do/water-planning/managingconstraints/constraints-overview/nsw.

Medeiros, E. S. and A. H. Arthington. 2011. Allochthonous and autochthonous carbon sources for fish in floodplain lagoons of an Australian dryland river. Environmental Biology of Fishes **90**:1-17.

Mitrovic, S. M. and D. S. Baldwin. 2016. Allochthonous dissolved organic carbon in river, lake and coastal systems: transport, function and ecological role. Marine and Freshwater Research **67**:i-iv.

Mulholland, P., C. S. Fellows, J. Tank, N. Grimm, J. Webster, S. Hamilton, E. Martí, L. Ashkenas, W. Bowden, and W. Dodds. 2001. Inter-biome comparison of factors controlling stream metabolism. Freshwater Biology **46**:1503-1517.

Nanson, G. C. and A. D. Knighton. 1996. Anabranching rivers: their cause, character and classification. Earth Surface Processes and Landforms **21**:217-239.

Neckles, H. A., H. R. Murkin, and J. A. Cooper. 1990. Influences of seasonal flooding on macroinvertebrate abundance in wetland habitats. Freshwater Biology **23**:311-322.

Nielsen, D., T. Hillman, and F. Smith. 1999. Effects of hydrological variation and planktivorous competition on macroinvertebrate community structure in experimental billabongs. Freshwater Biology **42**:427-444.

Nielsen, D., F. Smith, T. Hillman, and R. Shiel. 2000. Impact of water regime and fish predation on zooplankton resting egg production and emergence. Journal of Plankton Research **22**:433-446.

Nielsen, D. L., R. A. Cook, N. Ning, B. Gawne, and R. Petrie. 2015. Carbon and nutrient subsidies to a lowland river following floodplain inundation. Marine and Freshwater Research.

Nilsson, C., C. A. Reidy, M. Dynesius, and C. Revenga. 2005. Fragmentation and flow regulation of the world's large river systems. Science **308**:405-408.

Odum, E. P. and G. W. Barrett. 1971. Fundamentals of ecology. Saunders Philadelphia.

Odum, H. T. 1956. Primary production in flowing waters. Limnology and Oceanography:102-117.

Oliver, R., B. Hart, J. Olley, M. Grace, C. Rees, and G. Caitcheon. 1999. The Darling River: Algal growth and the cycling and sources of nutrients.

Oliver, R. L. and C. J. Merrick. 2006. Partitioning of river metabolism identifies phytoplankton as a major contributor in the regulated Murray River (Australia). Freshwater Biology **51**:1131-1148.

Polis, G. A., W. B. Anderson, and R. D. Holt. 1997. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. Annual review of ecology and systematics:289-316.

Pomeroy, L. R. 1974. The ocean's food web, a changing paradigm. BioScience **24**:499-504.

Robertson, A., S. Bunn, P. Boon, and K. Walker. 1999. Sources, sinks and transformations of organic carbon in Australian floodplain rivers. Marine and Freshwater Research **50**:813-829.

Robertson, A., A. Burns, and T. Hillman. 2016. Scale dependent lateral exchanges of organic carbon in a dryland river during a high flow experiment. Marine and Freshwater Research.

Ruhí, A., I. Muñoz, E. Tornés, R. J. Batalla, D. Vericat, L. Ponsatí, V. Acuña, D. Schiller, R. Marcé, and G. Bussi. 2016. Flow regulation increases food-chain length through omnivory mechanisms in a Mediterranean river network. Freshwater Biology **61**:1536-1549.

Schindler, D. E., S. R. Carpenter, J. J. Cole, J. F. Kitchell, and M. L. Pace. 1997. Influence of food web structure on carbon exchange between lakes and the atmosphere. Science **277**:248-251.

Sharley, T. and C. Huggan. 1995. Chowilla resource management plan: Final report. Murray–Darling Basin Commission, Australian Capital Territory.

Sheldon, F., A. J. Boulton, and J. T. Puckridge. 2002. Conservation value of variable connectivity: aquatic invertebrate assemblages of channel and floodplain habitats of a central Australian arid-zone river, Cooper Creek. Biological conservation **103**:13-31.

Sherman, B. S., I. T. Webster, G. J. Jones, and R. L. Oliver. 1998. Transitions between Auhcoseira and Anabaena dominance in a turbid river weir pool. Limnol. Oceanogr **43**:1902-1915.

Staehr, P. A., D. Bade, M. C. Van de Bogert, G. R. Koch, C. Williamson, P. Hanson, J. J. Cole, and T. Kratz. 2010. Lake metabolism and the diel oxygen technique: state of the science. Limnology and Oceanography: Methods **8**:628-644.

Staehr, P. A. and K. Sand-Jensen. 2007. Temporal dynamics and regulation of lake metabolism. Limnology and Oceanography **52**:108-120.

Staehr, P. A., J. M. Testa, W. M. Kemp, J. J. Cole, K. Sand-Jensen, and S. V. Smith. 2012. The metabolism of aquatic ecosystems: history, applications, and future challenges. Aquatic Sciences **74**:15-29.

Taylor, P. J., G. R. Walker, G. Hodgson, T. J. Hatton, and R. L. Correll. 1996. Testing of a GIS model ofEucalyptus Iargiflorens health on a semiarid, saline floodplain. Environmental management **20**:553-564.

Thomaz, S. M., L. M. Bini, and R. L. Bozelli. 2007. Floods increase similarity among aquatic habitats in river-floodplain systems. Hydrobiologia **579**:1-13.

Thoms, M. C. 2003. Floodplain–river ecosystems: lateral connections and the implications of human interference. Geomorphology **56**:335-349.

Thomson, C. 1994. The impact of river regulation on the natural flows of the Murray-Darling Basin. Murray-Darling Basin Commission.

Thorp, J. H. and M. D. Delong. 1994. The riverine productivity model: an heuristic view of carbon sources and organic processing in large river ecosystems. Oikos **70**:305-308.

Thorp, J. H. and M. D. Delong. 2002. Dominance of autochthonous autotrophic carbon in food webs of heterotrophic rivers. Oikos **96**:543-550.

Thorp, J. H., M. D. Delong, K. S. Greenwood, and A. F. Casper. 1998. Isotopic analysis of three food web theories in constricted and floodplain regions of a large river. Oecologia **117**:551-563.

Tockner, K., F. Malard, and J. Ward. 2000. An extension of the flood pulse concept. Hydrological Processes **14**:2861-2883.

Tockner, K., D. Pennetzdorfer, N. Reiner, F. Schiemer, and J. Ward. 1999. Hydrological connectivity, and the exchange of organic matter and nutrients in a dynamic river–floodplain system (Danube, Austria). Freshwater Biology **41**:521-535.

Tockner, K. and J. Ward. 1999. Biodiversity along riparian corridors. Large Rivers **11**:293-310.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The river continuum concept. Canadian journal of fisheries and aquatic sciences **37**:130-137.

Walker, K. 1985. A review of the ecological effects of river regulation in Australia. Pages 111-129 Perspectives in Southern Hemisphere Limnology. Springer.

Walker, K. F., F. Sheldon, and J. T. Puckridge. 1995. A perspective on dryland river ecosystems. Regulated Rivers: Research & Management **11**:85-104.

Wallace, T. A. and D. Furst. 2016. Open water metabolism and dissolved organic carbon in response to environmental watering in a lowland river–floodplain complex. Marine and Freshwater Research.

Ward, J. and J. Stanford. 1995. Ecological connectivity in alluvial river ecosystems and its disruption by flow regulation. Regulated Rivers: Research & Management **11**:105-119.

Ward, J., K. Tockner, and F. Schiemer. 1999. Biodiversity of floodplain river ecosystems: ecotones and connectivity. Regulated Rivers: Research & Management **15**:125-139.

Watkins, S. C., G. Quinn, and B. Gawne. 2010. Changes in organic-matter dynamics and physicochemistry, associated with riparian vegetation loss and river regulation in floodplain wetlands of the Murray River, Australia. Marine and Freshwater Research **61**:1207-1217.

Wolfenden, B. J., S. M. Wassens, K. M. Jenkins, D. S. Baldwin, T. Kobayashi, and J. Maguire. 2017. Adaptive Management of Return Flows: Lessons from a Case Study in Environmental Water Delivery to a Floodplain River. Environmental management:1-16.

Woodwell, G. M. and R. H. Whittaker. 1968. Primary production in terrestrial ecosystems. American Zoologist **8**:19-30.

Young, R. G. and A. D. Huryn. 1996. Interannual variation in discharge controls ecosystem metabolism along a grassland river continuum. Canadian journal of fisheries and aquatic sciences **53**:2199-2211.

Zampatti, B. P., C. M. Bice, and P. R. Jennings. 2010. Temporal variability in fish assemblage structure and recruitment in a freshwater-deprived estuary: The Coorong, Australia. Marine and Freshwater Research **61**:1298-1312.

Zeug, S. C. and K. O. Winemiller. 2008. Evidence supporting the importance of terrestrial carbon in a large-river food web. Ecology **89**:1733-1743.

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Overall percentage (%)	80 %		
Certification:	This paper reports on original research I conducted during the period of my Higher Degree by Research candidature and is not subject to any obligations or contractual agreements with a third party that would constrain its inclusion in this thesis. I am the primary author of this paper.		
Signature		Date	25 May 2017

Co-author Contributions

By signing the Statement of Authorship, each author certifies that:

i. the candidate's stated contribution to the publication is accurate (as detailed above);
ii. permission is granted for the candidate in include the publication in the thesis; and
iii. the sum of all co-author contributions is equal to 100% less the candidate's stated contribution

Name of Co-author	Roderick Oliver		
Contribution to the paper	Provided input in conceiving the study and design of experiments; supervised data analysis and interpretation; reviewed the manuscript		
Signature		Date	25 May 2017

Name of Co-author	Kane Aldridge		
Contribution to the paper	Provided input in conceiving the study and design of experiments; supervised data analysis and interpretation; reviewd the manuscript		
Signature		Date	25 May 2017

Name of Co-author	Todd Wallace		
Contribution to the paper	Provided input in conceiving the study and design of experiments; helped in field data collection; reviewed the manuscript		
Signature		Date	25 May 2017

Name of Co-author	Justin Brookes		
Contribution to the paper	Provided input in conceiving the study and design of experiments; supervised data analysis and interpretation; reviewed the manuscript		
Signature		Date	25 May 2017

CHAPTER 2

SPATIO-TEMPORAL VARIABILITY IN ECOSYSTEM METABOLISM DURING A MANAGED FLOODPLAIN INUNDATION IN THE LOWER RIVER MURRAY, SOUTH AUSTRALIA

ABSTRACT

The importance of floods in mobilising and transporting terrestrial carbon and nutrients and enhancing riverine productivity has been well documented. However, the magnitude and duration of natural flooding regimes is highly altered in regulated rivers, disrupting the lateral exchange of organic material between habitats. With constraints to environmental water delivery, management authorities are constructing and operating floodplain environmental flow regulators that help inundate greater areas of floodplains at specified flow levels. This technique provides new management opportunities to reinstate lateral connectivity between habitats. In this study, we compared ecosystem metabolism at two sites in an anabranch creek of the Chowilla Floodplain adjacent to lower River Murray in South Australia. Measurements were made during periods of lateral hydrologic connection and disconnection of the anabranch creek to the adjacent floodplain, resulting from the operation of a newly constructed environmental flow regulator. We observed substantial increase in ecosystem productivity rates at both sites in the anabranch as compared to the river reference site, both during an initial rise in the anabranch water level that resulted from increased river flow to South Australia just prior to the operation of the regulator, and during a managed inundation event using the regulator. However, net ecosystem productivity (NEP) rates were different between anabranch sites during the managed inundation event; with net autotrophy ($NEP > 0$) observed at the upstream site compared to balanced metabolism ($NEP \sim 0$) at the downstream site. Spatial variability in the metabolic activity in the anabranch also occurred in response to increased river flows that connected the anabranch creek to the floodplain. Further studies on the importance of the drivers of this spatial and temporal variability is required to enable optimal management of floodplain inundation. To achieve this, we need better understanding of how the mosaic of habitats present on the floodplain moderate the benefits of enhanced connectivity through differences in geomorphology and water quality. This information will be important in supporting improved ecosystem productivity in large and regulated floodplain rivers where environmental water provisions are managed by the operation of floodplain regulators.

KEY WORDS: Ecosystem metabolism, managed inundation, environmental flow, floodplain rivers

INTRODUCTION

River ecosystems obtain energy from two primary sources of organic materials: autochthonous materials, which are produced within the river by photosynthetic organisms and include primary producers such as phytoplankton, benthic algae and aquatic plants (Thorp and Delong 1994, 2002, Bunn et al. 2003); and allochthonous materials, which are imported into the river from the surrounding floodplain, primarily through flooding and surface runoff (Thorp et al. 1998, Medeiros and Arthington 2011, Bartels et al. 2012). Several conceptual models of river ecosystem functioning make differing predictions about the primary sources of organic material in lowland rivers, in relation to varying patterns of connectivity to upstream reaches, riparian zones and floodplains (Vannote et al. 1980, Junk et al. 1989, Thorp and Delong 1994, 2002). The input, transformation, and movement of the organic material through food webs are key processes for the functioning of river ecosystems.

During dry periods, floodplains accumulate organic carbon, primarily through leaf litter and detritus, which can be transported to the river channel through flooding, providing a pulse of energy to riverine food-webs (Baldwin 1999, Burford et al. 2008). Thus, flooding is a critical process for driving the productivity of floodplain-river ecosystems (Junk et al. 1989, Robertson et al. 1999, Tockner et al. 1999). In such systems, aquatic biota are dependent on seasonal flooding not only for providing physical connectivity allowing exchange of individuals, but also by introducing additional carbon sources into the system (Medeiros and Arthington 2008, Abrantes and Sheaves 2010, Medeiros and Arthington 2011, Bartels et al. 2012). However, despite the apparent importance of floodplain inundation in stimulating riverine productivity, many lowland rivers increasingly have reduced connections to adjacent floodplains because of lowered flow levels, a result of over extraction, diversion and regulation. This has reduced the frequency, duration and magnitude of floods, thereby disrupting the exchange of resources between the floodplains and rivers (Junk et al. 1989, Robertson et al. 1999, Tockner et al. 1999, Benke et al. 2000, Nilsson et al. 2005, Gawne et al. 2007). As a consequence, river metabolism tends to shift towards autotrophy due to the extended periods of reduced delivery of allochthonous nutrients and carbon, a condition believed to mostly reduce system respiration (Dahm et al. 2003, Zeug and Winemiller 2008).

Several studies conducted in Australian regulated rivers have observed balanced or energy-limited systems, with the net ecosystem production being close to zero (Vink et al. 2005, Oliver and Merrick 2006); and have concluded that the autotrophic sources of carbon dominate the food webs (Bunn et al. 2003, Oliver and Merrick 2006, Hadwen et al. 2010). However, these studies were largely conducted during periods when there was no or limited connectivity with the adjacent floodplain, thus precluding an assessment of the role floodplain resources have in supporting river metabolism. A plethora of studies on the influence of natural flood events in rivers have demonstrated how floodplain inundation results in the transportation of floodplain resources to the main river channel (MRC), for example, dissolved organic carbon (DOC) (McGinness and Arthur 2011, Nielsen et al. 2015), nutrients (Nielsen et al. 2015), phytoplankton (Tockner et al. 1999, Nielsen et al. 2015) and zooplankton (Furst et al. 2014, Nielsen et al. 2015). These studies confirm the important role of floodplains in stimulating ecosystem productivity (Junk et al. 1989, Robertson et al. 1999, Tockner et al. 1999), and highlight the need to understand the role floodplain habitats play in supporting riverine productivity during managed flooding events, especially where natural flood events are significantly reduced due to river regulation.

Environmental flows have emerged as a major restoration tool in regulated rivers, as they can enhance the ecological conditions, impaired as a result of regulation, by partially reinstating the connectivity between floodplain and riverine habitats (Arthington et al. 2006, Lind et al. 2007, King et al. 2010, Baldwin et al. 2016). However, in such systems, there are multiple constraints to providing adequate flows at large spatial scales. (MDBA 2014). As a result, management authorities are increasingly considering the use of floodplain regulators to enable the inundation of larger areas of floodplains for a given flow in order to increase the frequency, duration and extent of floodplain inundation.

Floodplain anabranches are known to be comparatively easy to target for management, as they require relatively small amounts of water to maintain lateral hydrological connection compared to other floodplain habitats (McGinness and Arthur 2011), and they provide suitable sites for constructing regulators. Anabranch channels are restricted in their area of direct influence at low flows, but during periods of higher flows, floodplain anabranch creeks become connected to low lying temporary creeks, wetlands, and lakes and eventually the extended floodplain. Consequently, the ecological response at an individual anabranch site will be affected by its position in relation to the nearby peripheral floodplain habitats and its location in the increasingly complex floodplain stream network. Its direct and indirect connections to the river is expected to impact the ecological response, as these conditions influence the flood residence times and the physico-chemical characteristics of the source water (Thomaz et al. 2007). Understanding the role of anabranch habitats in connecting floodplain components with the river and improving ecosystem productivity is therefore a critical area of research, and can inform how the use of environmental regulators can be optimised to maximise ecological benefits.

In this study, we measured the ecosystem metabolism at two anabranch sites in Chowilla Creek during a period of increased connectivity with the adjacent floodplain, established through the operation of a newly installed regulator, and compared the results against a reference site in the main channel of the River Murray. The operation of the regulator facilitated the managed inundation of approximately 23 km^2 area of the floodplain, about 33% of the potential maximum inundation extent that could be achieved (Wallace and Furst 2016). We tested the hypothesis that floodplain inundation can stimulate ecosystem productivity within floodplain anabranches by mobilising floodplain DOC and nutrients.

METHODS

Study Area Description

Chowilla Floodplain (Figure 2-1) (33°57′ S, 140°56′29 E) is one of the major floodplain complexes adjoining the River Murray. Covering an area of 17,700 hectares, it has a semi-arid climate with an annual rainfall of 250 mm yr^{-1} (Kingsford 2000) and is one of the six Icon Sites in the Murray Darling Basin Authority's *The Living Murray Program* (MDBA 2012). It also forms part of the Riverland Ramsar site, a wetland of international importance under the Ramsar Convention (Taylor et al. 1996, MDBA 2012). Chowilla Floodplain contains a large diversity of habitat types as a result of its complex geomorphology and hydrological variability. It comprises a combination of lentic and lotic habitats, including lakes, wetlands, anabranches, and shallow depressions. There are numerous inlet creeks from the River Murray that feed into the permanent Chowilla Creek, which, during periods of high flow, becomes connected to a series of temporary creeks, wetlands and lakes (Wallace and Furst 2016). Water diverted from the MRC upstream of Lock 6 (Figure 2-1) enters into a network of streams and passes into the main anabranch of the floodplain, Chowilla Creek, which passes back into the MRC approximately 8 kms downstream of Lock 6 (Jolly et al. 1994). More detailed description on the position and operation of Lock 6 can be obtained from Wallace and Furst (2016).

The Chowilla Environmental Regulator (CER) was constructed in 2014 in Chowilla Creek, approximately 1.45 km upstream from where Chowilla Creek re-enters the Murray River, with the purpose of improving the ecological conditions of the floodplain by increasing the frequency, duration, and extent of floodplain inundation. On 10 September 2014, the first testing of the structural integrity of the CER was undertaken, providing the opportunity to investigate how aquatic ecosystem metabolism responds to managed inundations.

Study Sites

Ecosystem metabolism was assessed and compared between two sites (Figure 2-1), approximately 10 km apart in the Chowilla Creek. These sites were established, and maintained, by the South Australian Government's Department of Environment,

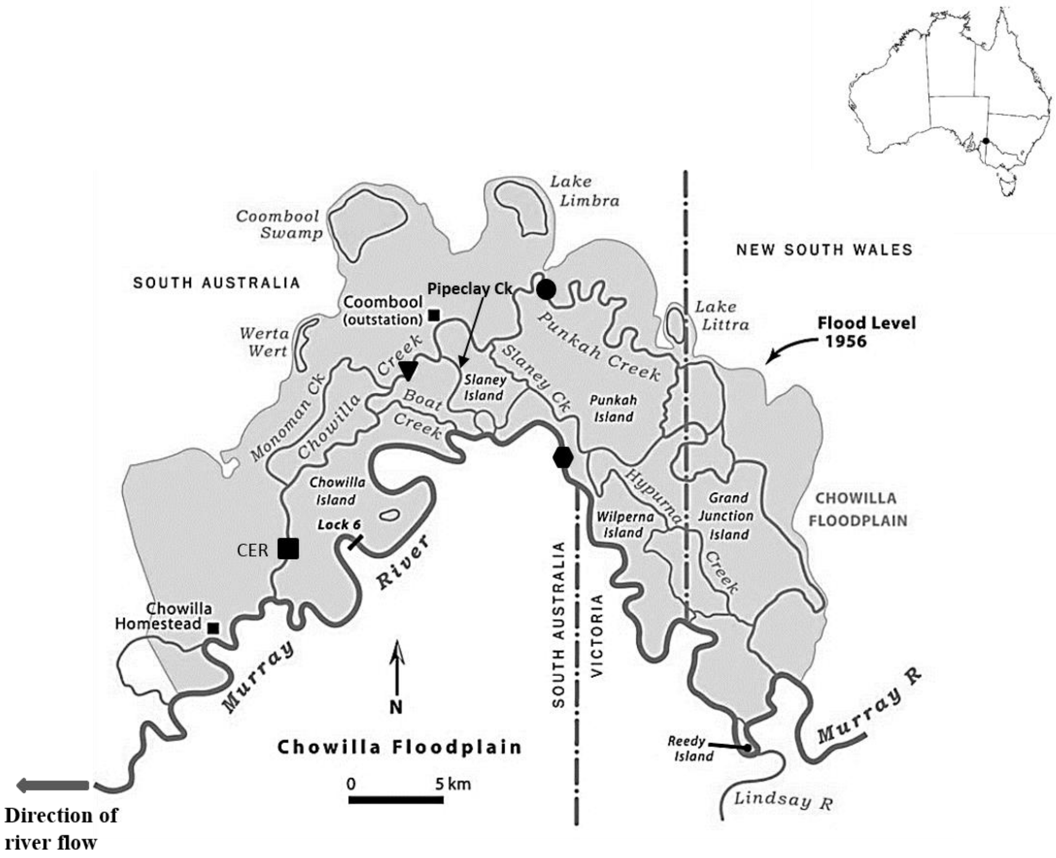

Figure 2-1: The Chowilla Floodplain and the adjacent River Murray (modified from MDBA 2012) showing: the upstream (black circle) and downstream (inverted triangle) sites on the anabranch, along with the Chowilla Environmental Regulator (black rectangle); the reference site (black hexagon) on the MRC of the River Murray; and the direction of flow (arrow). The boundary of the floodplain (shaded grey) is defined by the extent of the historically significant 1956 flood.

Water and Natural Resources (DEWNR) and the Murray-Darling Basin Authority (MDBA). The two sites chosen vary in terms of channel network and morphology. Two inlet creeks from the River Murray, Slaney and Pipeclay, enter between the upstream and downstream sites (Figure 2-1). During periods of high inflows into the Chowilla creek, the upstream site becomes connected with shallow wetland habitats, while the downstream site is affected by the inlet creeks from the River Murray (Wallace et al. 2015). A site in the MRC (Figure 2-1), upstream of the outlet of Chowilla Creek was chosen as a reference site for the study. This site acted as an indicator of ambient water quality and productivity under non-inundated conditions.

Discharge and Chowilla Environmental Regulator Operations

The study period went from June to December 2014, with the managed floodplain inundation commencing on the 10 September (Figure 2-2). The water level at the CER is typically 16.3 m Australian Height Datum (AHD) under normal river operation conditions (Wallace and Furst 2016). About fifty days prior to the managed inundation, a small rise in the water level was recorded at the CER with a peak of 16.85 m AHD on 12 August which dropped back to 16.3 m AHD again in early September. This was the result of a significant increase in flow to South Australia from upstream, which peaked for a short duration at 18,000 ML d^{-1} compared to a previous flow of 4,500 ML d^{-1} (Figure 2-2). This increased flow raised the water level in Lock 5, creating backwater curve causing the initial increase in water level in the anabranch. In comparison, during the managed inundation of the floodplain that commenced on 10 September, discharge in the River Murray upstream of the Chowilla inlet was in the range of 5,000 to 10,000 ML day^{-1}.

The maximum achievable operating height for the CER is 19.87 m AHD, but for the managed inundation event, the maximum height of the regulator was set to 19.10 m AHD. Accordingly, water level at the CER was raised gradually from 16.90 m AHD to 19.10 m AHD between 10 September and 14 October 2014, which inundated a floodplain area of approximately 23 km^2. This period is considered the 'rising phase of the hydrograph.' Water was then held at the level of about 19.10 m AHD for two weeks, between 15 October and 28 October 2014, which is considered the 'peak of the hydrograph.' Water level decreased from 29 October to 03 December 2014, and returned to the level prior to the inundation, which is considered the 'falling phase of the hydrograph.' The period from 03 December to 10 December 2014 is considered the 'post inundation phase.'

Sampling Regime

Water quality sampling stations were established at all three sites, and were maintained by DEWNR and the MDBA. Dissolved oxygen (DO) data was collected using D'Opto loggers (ZebraTech, New Zealand), deployed about 0.6 m below the surface at each station, and recorded at 5 min intervals. Water samples for DOC, chlorophyll *a* (chl *a*) and nutrient analysis were collected at six weekly intervals prior to the inundation and weekly after the commencement of inundation. Nutrients (total phosphorus (TP), total nitrogen (TN), filterable reactive phosphorus (FRP), nitrate (NO_3) and ammonia (NH_3)) were analysed by the Environmental Analysis Laboratory, an accredited laboratory of the National Association of Testing Authorities, using standard techniques. Measurements of solar radiation, wind speed and barometric pressure were made at 10 min intervals by an automated weather station established on the Chowilla Island in February 2014 by the DEWNR.

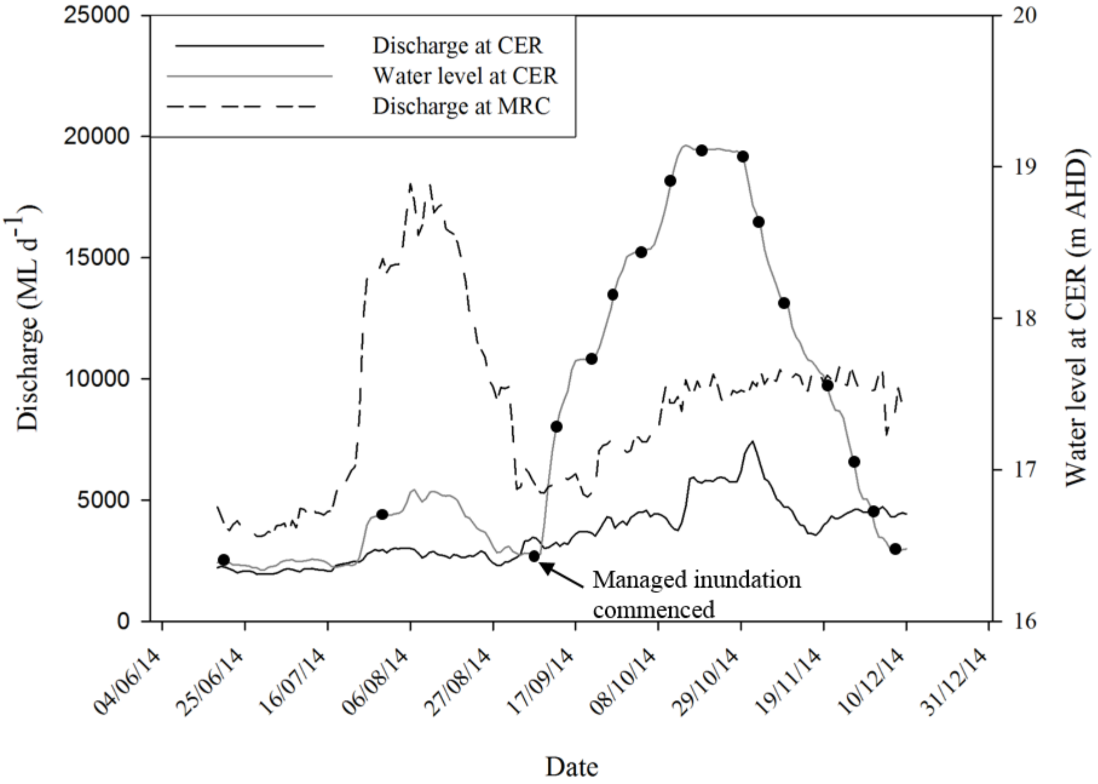

Figure 2-2: Hydrographs of flow (ML d^{-1}) at CER (black solid line) and in the MRC (black dotted line), and the water level (m AHD) at CER (grey solid line). Black dots indicate the days when water samples were collected at each study site.

Open Water Primary Production and Respiration Measurements

Open water metabolism was estimated from analyses of the daily time series of DO concentrations and light intensities using the single station analytical method (Odum 1956, Young and Huryn 1996, Oliver and Merrick 2006). The rate of change in DO concentration ($\frac{dO}{dt}$) in the open water is a function of photosynthesis, respiration and the oxygen exchange at the air-water interface:

$$\frac{dO}{dt} = AE_t^p + kD + CR \quad (Equation\ 1)$$

where, AE_t^p describes the dependence of integral gross primary production (GPP) on irradiance intensity (Kosinski 1984, Young and Huryn 1996, Oliver and Merrick 2006), *A* and *p* being coefficients. E_t is the incident photosynthetically active solar radiation (PAR, μmol photons m^{-2} s^{-1}) at time *t*. The exponent *p* accounts for the possibility that the integrated GPP shows a saturating response to irradiance through the day (Kosinski 1984). *kD* is the atmospheric gas exchange, where, *k* = re-aeration coefficient ($time^{-1}$) *and D* is the oxygen deficit, which is the difference between the saturation oxygen concentration and the measured oxygen concentration in the water (Odum 1956, McCutchan Jr et al. 1998). *CR* is the community respiration rate, which is assumed to be constant over the duration of a 24 hrs period.

Saturated oxygen concentrations were calculated from the measured water temperatures using formulae from the International Oceanographic Tables (1973) without salinity correction. $\frac{dO}{dt}$ *and D* were estimated over 10 min intervals using the DO data and the respective calculated saturated oxygen concentrations at the given water temperature. E_t was obtained from the automated weather station at Chowilla Island. A three dimensional, non-linear regression curve was fitted to Equation 1 using the time series data to estimate average values for *A, p, k and CR*. *Equation 1* was then used to calculate *GPP* (AE_t^p), and values were calculated for 10 minute time intervals and summed over the day (Oliver and Merrick 2006, Oliver and Lorenz 2013). The difference between daily rates of GPP and CR was subsequently calculated to provide an estimate of daily Net Ecosystem Production (NEP).

Statistical Analyses

To evaluate the temporal differences in the water quality parameters and examine when significant changes occurred across the three sites, a set of linear mixed effects models were fitted by analysing ‘day of year’ as a factor. Planned contrasts and a series of sequential tests were then constructed for pairwise comparisons between sampling points for each site separately to evaluate at what time-points the threshold changes occurred at the sampling sites. However, for chl *a*, the lack of data prior to inundation precluded pairwise comparisons of concentrations prior to and during inundation. Instead, two-way ANOVA tests were performed to compare the concentrations between sites and between different phases of the hydrograph during the managed inundation period.

Time series analysis of the ecosystem metabolism data was conducted by fitting a generalised additive mixed model, and the autocorrelation in the data over time was adjusted using a continuous autoregressive model (corAR1). P values were compared with and without site interaction to test the effect of the site. One sample t-test was performed to test if average NEP for the entire study period was significantly different from zero at all three sites.

The initial water level rise that occurred prior to the managed inundation period was unexpected, and water quality parameters were sampled only twice prior to the managed inundation, once before any water level rise and once during the unexpected initial rise. The resulting lack of data for the period prior to the managed inundation made it difficult to directly assess the influence of the initial water level rise on chl *a*, DOC and nutrients. However, comparisons of ecosystem metabolism rates, for the period prior to either of the inundation events, and during the various stages of the managed inundation were possible due to the availability of the continuous time-series data. As the initial rise in water level was relatively small, water quality data collected before the commencement of the managed inundation was used in some cases to estimate the prior conditions.

RESULTS

Water Column Nutrients

All sites had similar nutrient concentrations prior to the managed inundation period (Figure 2-3). TN ranged from 0.27 (±0.007) to 0.50 (±0.012) mg L^{-1} (mean ± SEM) at the reference site in the MRC, 0.31 (±0.009) to 0.71 (±0.018) mg L^{-1} at the upstream site, and 0.28 (±0.007) to 0.48 (±0.009) mg L^{-1} at the downstream site in the anabranch. Pairwise comparisons indicated that the concentration of TN increased significantly during the managed inundation event at the anabranch upstream site ($p < 0.05$), mainly during the rising phase of the hydrograph, as compared to the other two sites, which were not significantly different from each other or with the concentration prior to the managed inundation period ($p > 0.05$).

TP ranged from 0.035 (±0.001) to 0.079 (±0.001) mg L^{-1} at the reference site, 0.047 (±0.003) to 0.111 (±0.001) mg L^{-1} at the upstream site, and 0.043 (±0.003) to 0.088 (±0.002) mg L^{-1} at the downstream site. Pairwise comparisons indicated that the concentrations of TP were similar at all three sites prior to the managed inundation period, but the concentrations at the anabranch sites increased significantly compared to the reference site during the rising phase of the hydrograph of the managed inundation event ($p < 0.05$) (Figure 2-3). The concentration of TP at the upstream site remained significantly higher throughout the following phases of the hydrograph, as compared to the other two sites while during the peak of the hydrograph, the concentrations at the reference and downstream sites were similar. During the falling phase of the hydrograph the concentrations at both these sites increased, with the concentrations at the downstream site in the anabranch being higher than the reference site ($p < 0.05$), and concentrations significantly different between all three sites ($p < 0.05$).

Among dissolved nutrients, FRP ranged from 0.001 (±0.001) to 0.046 (±0.001) at the reference site, 0.003 (±0.001) to 0.044 (±0.002) at the upstream site, and 0.001 (±0.001) to 0.048 (±0.001) at the downstream site. NO_3 ranged from 0.001 (±0.001) to 0.011 (±0.005) at the reference site, 0.001 (±0.001) to 0.019 (±0.019) at the upstream site, and 0.001 (±0.001) to 0.015 (±0.001) at the downstream site. NH_3 ranged from 0.002 (±0.001) to 0.016 (±0.010) at the reference site, 0.003 (±0.001) to 0.013 (±0.002) at the upstream site, and 0.001 (±0.001) to 0.013

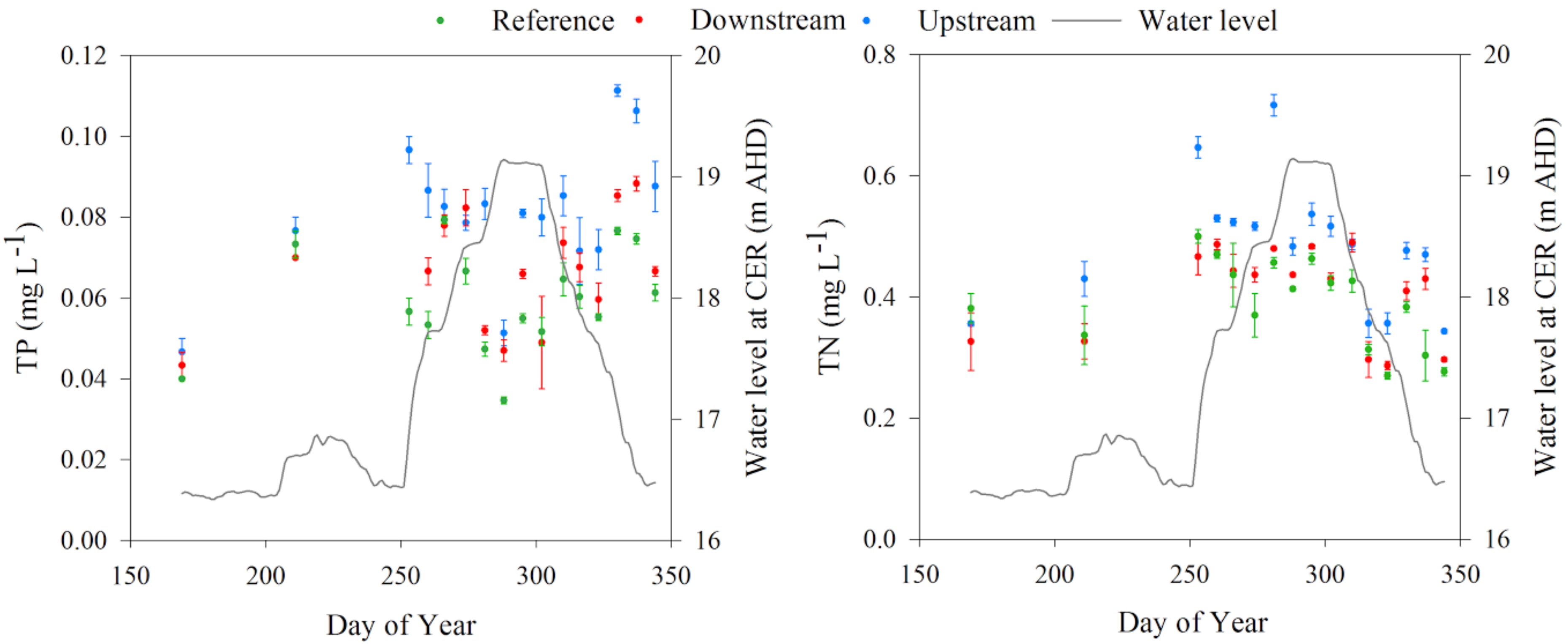

Figure 2-3: TP and TN concentrations (mg L^{-1}) at three sites during the study period. Error bars represent the 95% confidence interval of the mean.

(±0.002) at the downstream site. Pairwise comparisons indicated no significant difference in the concentrations of dissolved nutrients, either between sites or at any point of time throughout the sampling periods as compared to the concentrations prior to the managed inundation ($p > 0.05$).

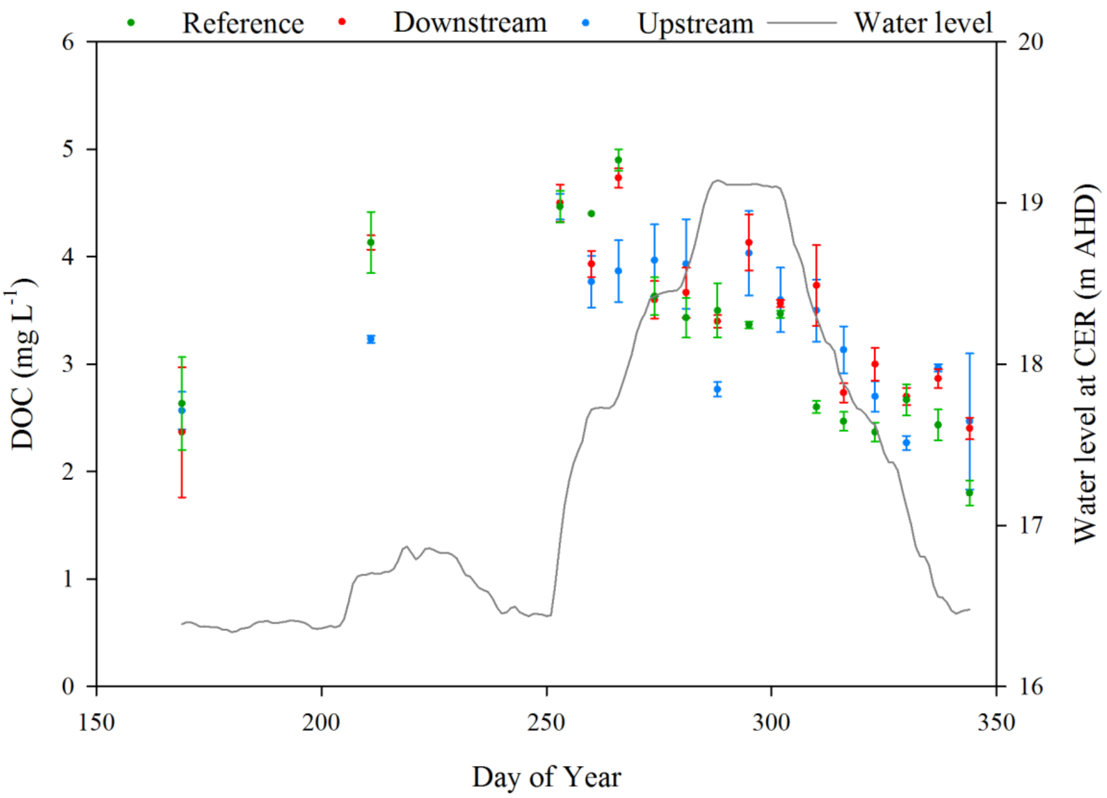

Figure 2-4: DOC concentrations (mg L^{-1}) at three sites during the study period. Error bars represent the 95% confidence interval of the mean.

Dissolved Organic Carbon

Throughout the sampling period, DOC ranged from 1.8 (±0.10) to 4.9 (±0.10) mg L^{-1} at the reference site in the MRC, 2.55 (±0.15) to 4.45 (±0.10) mg L^{-1} at the upstream site, and 2.15 (±0.05) to 4.75 (±0.10) mg L^{-1} at the downstream site in the anabranch (Figure 2-4). Pairwise comparison indicated no significant change in DOC concentrations at any of the sites during the managed inundation period, when compared to the concentrations prior to inundation ($p > 0.05$). There were no significant differences in concentrations between anabranch sites throughout the study ($p > 0.05$). However, significant differences in the DOC concentrations were observed between anabranch and MRC sites ($p < 0.05$) during the periods coinciding with the peak and the falling phases of the hydrograph. The difference observed was a result of a decline in the DOC concentrations at the reference site in the MRC during the peak and the falling phase of the hydrograph (Figure 2-4).

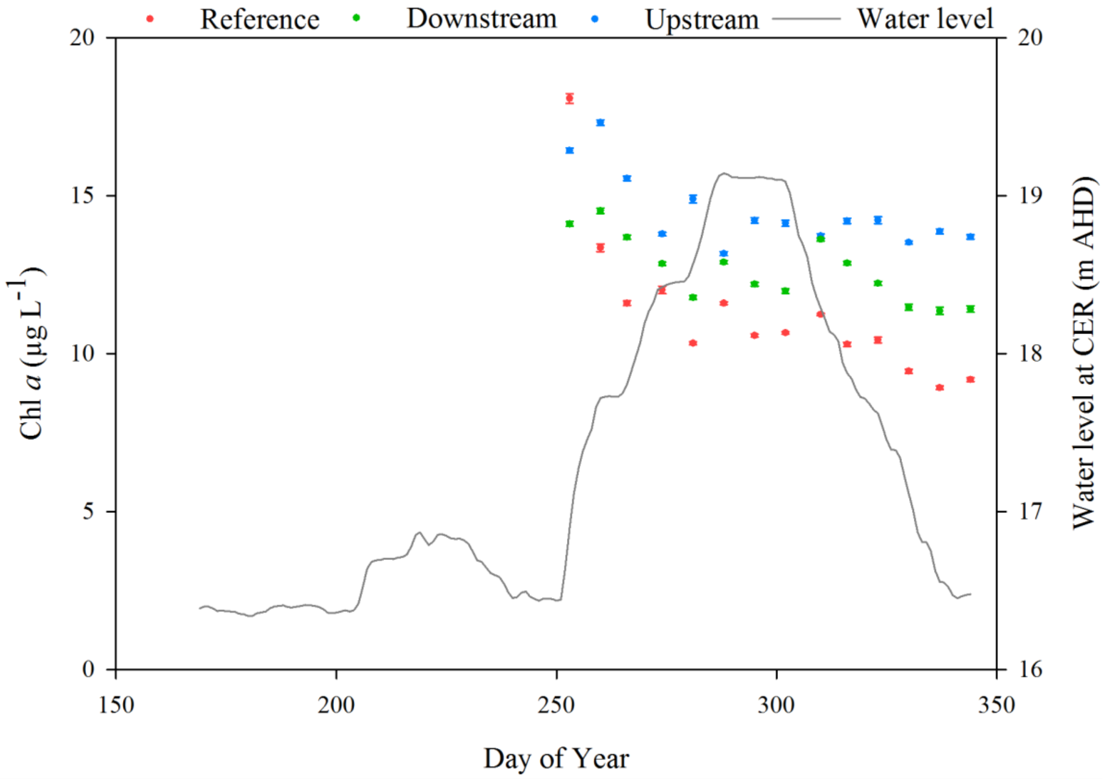

Figure 2-5: Chl *a* concentrations (µg L^{-1}) at study sites during the managed inundation period. Error bars represent the 95% confidence interval of the mean.

Phytoplankton Biomass

Phytoplankton biomass ranged from 8.91 (±0.05) to 18.07 (±0.15) µg L^{-1} at the reference site, 13.16 (±0.06) to 17.31 (±0.08) µg L^{-1} at the upstream site, and 11.35 (±0.11) to 14.52 (±0.08) µg L^{-1} at the downstream site in the anabranch. A two- way ANOVA linear model indicated a significant temporal variation in concentrations of chl *a* at the three sites ($p < 0.05$) during the managed inundation event, which varied significantly between sites ($p < 0.05$); and the effect of the site was dependent upon the time of the year ($p < 0.05$). The chl *a* concentrations at the upstream site in the anabranch were always higher than the downstream site and the reference site in the MRC, except during the first sampling of the managed inundation period (Figure 2-5), when the concentration at the reference site was higher than at anabranch sites. Due to the lack of chl *a* data for the period prior to the inundation period, comparisons could not be made to test if the concentrations increased during the managed inundation events, relative to the concentrations prior to the inundation.

Ecosystem Metabolism

We observed strong non-linear responses in ecosystem productivity rates at anabranch sites, and there were notable spatio-temporal patterns, with higher rates in anabranch sites compared to the reference site throughout the study period (Figure 2-6). Based on the regression models of metabolism, GPP rates at the anabranch sites were greater than at the reference site in the MRC, with rates at the upstream site greater by 1.17 mg O_2 L^{-1} d^{-1} and at the downstream site by 0.6 mg O_2 L^{-1} d^{-1}. Similarly, CR rates at the upstream site were greater than the reference site by a magnitude of 0.95 mg O_2 L^{-1} d^{-1} and at downstream site by 0.80 mg O_2 L^{-1} d^{-1}. These estimates were significantly different from zero for all three sites ($p < 0.05$), and the effect of the site was dependent upon the time of year ($p < 0.05$). ANOVA tests performed to test the effect of site interaction for GPP, CR and NEP showed that the non-linear pattern of ecosystem metabolic rates differed significantly between sites over time ($p < 0.05$).

We observed a large increase in both GPP and CR rates at both anabranch sites during the initial water level rise that occurred between late July and early August (Figure 2-6; P1), prior to the commencement of the managed inundation ($p < 0.05$). However, the rates decreased as the water level dropped, although they did not return to the levels observed prior to the water level increase. Once the managed inundation commenced (Figure 2-6; P2 onwards), metabolic rates gradually increased to levels higher than those observed during the initial unmanaged water level rise. During both the unmanaged and the managed water level rises, GPP rates were always higher at the upstream site than the downstream site in the anabranch and both were higher than the reference site in the MRC ($p < 0.05$). In contrast, CR rates at the downstream site in the anabranch were greater than both upstream and the reference sites during the initial water level rise prior to the managed inundation period ($p < 0.05$). Then, during the managed

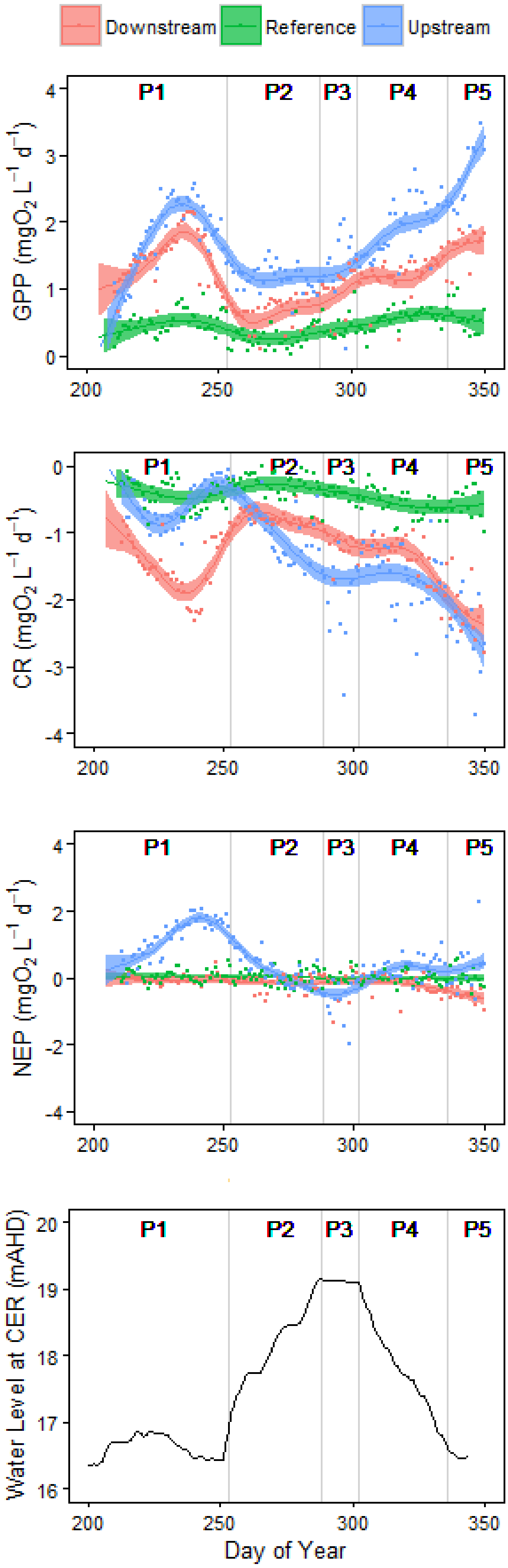

Figure 2-6: Time-series visualization of the regression (Visreg) plots for daily GPP, CR and NEP rates throughout the study period, and the hydrograph showing the water level in m AHD at CER. P1 = prior to inundation period; P2 = rising phase of the hydrograph; P3 = peak of the hydrograph; P4 = falling phase of the hydrograph; and P5 = post-inundation phase. Respiration rates are shown as negative values. Shaded blue, red and green bands represent +/-95% confidence interval of the mean values of GPP, CR and NEP.

inundation, the rates at the upstream site increased significantly and became higher than the downstream site and continued until the post-inundation phase when rates at both anabranch sites were similar, but greater than the reference site ($p < 0.05$). While the GPP and CR rates at anabranch sites responded to changes in water levels, rates at the reference site in the MRC remained steady throughout the study period.

One sample t-test indicated that NEP at the upstream anabranch site was significantly different from zero [M= 0.56, t (181) = 10.80, $p < 0.05$]. NEP was positive at the upstream site during the unmanaged water level rise prior to the managed inundation period, indicating autotrophy (Figure 2-6). During the managed inundation, the rates were negative for a short duration of time during the peak of the hydrograph, but switched back to positive in the post-inundation phase. At the downstream site, NEP values were also significantly different from zero [M= -0.15, t (181) = -8.15, $p < 0.05$]. However, NEP was more negative mainly during the peak and the falling phase of the hydrograph during the managed inundation period, indicating heterotrophy, reflecting a greater change in CR relative to GPP. NEP rates were generally balanced at the reference site in the MRC, with GPP and CR changing at similar rates. However, a t-test indicated that the mean value of NEP was slightly positive [M= 0.03, t (181) = 1.99, $p < 0.05$].

DISCUSSION

The capacity of floodplains to support the productivity of riverine ecosystems relies on periods of hydrological connectivity between the dynamic spatial mosaics of river-floodplain systems (Junk et al. 1989, Robertson et al. 1999, Tockner et al. 2000). Such connectivity facilitates the mobilisation of terrestrially derived organic carbon and nutrients, stimulating primary productivity and heterotrophic respiration (Edwards and Meyer 1987, Baldwin 1999, Tockner et al. 1999, Burford et al. 2008). In this study, we investigated how managed floodplain inundation effects ecosystem productivity by mobilising terrestrial sources of nutrients and DOC in an anabranch system of a highly regulated, complex river-floodplain ecosystem.

Nutrient Concentrations

We observed an increase in total nutrient concentrations at the anabranch sites during the managed inundation event. This indicated contributions from the peripheral floodplain habitats during the period of improved connectivity resulting from the higher water level. The increased concentrations during the period coinciding with the rising phase of the hydrograph, likely occurred partly from the mobilisation of nutrients deposited in the floodplain during previous floods, and partly from the breakdown of terrestrial organic material accumulated on the floodplain since the previous flood.

The breakdown of fine organic material accumulated in the soil provides a surge of nutrients to the water column as the soil gets wet (Tockner et al. 1999). The observed increase in TP concentrations at both anabranch sites and at the reference site during the falling phase of the hydrograph indicated an increased nutrient supply from the upstream reaches of the Murray River, but with additional contributions from the floodplain to the anabranch sites. The observed differences in the concentrations between the anabranch sites, suggests there could be deposition of material or benthic utilisation of the nutrients during transportation downstream from the upstream site. However, it is also likely that inflows through the two inlet creeks that enter between the two sites contributed lower amount of nutrients, thereby leading to lower nutrient concentrations at the downstream site in the anabranch, as was also observed by Wallace et al. (2015).

The concentrations of dissolved nutrients observed in this study were comparable to the concentrations observed by Aldridge et al. (2012) during a low flow period at Lock 5, where the Chowilla anabranch returns to the MRC. However, they observed substantial increases in the concentrations of dissolved nutrients during a flood. The lack of increase in dissolved nutrients at the anabranch sites in this study was potentially caused by rapid uptake by microorganisms, as the elevated total nutrient concentrations indicated an increase in nutrient supply deriving from the flooded areas.

Dissolved Organic Carbon Concentrations

DOC concentrations observed during the low flow periods were similar to those reported within the Murray-Darling Basin. For example, our results were comparable to observations by Cook et al. (2015) and Nielsen et al. (2015) during their sampling at the mid-River Murray downstream of an extensive floodplain prior to a flood, and by Aldridge et al. (2012) prior to flooding at their site at Lock 5 of the lower River Murray. However, these studies observed large increases in DOC concentrations during flooding in contrast to this study, where we did not observe elevated DOC concentrations at our anabranch sites during the managed inundation period. A key difference is that the previous studies were conducted during large natural flood events that resulted in overbank flooding inundating large areas of the floodplain with the return of significant amounts of water back into the MRC.

During this study, a much smaller area was flooded during the managed inundation event. For comparison, flooding during the study by Aldridge et al. (2012) inundated 67 km^2 area of the Chowilla Floodplain as compared to about 23 km^2 during the managed inundation event in this study. Similarly, flooding during the study by Nielsen et al. (2015) and Cook et al. (2015) flooded 80 % of 66, 000 ha total floodplain area. Moreover, concentrations of DOC would also be influenced by factors such as periods between flood pulses (Baldwin 1999). It is possible that the initial water level rise that occured prior to the managed inundation period led to the dissolution and importation of DOC into the stream channel, thereby reducing the increase in DOC during the managed inundation period. However, the lack of data during the initial water level rise, makes it difficult to conclude with confidence if this was the case.

Phytoplankton Biomass

The higher chl *a* concentrations observed at the upstream site compared to both the downstream site in the anabranch and the reference site in the MRC are likely related to improved planktonic growth conditions. The longer water residence time at the upstream site, would promote establishment of larger populations (Beaver et al. 2015). The shallower depth relative to the other two sites, improves light conditions in the water column, leading to higher growth rates that are supported by the increased nutrient concentrations. Together these factors support enhanced phytoplankton growth in the upstream anabranch site. In addition, the adjacent inundated areas include shallow wetland habitats and a number of large open lakes that are conducive to increased phytoplankton growth (Baker et al. 2000) and transport across the inundated areas. Higher chl *a* concentrations in floodplain waters compared to associated rivers have also been observed in other large river systems (Van den Brink et al. 1992, Stoyneva 1994, Preiner et al. 2008).

Ecosystem Metabolism

We observed substantial increases in GPP and CR rates at anabranch sites, during both the initial unmanaged water level rise and the managed inundation period. This demonstrates high sensitivity of anabranch habitats to even a small change in water level. In the MRC, metabolic rates remained closely balanced with the net production being near to zero. Similar balanced responses in the MRC of the River Murray were also observed by Oliver and Merrick (2006), and they hypothesized that such observations resulted from full heterotrophic utilisation of the autotrophic food resources, suggesting restriction in food-web production by the autotrophic energy supply. Regulated, dryland rivers like the River Murray, often tend to exhibit light and nutrient limitations (Baker et al. 2000) that reduce the primary production by in-stream autotrophs (Oliver et al. 1999). Consequently additional input from allochthonous sources are important in subsidising the carbon supplies to the system to enhance secondary productivity (Polis et al. 1997, Dolbeth et al. 2012).

Our observation of increased GPP and CR rates in the anabranch sites during the managed inundation supports the observations made by Wallace and Furst (2016) at their anabranch site further downstream and closer to the CER. However, a strongly heterotrophic response they observed at their site was driven by large increases in CR relative to GPP, and was positively coupled with changing DOC concentrations. In contrast, we did not observe elevated DOC concentrations at our anabranch sites during the managed inundation period. Moreover, at the upstream anabranch site, we observed a strongly autotrophic response, which suggests that improved growth conditions associated with shallower depth and contributions by phytoplankton from the peripheral floodplain habitats during the increased connection enhanced the primary production. Shallower depths may also result in additional contributions from benthic photoautotrophs to the water column metabolism (Van de Bogert et al. 2012), however, the lack of data on benthic measurements makes it difficult to conclude with confidence if this was the case.

At the downstream site in the anabranch, the NEP rates shifted to more negative values as the managed inundation progressed, mainly during the peak of the hydrograph, indicating the influence of external carbon supplies and a shift to heterotrophy. It is possible that the increased CR was a result of the utilization of carbon from upstream sources being transported and metabolized. The heterotrophy observed at our downstream anabranch site was similar to that observed by Wallace and Furst (2016) at their site closer to the CER, which was positively coupled with changing DOC concentrations. However, at our site there were no observed elevated DOC concentrations to suggest it was a major driver of the change in CR. These observations highlight the limitation of discrete data series in interpreting system responses, and supports the importance of frequently monitored water quality data for assessing the drivers of the change in metabolism in complex river-floodplain ecosystems.

The different responses for total nutrients, phytoplankton biomass and metabolic rates observed between the anabranch sites suggest a strong influence of local driving forces on the return waters from the managed flood. River floodplains have a high degree of heterogeneity (Junk et al. 1989, Tockner et al. 2000), created by geomorphic complexity and hydrological variability, and this results in distinct physical, chemical and biological characteristics varying across the spatial and temporal gradients (Walker et al. 1995, Ward et al. 1999, Thoms 2003, Humphries et al. 2014). In such systems, large floods are often considered to homogenize connections across the floodplain, as they facilitate the mixing and exchange of resources between the patches of habitats, and thereby tend to reduce the spatial variability (Agostinho and Zalewski 1995, Agostinho et al. 2000, Neiff et al. 2001, Thomaz et al. 2007). Several studies, mainly from the Neo-tropical and northern temperate floodplains have supported this generalised pattern through the observation of decreasing variability in limnological variables, such as nutrients, conductivity and chl *a*, with increasing water level (Furch and Junk 1985, Hamilton and Lewis Jr 1990, Tockner and Ward 1999, Tockner et al. 2000, Ward and Tockner 2001). The composition of phytoplankton, zooplankton and fish tend to be more similar during large floods (Bonecker et al. 1998, Agostinho et al. 2000, Huszar et al. 2000, Aoyagui and Bonecker 2004, Miranda 2005). However, as managed floods are generally smaller in magnitude than the range of natural floods, they are less likely to homogenise hydrological conditions across larger areas and thereby tend to be more influenced by the floodplain mosaic (Tockner et al. 1999, Tockner et al. 2000, Thomaz et al. 2007), as observed in this study.

A major factor inducing heterogeneity in flood waters is the inputs from the lateral, interconnected floodplain creeks with distinct physical and chemical characteristics, such as temperature, turbidity and nutrient contents (Devol et al. 1988, Schemel et al. 2004). During periods of high flow, the Chowilla anabranch creek is connected to a series of different habitats, such as temporary creeks, wetlands and lakes (Wallace and Furst 2016), and therefore, depending on its network position, an individual site within the anabranch creek can receive water inputs from different habitat sources on the floodplain. Such interaction can greatly influence habitat heterogeneity and ultimately the ecosystem productivity (Thomaz et al. 2007). More detailed information is needed on the effects of managed inundation events on ecosystem productivity before generalizing the impact for a larger spatial extent. The findings from this study, highlight the need for considering spatial variability in terms of ecosystem productivity while planning for future managed inundation events.

Currently, there is limited information demonstrating the influence of managed inundation events on ecosystem productivity in dryland rivers. This study suggests that managed inundation events have the potential to stimulate ecosystem productivity even during periods of low water availability. However, managed floods tend to show high variability in water quality and productivity, and therefore greater understanding of the drivers of this variability is required, so that managers are aware of how the mosaic of habitats present on the floodplain differentially modify the ecological benefits of enhanced connectivity through characteristics including geomorphology and water quality. More frequently monitored water quality parameters and the use of multiple sensors in various floodplain habitats will greatly improve our ability to understand and identify the drivers of such large changes in the metabolic rates. Moreover, more work is needed to fully understand the broader impacts of managed floods. This is because whether detrital or newly derived organic material passes up through the food web and influences the biomass of organisms at higher trophic level will not only depend upon the quantity of the organic material delivered by the flood, but also upon its quality and bio-availability.

REFERENCES

Abrantes, K. G. and M. Sheaves. 2010. Importance of freshwater flow in terrestrial–aquatic energetic connectivity in intermittently connected estuaries of tropical Australia. Marine Biology **157**:2071-2086.

Agostinho, A., S. Thomaz, C. Minte-Vera, and K. Winemiller. 2000. Biodiversity in the high Paraná River floodplain. Biodiversity in wetlands: assessment, function and conservation **1**:89-118.

Agostinho, A. A. and M. Zalewski. 1995. The dependence of fish community structure and dynamics on floodplain and riparian ecotone zone in Parana River, Brazil. Pages 141-148 The Importance of Aquatic-Terrestrial Ecotones for Freshwater Fish. Springer.

Aldridge, K., Z. Lorenz, R. Oliver, and J. Brookes. 2012. Changes in water quality and phytoplankton communities in the Lower River Murray in response to a low flow-high flow sequence. Goyder Institute for Water Research Technical Report Series.

Aoyagui, A. S. and C. C. Bonecker. 2004. Rotifers in different environments of the Upper Paraná River floodplain (Brazil): richness, abundance and the relationship with connectivity. Hydrobiologia **522**:281-290.

Arthington, A. H., S. E. Bunn, N. L. Poff, and R. J. Naiman. 2006. The challenge of providing environmental flow rules to sustain river ecosystems. Ecological Applications **16**:1311-1318.

Baker, P. D., J. D. Brookes, M. D. Burch, H. R. Maier, and G. G. Ganf. 2000. Advection, growth and nutrient status of phytoplankton populations in the lower River Murray, South Australia. Regulated Rivers: Research & Management **16**:327-344.

Baldwin, D. S. 1999. Dissolved organic matter and phosphorus leached from fresh and 'terrestrially'aged river red gum leaves: implications for assessing river–floodplain interactions. Freshwater Biology **41**:675-685.

Baldwin, D. S., M. J. Colloff, S. M. Mitrovic, N. R. Bond, and B. Wolfenden. 2016. Restoring dissolved organic carbon subsidies from floodplains to lowland river food webs: a role for environmental flows? Marine and Freshwater Research.

Bartels, P., J. Cucherousset, C. Gudasz, M. Jansson, J. Karlsson, L. Persson, K. Premke, A. Rubach, K. Steger, and L. J. Tranvik. 2012. Terrestrial subsidies to lake food webs: an experimental approach. Oecologia **168**:807-818.

Beaver, J. R., K. C. Scotese, E. E. Manis, S. T. Juul, J. Carroll, and T. R. Renicker. 2015. Variation in water residence time is the primary determinant of phytoplankton and zooplankton composition in a Pacific Northwest reservoir ecosystem (Lower Snake River, USA). River Systems **21**:241-255.

Benke, A. C., I. Chaubey, G. M. Ward, and E. L. Dunn. 2000. Flood pulse dynamics of an unregulated river floodplain in the southeastern US coastal plain. Ecology **81**:2730-2741.

Bonecker, C. C., F. A. Lansac-Tôha, and D. C. Rossa. 1998. Planktonic and non-planktonic rotifers in two environments of the Upper Paraná River floodplain, State of Mato Grosso do Sul, Brazil. Brazilian Archives of Biology and Technology **41**:447-456.

Bunn, S. E., P. M. Davies, and M. Winning. 2003. Sources of organic carbon supporting the food web of an arid zone floodplain river. Freshwater Biology **48**:619-635.

Burford, M. A., A. J. Cook, C. S. Fellows, S. R. Balcombe, and S. E. Bunn. 2008. Sources of carbon fuelling production in an arid floodplain river. Marine and Freshwater Research **59**:224-234.

Cook, R. A., B. Gawne, R. Petrie, D. S. Baldwin, G. N. Rees, D. L. Nielsen, and N. S. Ning. 2015. River metabolism and carbon dynamics in response to flooding in a lowland river. Marine and Freshwater Research.

Dahm, C. N., M. A. Baker, D. I. Moore, and J. R. Thibault. 2003. Coupled biogeochemical and hydrological responses of streams and rivers to drought. Freshwater Biology **48**:1219-1231.

Devol, A., B. R. Forsberg, J. E. Richey, and D. Sandtos. 1988. Factors controlling nutrient concentrations in Amazon floodplain lakes.

Dolbeth, M., M. Cusson, R. Sousa, and M. A. Pardal. 2012. Secondary production as a tool for better understanding of aquatic ecosystems. Canadian journal of fisheries and aquatic sciences **69**:1230-1253.

Edwards, R. and J. Meyer. 1987. Metabolism of a sub-tropical low gradient black water river. Freshwater Biology **17**:251-263.

Furch, K. and W. J. Junk. 1985. Dissolved carbon in a floodplain lake of the Amazon and in the river channel. Transport of Carbon and Minerals in major World rivers, Part **3**:285-298.

Furst, D. J., K. T. Aldridge, R. J. Shiel, G. G. Ganf, S. Mills, and J. D. Brookes. 2014. Floodplain connectivity facilitates significant export of zooplankton to the main River Murray channel during a flood event.

Gawne, B., C. Merrick, D. G. Williams, G. Rees, R. Oliver, P. M. Bowen, S. Treadwell, G. Beattie, I. Ellis, and J. Frankenberg. 2007. Patterns of primary and heterotrophic productivity in an arid lowland river. River Research and Applications **23**:1070-1087.

Hadwen, W. L., C. S. Fellows, D. P. Westhorpe, G. N. Rees, S. M. Mitrovic, B. Taylor, D. S. Baldwin, E. Silvester, and R. Croome. 2010. Longitudinal trends in river functioning: patterns of nutrient and carbon processing in three Australian rivers. River Research and Applications **26**:1129-1152.

Hamilton, S. K. and W. M. Lewis Jr. 1990. Basin morphology in relation to chemical and ecological characteristics of lakes on the Orinoco River floodplain. Venezuela. Arch. Hydrobt'ol **119**:393-425.

Humphries, P., H. Keckeis, and B. Finlayson. 2014. The river wave concept: integrating river ecosystem models. BioScience:biu130.

Huszar, V., R. L Bozelli, F. Esteves, and F. Roland. 2000. Fitoplâncton. Lago Batata: impacto e recuperação de um ecossistema amazônico. Rio de Janeiro: IB-UFRJ/SBL:91-104.

Jolly, I. D., G. R. Walker, and K. A. Narayan. 1994. Floodwater recharge processes in the Chowilla anabranch system, South Australia. Soil Research **32**:417-435.

Junk, W. J., P. B. Bayley, and R. E. Sparks. 1989. The flood pulse concept in river-floodplain systems. Canadian special publication of fisheries and aquatic sciences **106**:110-127.

King, A., K. Ward, P. O’connor, D. Green, Z. Tonkin, and J. Mahoney. 2010. Adaptive management of an environmental watering event to enhance native fish spawning and recruitment. Freshwater Biology **55**:17-31.

Kingsford, R. T. 2000. Ecological impacts of dams, water diversions and river management on floodplain wetlands in Australia. Austral Ecology **25**:109-127.

Kosinski, R. J. 1984. A comparison of the accuracy and precision of several open-water oxygen productivity techniques. Hydrobiologia **119**:139-148.

Lind, P., B. Robson, and B. Mitchell. 2007. Multiple lines of evidence for the beneficial effects of environmental flows in two lowland rivers in Victoria, Australia. River Research and Applications **23**:933-946.

McCutchan Jr, J. H., W. M. Lewis Jr, and J. Saunders III. 1998. Uncertainty in the estimation of stream metabolism from open-channel oxygen concentrations. Journal of the North American Benthological Society:155-164.

McGinness, H. M. and A. D. Arthur. 2011. Carbon dynamics during flood events in a lowland river: the importance of anabranches. Freshwater Biology **56**:1593-1605.

MDBA. 2012. Chowilla Floodplain Environmental Water Management Plan 2012. Australian Government: Canberra, ACT.

MDBA. 2014. Preliminary Overview of Constraints to Environmental Water Delivery in the Murray–Darling Basin. Retrieved 1/04/2014, 2014, from http://www. mdba. gov. au/what-we-do/water-planning/managingconstraints/constraints-overview/nsw.

Medeiros, E. S. and A. H. Arthington. 2008. The importance of zooplankton in the diets of three native fish species in floodplain waterholes of a dryland river, the Macintyre River, Australia. Hydrobiologia **614**:19-31.

Medeiros, E. S. and A. H. Arthington. 2011. Allochthonous and autochthonous carbon sources for fish in floodplain lagoons of an Australian dryland river. Environmental Biology of Fishes **90**:1-17.

Miranda, L. 2005. Fish assemblages in oxbow lakes relative to connectivity with the Mississippi River. Transactions of the American Fisheries Society **134**:1480-1489.

Neiff, J., B. Gopal, and W. Junk. 2001. Diversity in some tropical wetland systems of South America. Biodiversity in wetlands: assessment, function and conservation **2**:157-186.

Nielsen, D. L., R. A. Cook, N. Ning, B. Gawne, and R. Petrie. 2015. Carbon and nutrient subsidies to a lowland river following floodplain inundation. Marine and Freshwater Research.

Nilsson, C., C. A. Reidy, M. Dynesius, and C. Revenga. 2005. Fragmentation and flow regulation of the world's large river systems. Science **308**:405-408.

Odum, H. T. 1956. Primary production in flowing waters. Limnology and Oceanography:102-117.

Oliver, R., B. Hart, J. Olley, M. Grace, C. Rees, and G. Caitcheon. 1999. The Darling River: Algal growth and the cycling and sources of nutrients.

Oliver, R. L. and Z. Lorenz. 2013. Changes in metabolic activity in the South Australian section of the Murray River during the 2010/11 flood that followed a ten year drought. Goyder Institute for Water Research Technical Report Series.

Oliver, R. L. and C. J. Merrick. 2006. Partitioning of river metabolism identifies phytoplankton as a major contributor in the regulated Murray River (Australia). Freshwater Biology **51**:1131-1148.

Polis, G. A., W. B. Anderson, and R. D. Holt. 1997. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. Annual review of ecology and systematics:289-316.

Preiner, S., I. Drozdowski, M. Schagerl, F. Schiemer, and T. Hein. 2008. The significance of side-arm connectivity for carbon dynamics of the River Danube, Austria. Freshwater Biology **53**:238-252.

Robertson, A., S. Bunn, P. Boon, and K. Walker. 1999. Sources, sinks and transformations of organic carbon in Australian floodplain rivers. Marine and Freshwater Research **50**:813-829.

Schemel, L. E., T. R. Sommer, A. B. Müller-Solger, and W. C. Harrell. 2004. Hydrologic variability, water chemistry, and phytoplankton biomass in a large floodplain of the Sacramento River, CA, USA. Hydrobiologia **513**:129-139.

Stoyneva, M. P. 1994. Shallows of the lower Danube as additional sources of potamoplankton. Pages 171-178 Phytoplankton in Turbid Environments: Rivers and Shallow Lakes. Springer.

Taylor, P. J., G. R. Walker, G. Hodgson, T. J. Hatton, and R. L. Correll. 1996. Testing of a GIS model ofEucalyptus Iargiflorens health on a semiarid, saline floodplain. Environmental management **20**:553-564.

Thomaz, S. M., L. M. Bini, and R. L. Bozelli. 2007. Floods increase similarity among aquatic habitats in river-floodplain systems. Hydrobiologia **579**:1-13.

Thoms, M. C. 2003. Floodplain–river ecosystems: lateral connections and the implications of human interference. Geomorphology **56**:335-349.

Thorp, J. H. and M. D. Delong. 1994. The riverine productivity model: an heuristic view of carbon sources and organic processing in large river ecosystems. Oikos **70**:305-308.

Thorp, J. H. and M. D. Delong. 2002. Dominance of autochthonous autotrophic carbon in food webs of heterotrophic rivers. Oikos **96**:543-550.

Thorp, J. H., M. D. Delong, K. S. Greenwood, and A. F. Casper. 1998. Isotopic analysis of three food web theories in constricted and floodplain regions of a large river. Oecologia **117**:551-563.

Tockner, K., F. Malard, and J. Ward. 2000. An extension of the flood pulse concept. Hydrological Processes **14**:2861-2883.

Tockner, K., D. Pennetzdorfer, N. Reiner, F. Schiemer, and J. Ward. 1999. Hydrological connectivity, and the exchange of organic matter and nutrients in a dynamic river–floodplain system (Danube, Austria). Freshwater Biology **41**:521-535.

Tockner, K. and J. Ward. 1999. Biodiversity along riparian corridors. Large Rivers **11**:293-310.

Van de Bogert, M. C., D. L. Bade, S. R. Carpenter, J. J. Cole, M. L. Pace, P. C. Hanson, and O. C. Langman. 2012. Spatial heterogeneity strongly affects estimates of ecosystem metabolism in two north temperate lakes. Limnology and Oceanography **57**:1689.

Van den Brink, F., J. De Leeuw, G. Van der Velde, and G. Verheggen. 1992. Impact of hydrology on the chemistry and phytoplankton development in floodplain lakes along the Lower Rhine and Meuse. Biogeochemistry **19**:103-128.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The river continuum concept. Canadian journal of fisheries and aquatic sciences **37**:130-137.

Vink, S., M. Bormans, P. Ford, and N. Grigg. 2005. Quantifying ecosystem metabolism in the middle reaches of Murrumbidgee River during irrigation flow releases. Marine and Freshwater Research **56**:227-241.

Walker, K. F., F. Sheldon, and J. T. Puckridge. 1995. A perspective on dryland river ecosystems. Regulated Rivers: Research & Management **11**:85-104.

Wallace, T., D. Furst, S. Upadhyay, and R. Daly. 2015. Science to inform operational decisions of major environmental infrastructure on the Chowilla Floodplain and other regulated floodplains in the SA River Murray. Goyder Institute for Water Research Technical Report Series.

Wallace, T. A. and D. Furst. 2016. Open water metabolism and dissolved organic carbon in response to environmental watering in a lowland river–floodplain complex. Marine and Freshwater Research.

Ward, J. and K. Tockner. 2001. Biodiversity: towards a unifying theme for river ecology. Freshwater Biology **46**:807-820.

Ward, J., K. Tockner, and F. Schiemer. 1999. Biodiversity of floodplain river ecosystems: ecotones and connectivity. Regulated Rivers: Research & Management **15**:125-139.

Young, R. G. and A. D. Huryn. 1996. Interannual variation in discharge controls ecosystem metabolism along a grassland river continuum. Canadian journal of fisheries and aquatic sciences **53**:2199-2211.

Zeug, S. C. and K. O. Winemiller. 2008. Evidence supporting the importance of terrestrial carbon in a large-river food web. Ecology **89**:1733-1743.

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Certification:	This paper reports on original research I conducted during the period of my Higher Degree by Research candidature and is not subject to any obligations or contractual agreements with a third party that would constrain its inclusion in this thesis. I am the primary author of this paper.		
Signature		Date	25 May 2017

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By signing the Statement of Authorship, each author certifies that:

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Name of Co-author	Roderick Oliver		
Contribution to the paper	Provided input in conceiving the study and design of experiments; supervised data analysis and interpretation; reviewed the manuscript		
Signature		Date	25 May 2017

Name of Co-author	Kane Aldridge		
Contribution to the paper	Provided input in conceiving the study and design of experiments; supervised data analysis and interpretation; reviewd the manuscript		
Signature		Date	25 May 2017

Name of Co-author	Todd Wallace		
Contribution to the paper	Provided input in conceiving the study and design of experiments; helped in field data collection; reviewed the manuscript		
Signature		Date	25 May 2017

Name of Co-author	Justin Brookes		
Contribution to the paper	Provided input in conceiving the study and design of experiments; supervised data analysis and interpretation; reviewed the manuscript		
Signature		Date	25 May 2017

CHAPTER 3

MANAGED INUNDATION OF A DRYLAND RIVER FLOODPLAIN STIMULATES ECOSYSTEM PRODUCTIVITY IN THE RIVER CHANNEL

ABSTRACT

Environmental flows have emerged as a major restoration tool in regulated rivers, as they can enhance ecological conditions impaired through river regulation, by partially reinstating the connectivity between floodplain and riverine habitats. Increasing demands for water to supply human uses have constrained environmental flow delivery. To compensate, environmental flow regulators are being used as a mechanism to inundate larger areas of floodplain to achieve desired ecological outcomes. Identifying how to deliver environmental water to produce a useful pulse in riverine ecosystem productivity is a crucial component of river management, especially in drier regions of the world. In this study, we assessed the effectiveness of a managed inundation event using a newly constructed environmental flow regulator on stimulating riverine productivity in the main channel of the River Murray in South Australia. A large increase in the gross primary production (GPP) and community respiration (CR) was observed at river sites downstream of the floodplain. A greater increase in GPP was observed at a site immediately downstream of the confluence of the floodplain anabranch to the main river channel (MRC), resulting in a switch of the net ecosystem productivity (NEP = GPP – CR) from near zero upstream to a strongly autotrophic state (NEP >> 0). At a site located 40 km further downstream, a larger increase in CR, resulted in a switch of the metabolic balance to strongly a heterotrophic state (NEP << 0). Our results suggest that return flows from managed inundation events have the potential to influence riverine productivity at largeer spatial scale; by contributing additional carbon and nutrients sources from the floodplain, even during periods of regulated low river flow.

KEY WORDS: Ecosystem metabolism, managed inundation, environmental flow, floodplain rivers, metabolic rates

INTRODUCTION

Despite the perceived importance of floodplain derived resources in stimulating riverine productivity (Junk et al. 1989, Baldwin 1999, Robertson et al. 1999, Tockner et al. 1999, Atkinson et al. 2009, Nielsen et al. 2015), many managed rivers have limited connectivity with their adjacent floodplain as an outcome of intensive flow regulations, irrigation diversions and climatic pressures (Pittock and Finlayson 2011, Baldwin et al. 2015, Cook et al. 2015, Nielsen et al. 2015). Restoring the natural connections that facilitate energy and material flows between the two habitats to support river-floodplain ecosystems becomes a major challenge with the competing pressures (Opperman et al. 2009, Watts et al. 2011, Roseman and DeBruyne 2015).

In highly regulated river systems, environmental flows have become a major river restoration tool to facilitate the lateral connectivity between the main river channel (MRC) and its adjacent floodplain even during periods of regulated low flows (Arthington 2012, Baldwin et al. 2016). Environmental flows are defined as the quantity, timing and quality of water flow required to sustain and protect ecosystem and social values (Arthington et al. 2010). With growing water demands increasing the constraints to the delivery of environmental flows, management authorities are constructing and operating environmental flow regulators that inundate larger areas of floodplains for a given amount of flow. In combination with environmental flows, the environmental regulators can increase the frequency and duration of floodplain inundation to achieve desired ecological outcomes (MDBA 2014). Throughout the Murray-Darling Basin in Australia, the primary goals of flooding the floodplain through the use of environmental flows have often focussed on maintaining and improving the conditions of floodplain vegetation and structuring of floodplain biotic communities reliant on inundated floodplains (Baldwin et al. 2016). However, a recent study suggests that environmental flows may also alter the sources and transport of resources available for uptake into the food web (Cross et al. 2011). Understanding how to deliver environmental water to produce a useful pulse in riverine ecosystem productivity, by restoring subsidies of nutrients and organic carbon that supports riverine food webs, without leading to unintended outcomes such as hypoxic blackwater events and problematic algal blooms is a less studied but critical area of research.

Studies that have been conducted during managed high flow periods (Valett et al. 2005, Robertson et al. 2016), and natural flood events (Furst et al. 2014, Cook et al. 2015, Nielsen et al. 2015) provide evidence on the capacity of floodplain habitats in contributing resources that support the riverine ecosystem food webs. However, ecosystem responses tend to vary greatly with flow regimes (Bunn and Arthington 2002). Therefore, whether managed floodplain inundations will produce similar improvements in riverine productivity as those associated with unregulated inundations is poorly understood. This is because managed floods are generally smaller in magnitude than the range of natural floods, and are less likely to homogenise hydrological conditions across the spatial gradients in the floodplain as do the larger floods (Thomaz et al. 2007). Therefore, more information is required to assess the effectiveness of managed floods in supporting riverine productivity to make robust and defensible management decisions. This understanding is important if specific management objectives are to be achieved through constrained environmental water allocations.

In this study, we assessed the influence of the return flows from a managed floodplain inundation on the ecosystem productivity of the MRC of the Lower River Murray. Managed inundation was facilitated by the first testing of a newly constructed environmental flow regulator on the permanent anabranch creek of the Chowilla Floodplain of the Lower River Murray. Two sites in the MRC downstream of the inundated floodplain, approximately 40 km apart, were chosen to assess the influence of the return flows on the whole ecosystem metabolism. Comparisons were made with a reference site situated in the MRC of the River Murray, upstream of the outlet of the Chowilla Creek. A recent study by Wallace and Furst (2016) evaluated the impact of these same return flows on ecosystem productivity in the MRC of River Murray immediately downstream of the inundated area, and suggested that the managed inundation event could modulate riverine productivity. This study extends these findings by investigating whether the return flows from the managed inundation have a larger spatial impact on riverine productivity, beyond the immediate vicinity of the inundated floodplain areas. The study focussed particularly on the effect of flooding on concentrations of nutrients and dissolved organic carbon (DOC) and changes in gross primary production (GPP), community respiration (CR) and net ecosystem production (NEP).

METHODS

Study Area Descriptiona

The Murray River is located in the southeast of Australia and together with the Darling River drains a catchment of 1 x 10^6 km^2 (Mackay 1990). Chowilla Floodplain (33°57′ S, 140°56′29 E) is one of the major floodplain complexes adjoining the lower River Murray in South Australia and New South Wales. The floodplain is located downstream of the junction of the Murray and Darling Rivers and covers an area of 17,700 hectares. Water diverted from the River Murray main channel upstream of Lock 6 (Figure 3-1) enters into a network of streams and then passes into the main anabranch of the floodplain, Chowilla Creek, which passes back into the main river channel below Lock 6 (Jolly et al. 1994).

The floodplain is one of the six Icon Sites in the Murray Darling Basin Authority's *The Living Murray Program* (MDBA 2012), and it also forms part of the Riverland Ramsar site, a wetland of international importance under the Ramsar Convention (Taylor et al. 1996, MDBA 2012). However, due to the effect of flow regulation, irrigation diversions and climatic pressures, the main channel of the River Murray has reduced connectivity with the floodplain, and the environmental condition of the Chowilla Floodplain has severely declined over time (Saintilan and Overton 2010).

The Chowilla Environmental Regulator (CER) was constructed in 2014 on Chowilla Creek, the major outlet from the floodplain that drains into the MRC in the South Australian section of the Lower River Murray. The CER is approximately 1.45 km upstream of the confluence of Chowilla Creek with the River Murray. The CER was built under *The Living Murray Program*, with the purpose of improving ecological conditions and functions of the floodplain by reinstating a flooding regime closer to natural patterns in terms of frequency, duration and extent of floodplain inundation. On 10 September 2014, corresponding to the 253rd day of the year (DOY), the first testing of the structural integrity of the CER was undertaken, providing the opportunity to investigate longitudinal influences of the operation of the regulator on the MRC ecosystem productivity.

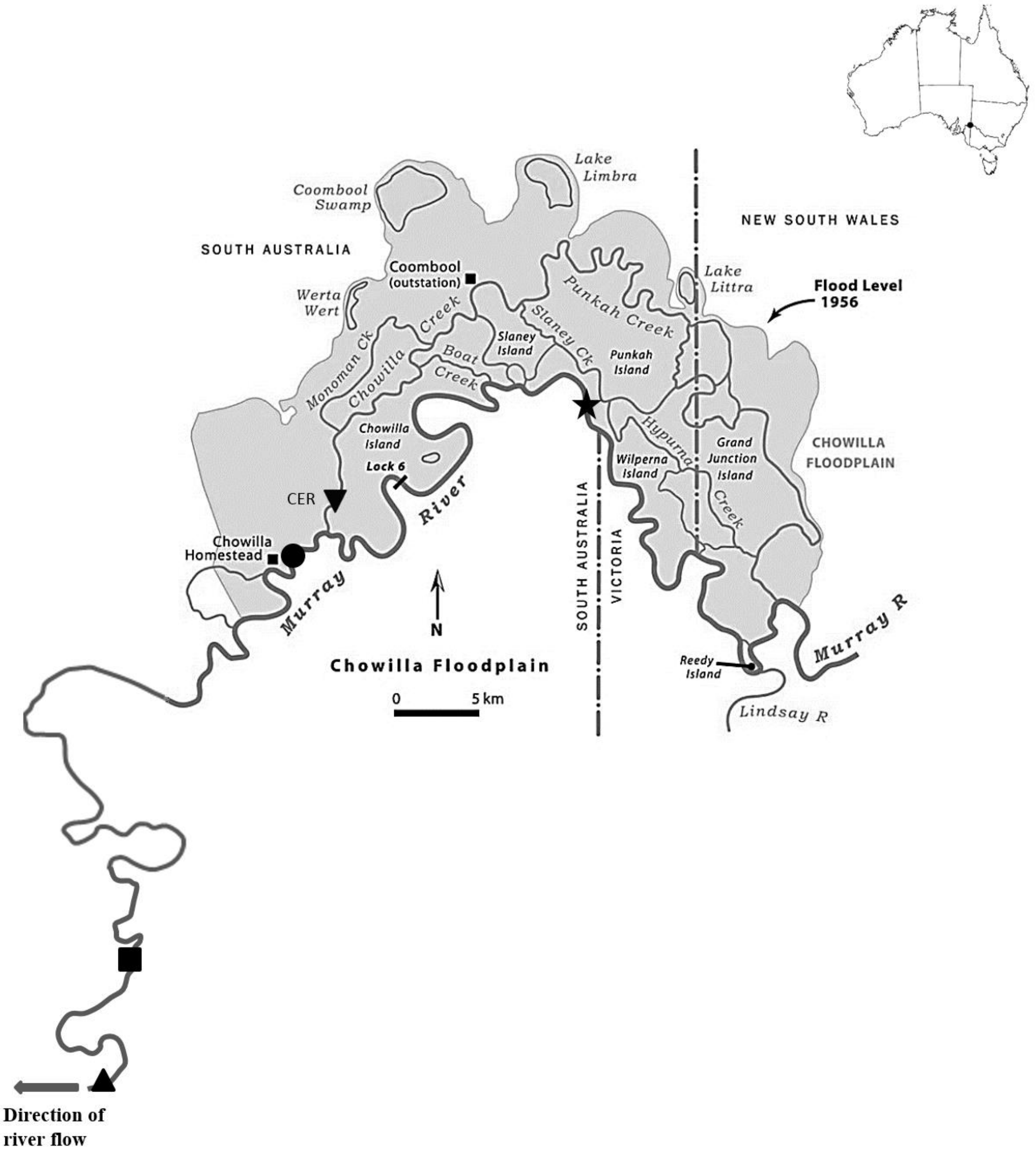

Figure 3-1: The Chowilla Floodplain and adjacent River Murray (modified from MDBA (2012)) showing Chowilla Environmental Regulator (black inverted triangle) on the Chowilla anabranch, the reference (black star), immediately downstream (black circle) and the further downstream (black square) sites, along with the Lock 5 (black triangle) on the MRC of the River Murray; and the direction of flow (arrow). The boundary of the floodplain (shaded grey) is defined by the extent of the historically significant 1956 flood.

Study Sites and Sampling Regime

The impact of the managed floodplain inundation on the MRC ecosystem productivity was assessed and compared between two sites – one immediately downstream (DS1, black circle, Figure 3-1), and the other 40 km downstream (DS2, black square, Figure 3-1) of the confluence of the Chowilla Floodplain with the main river channel of the River Murray. A site upstream of the outlet of Chowilla Creek was chosen as a reference site for the study (RS, black star, Figure 3-1). The RS acted as an indicator of ambient source water quality and productivity under non-inundated conditions. Water quality monitoring stations were established and maintained at all three sites by the South Australian Government Department of Environment, Water and Natural Resources (DEWNR) and the Murray-Darling Basin Authority (MDBA).

Data on dissolved oxygen (DO) were collected at all three sites at 5 min intervals using D'Opto loggers (ZebraTech, New Zealand), deployed about 0.6 m below the water surface. Data for DOC, chlorophyll *a* (Chl *a*) and nutrients were collected at six weekly intervals prior to the managed inundation event and weekly after the commencement of inundation. Nutrient analyses included total phosphorus (TP), total nitrogen (TN), filterable reactive phosphorus (FRP), nitrate (NO_3), nitrogen oxides (No_x) and ammonia (NH_3), and were analysed by the Environmental Analysis Laboratory at Southern Cross University, a National Association of Testing Authorities accredited laboratory. Measurements of solar radiation, wind speed and barometric pressure made at 10 min intervals by an automated weather station located on Chowilla Island were provided by the DEWNR.

Discharge and Chowilla Environmental Regulator Operations

The study period spanned from June to December 2014, with the managed floodplain inundation commencing on 10 September 2014 (Figure 3-2). About 50 days before the managed inundation commenced, there was a small rise in flow to South Australia, with discharge peaking at 18,000 ML d^{-1} for a short duration, compared to a pre-flow level of 4,500 ML d^{-1} (Figure 3-2). This inflow raised the water level in Lock 5, creating a backwater curve that increased the water level in the floodplain anabranch, prior to the managed inundation. Flow then declined prior to the managed inundation. During the testing period of the CER, discharge in the River Murray upstream of the Chowilla Creek inlet was in the range of 5,000 to 10,000 ML day^{-1}.

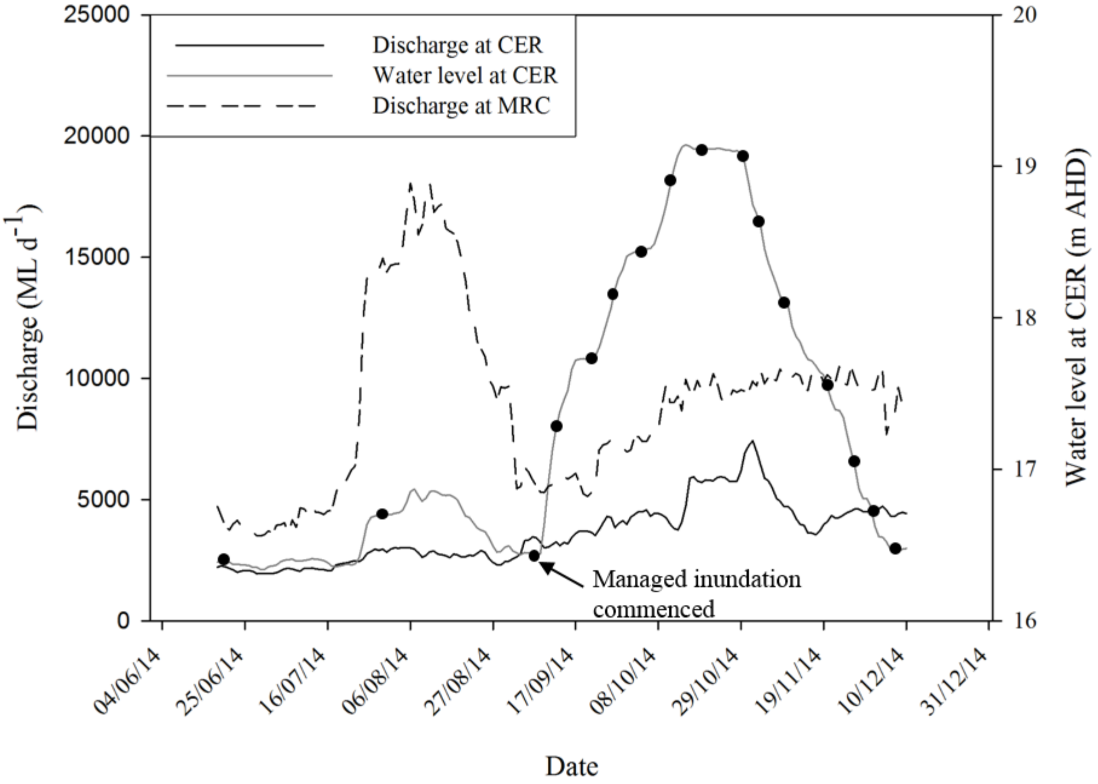

Figure 3-2: Hydrographs of flow (ML d^{-1}) at CER (black solid line) and in the MRC (black dotted line), and the water level (m AHD) at CER (grey solid line). Black dots indicate times when all sites were sampled in the MRC.

The water level at the CER is typically 16.3 m Australian Height Datum (AHD) under normal river operation conditions (Wallace and Furst 2016) and the maximum achievable operating height for the CER is 19.87 m AHD. For this inundation event, the maximum height of the regulator was set to 19.10 m AHD. Accordingly, water level at the CER was raised gradually from 16.90 m AHD to 19.10 m AHD between 10 September and 14 October 2014, which inundated a floodplain area of approximately 23 km^2. This period is considered the 'rising phase of the hydrograph.' Water was then held at the level of about 19.10 m AHD for two weeks, between 15 October and 28 October 2014, which is considered the 'peak of the hydrograph.' Water level decreased from 29 October to 03 December 2014, and returned to the level prior to the inundation, which is considered the ‘falling phase of the hydrograph.’ The period from 03 to 10 December 2014 is considered the ‘post inundation phase.’

Open Water Productivity Analyses

Open water metabolism was estimated from the daily time series of DO concentrations and light intensities using the single station analytical method (Odum 1956, Young and Huryn 1996, Oliver and Merrick 2006). See Chapter 2 of this thesis for further details on the estimation of the open water metabolism from high frequency measurements of DO.

Statistical Analyses

To evaluate the temporal differences in the water quality parameters and examine when significant changes occurred across the three sites, a set of linear mixed effects models were fitted to the data by analyzing ‘day of year’ as a factor. Planned contrasts and a series of sequential tests were then constructed for pairwise comparisons between sampling points for each site separately to evaluate the time points when the threshold changes occurred at the sampling sites. However, for Chl *a*, the lack of data prior to inundation precluded pairwise comparisons of concentrations prior to and during inundation. Instead, two-way ANOVA tests were performed to compare the concentrations between sites.

Time series analysis of the ecosystem metabolism data was conducted by fitting a generalized additive mixed model, with the autocorrelation in the data over time adjusted using a continuous autoregressive model (corAR1). P values were compared with and without site interaction to test the effect of the site. One sample t-tests were performed to determine if the average NEP during and prior to the managed inundation period, and during the different phases of the hydrograph of the managed inundation, were significantly different from zero at all three sites.

Water quality parameters were sampled only twice prior to the managed inundation period, as this was expected to be sufficient to characterize the baseline conditions. However, the initial unexpected water level rise that occurred prior to the managed inundation period made it difficult to use the prior data as representative of baseline conditions. Moreover, due to the lack of detailed data during the initial water level rise, we could not directly assess its influence on Chl *a*, DOC and nutrient concentrations. Therefore, the data analysis is primarily focused on comparing the concentrations of resources between the reference site and the two impacted sites downstream of the inundated floodplain, although in some cases water quality data collected before the commencement of the managed inundation was used to estimate prior conditions. With respect to ecosystem metabolism rates, the continuous measurements made it possible to compare responses during the both the initial water level and managed inundation event, as well as between pre- and post-inundation periods.

RESULTS

Water Column Nutrients

Prior to the managed inundation period, the concentrations of total nutrients were similar at all three MRC sites ($p > 0.05$), while during the managed inundation period, the concentrations at the two downstream sites increased significantly relative to the RS. An analysis of all data across all sites suggested that there was no significant difference in the concentrations during the managed inundation period when compared to the prior period ($p > 0.05$), a result of the large variability across sites, influenced in part by the early unmanaged inundation event. A comparison across the sites indicated that the downstream concentrations increased significantly relative to the RS, mainly during the peak and the early falling phase of the hydrograph (Figure 3-3).

Among dissolved nutrients, no significant differences were observed when compared either between prior to the managed inundation concentrations or between sites at any periods throughout the study period ($p > 0.05$). The average values of total and dissolved nutrients at the three study sites during the different phases of the managed inundation period are shown in Table 3-1.

Dissolved Organic Carbon

DOC ranged from 1.80 (± 0.11) to 4.90 (± 0.10) mg L^{-1} at RS, 1.80 (± 0.05) to 4.60 (± 0.11) mg L^{-1} at DS1, and 1.56 (± 0.09) to 4.46 (± 0.03) mg L^{-1} at DS2. The average DOC concentrations at the three study sites during different phases of the inundation period are shown in Table 3-1. Although DOC concentrations were

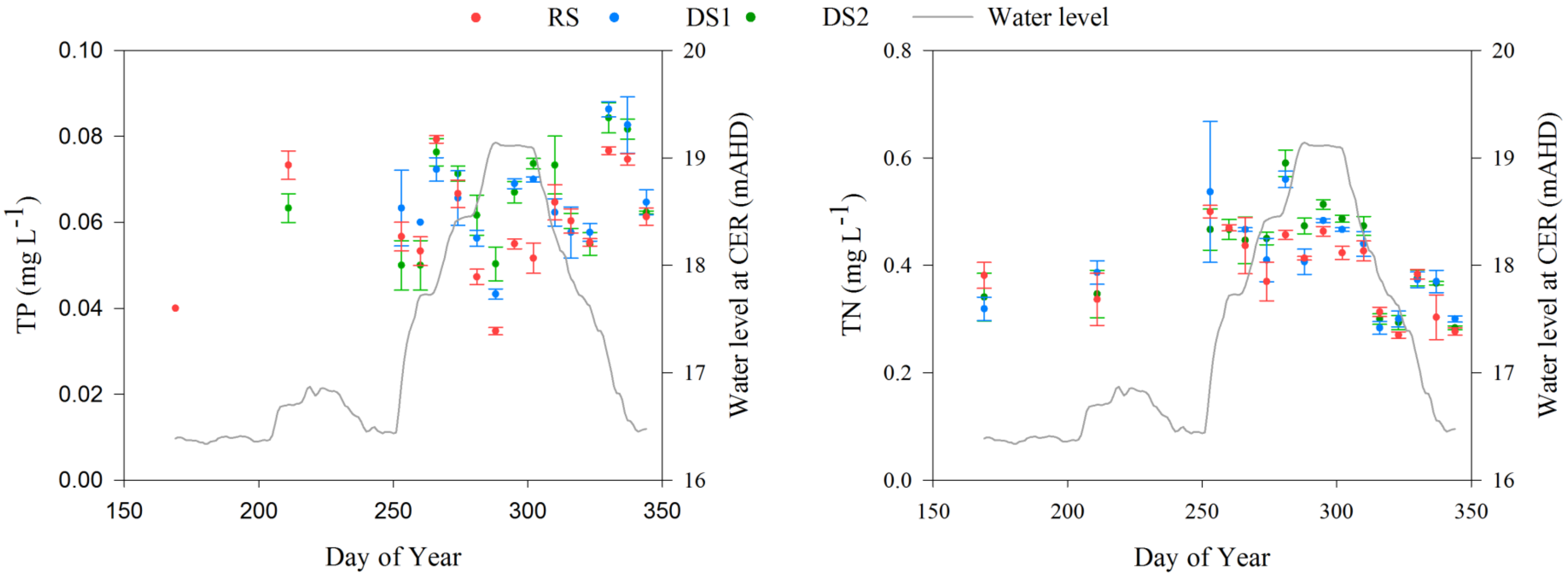

Figure 3-3: TP and TN concentrations (mg L^{-1}) at three sites during the study period. Error bars represent the 95% confidence interval of the mean.

Table 3-1: Average values of nutrients (TP, TN, FRP, NOx, and NH3), DOC in mg L^{-1} and Chl *a* in µg L^{-1} (± SE) during different phases of the inundation period at three study sites; RS- Reference Site, DS1- Immediate Downstream Site, and DS2- Site 40 km Downstream.

Sites	Phases	TP	TN	FRP	NOx	NH_3	DOC	Chl *a*
RS	Pre-inundation	0.057 (±0.008)	0.359 (±0.026)	0.008 (±0.003)	0.006 (±0.001)	0.006 (±0.001)	3.383 (±0.408)	-
	Rising	0.061 (±0.003)	0.447 (±0.016)	0.022 (±0.005)	0.006 (±0.001)	0.007 (±0.002)	4.167 (±0.156)	12.869 (±1.431)
	Peak	0.045 (±0.005)	0.438 (±0.012)	0.010 (±0.002)	0.013 (±0.002)	0.012 (±0.001)	3.433 (±0.117)	11.042 (±0.408)
	Falling	0.062 (±0.003)	0.363 (±0.017)	0.009 (±0.002)	0.007 (±0.001)	0.005 (±0.001)	2.713 (±0.110)	10.322 (±0.317)
	Post-inundation	0.068 (±0.003)	0.290 (±0.020)	0.006 (±0.001)	0.011 (±0.002)	0.004 (±0.001)	2.117 (±0.164)	9.013 (±0.022)
DS1	Pre- inundation	0.056 (±0.007)	0.354 (±0.021)	0.007 (±0.002)	0.005 (±0.001)	0.006 (±0.001)	2.923 (±0.302)	-
	Rising	0.063 (±0.002)	0.486 (±0.028)	0.022 (±0.005)	0.003 (±0.001)	0.005 (±0.001)	3.791 (±0.123)	13.672 (±1.506)
	Peak	0.056 (±0.006)	0.445 (±0.021)	0.014 (±0.002)	0.009 (±0.003)	0.009 (±0.001)	3.878 (±0.193)	11.314 (±0.071)
	Falling	0.067 (±0.003)	0.372 (±0.020)	0.008 (±0.001)	0.008 (±0.001)	0.006 (±0.001)	3.352 (±0.316)	11.286 (±0.266)
	Post-inundation	0.074 (±0.005)	0.334 (±0.019)	0.005 (±0.001)	0.012 (±0.003)	0.004 (±0.001)	2.169 (±0.186)	10.843 (±0.072)
DS2	Pre- inundation	0.052 (±0.005)	0.344 (±0.028)	0.006 (±0.002)	0.008 (±0.005)	0.007 (±0.001)	2.661 (±0.383)	-
	Rising	0.062 (±0.003)	0.476 (±0.017)	0.021 (±0.005)	0.006 (±0.001)	0.007 (±0.001)	4.003 (±0.109)	14.099 (±1.298)
	Peak	0.059 (±0.004)	0.492 (±0.012)	0.009 (±0.001)	0.004 (±0.002)	0.010 (±0.002)	3.790 (±0.174)	13.266 (±0.613)
	Falling	0.069 (±0.003)	0.386 (±0.022)	0.008 (±0.002)	0.021 (±0.006)	0.006 (±0.001)	3.219 (±0.134)	12.165 (±0.598)
	Post-inundation	0.072 (±0.004)	0.323 (±0.019)	0.005 (±0.001)	0.013 (±0.002)	0.006 (±0.002)	2.193 (±0.302)	11.371 (±0.071)

similar at all three sites prior to the inundation period ($p > 0.05$), the concentrations at the two downstream sites increased significantly, mainly during the peak and the early falling phase of the hydrograph ($p < 0.05$) relative to the RS (Figure 3-4). The concentrations at the two downstream sites decreased during the late falling phase of the hydrograph until similar to the concentrations observed at RS ($p > 0.05$) (Figure 3-4).

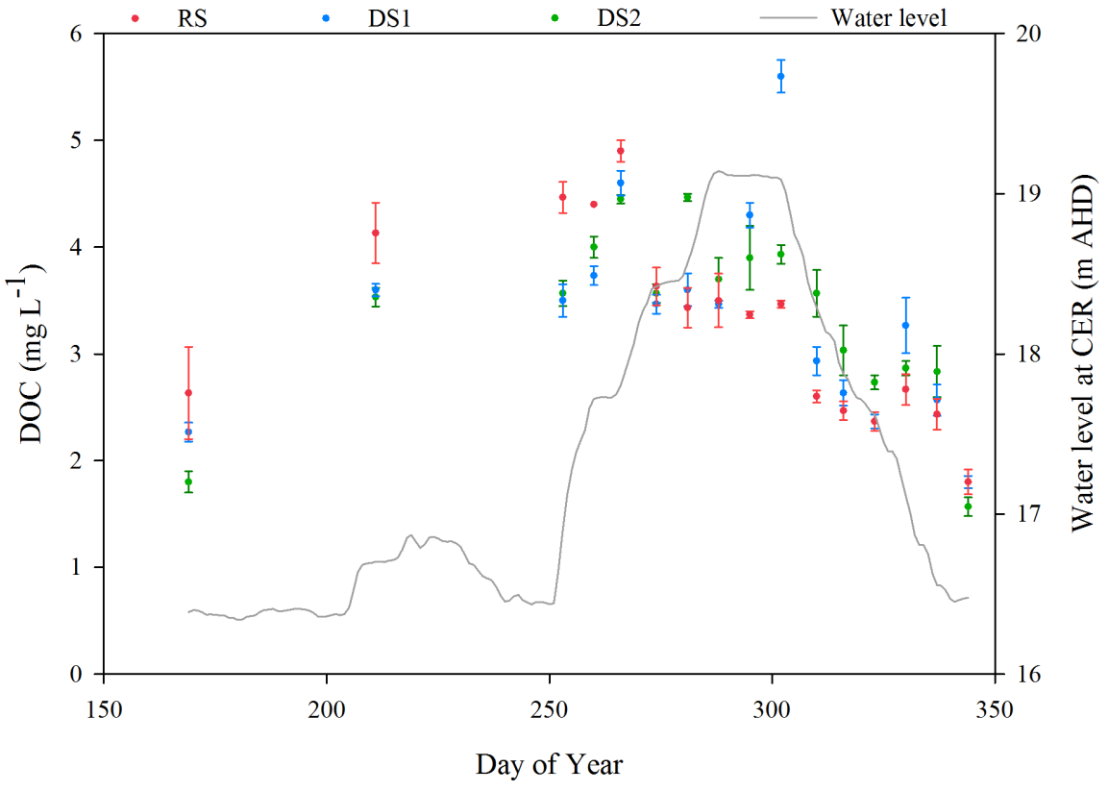

Figure 3-4: DOC concentrations in three study sites during the study period. Error bars represent 95% confidence interval of a mean.

Phytoplankton Biomass

Two-way ANOVA demonstrated a significant temporal variation in the concentration of Chl *a* ($p < 0.05$). Despite concentrations being in similar ranges at all sites (Table 3-1), significant differences in the concentrations were observed between RS and the two downstream sites. These were mainly associated with the peak and falling phases of the hydrograph during the managed inundation period, with higher concentration observed at downstream sites relative to RS ($p < 0.05$).

Ecosystem Metabolism

Strong temporal changes were observed in both GPP and CR rates in response to changes in water level, with noticeable differences in temporal patterns between the three sites (Figure 3-5). The ranges of the rates of GPP, CR and NEP observed at the three sites during different phases of the hydrograph are detailed in Table 3-2.

Table 3-2: Minimum and maximum rates of GPP, CR and NEP in mgO$_2$ L^{-1} d^{-1} during different phases of the inundation period at three study sites; RS- Reference Site, DS1- Immediate Downstream Site, and DS2- Site 40 km Downstream.

Sites	Phases	GPP		CR		NEP	
		Min	Max	Min	Max	Min	Max
RS	Pre-inundation	0.123	0.921	-0.097	-0.875	-0.620	0.497
	Rising	0.022	0.643	-0.010	-0.782	-0.407	0.434
	Peak	0.259	0.956	-0.223	-0.824	-0.315	0.441
	Falling	0.113	0.787	-0.141	-0.960	-0.374	0.278
	Post-inundation	0.357	0.990	-0.322	-0.693	-0.193	0.590
DS1	Pre- inundation	0.034	1.645	-0.122	-0.998	-0.346	0.968
	Rising	0.182	0.893	-0.051	-0.773	-0.166	0.687
	Peak	0.409	0.857	-0.402	-0.779	-0.134	0.455
	Falling	0.318	1.291	-0.251	-1.243	-0.266	0.351
	Post-inundation	0.289	1.119	-0.409	-1.089	-0.261	0.066
DS2	Pre-inundation	0.038	1.319	-0.027	-1.514	-0.601	1.179
	Rising	0.048	1.569	-0.163	-1.369	-1.059	1.569
	Peak	0.038	0.908	-0.308	-0.967	-0.432	0.322
	Falling	0.132	1.048	-0.508	-1.256	-0.813	0.489
	Post-inundation	0.025	1.288	-0.254	-0.492	-0.285	0.796

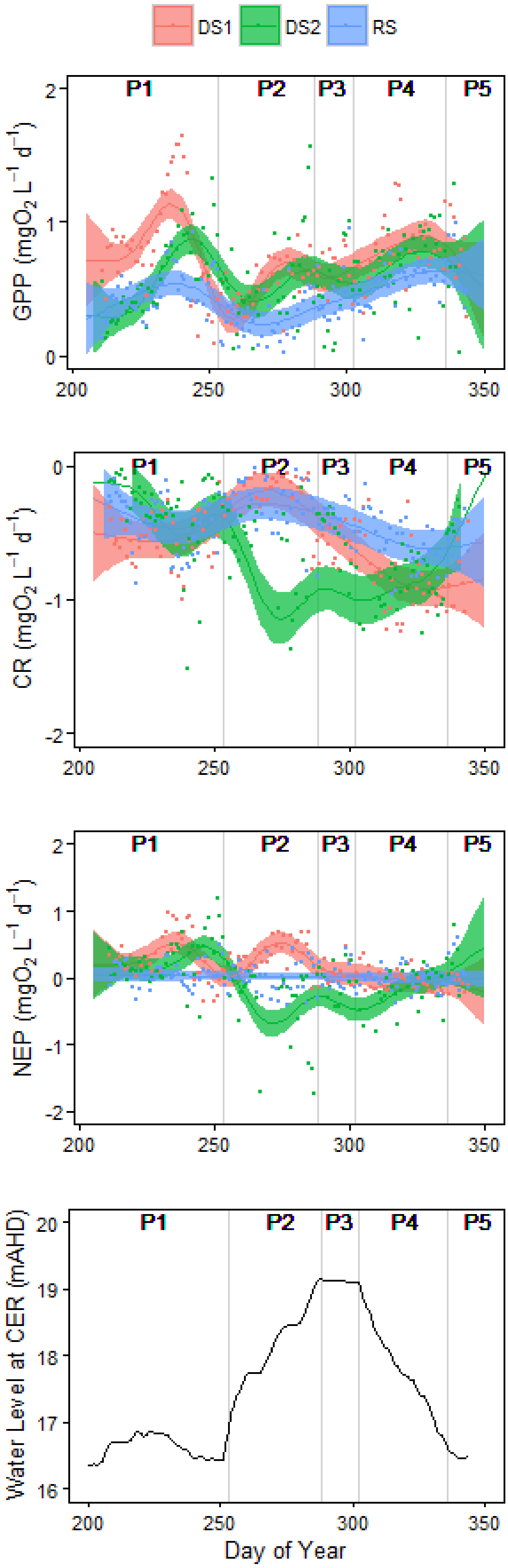

Figure 3-5: Time-series visualization of the regression (Visreg) plot for GPP, CR and NEP rates in mgO_2 L^{-1} d^{-1} at three sites in the MRC of the River Murray, and the hydrograph showing the water level in m AHD at CER. P1 = prior to inundation period; P2 = rising phase of the hydrograph; P3 = static phase/peak of the hydrograph; P4 = falling phase of the hydrograph; and P5 = post-inundation phase. Shaded blue, red and green bands represent +/-95% confidence interval of the mean values of GPP, CR and NEP.

GPP rates at DS1 were significantly higher than rates observed at the RS, even prior to the managed inundation period ($p < 0.05$) (Table 3-2). This early response aligned with the initial water level rise prior to the managed inundation. In contrast, the GPP rates at DS2 were comparable to the rates at RS prior to the inundation period ($p > 0.05$). GPP at the two downstream sites increased significantly during the managed inundation period, and were significantly different to the rates at RS ($p < 0.05$) (Figure 3-5). The rates between the two downstream sites were not generally significantly different, except during the peak of the hydrograph ($p < 0.05$).

CR rates at RS were similar to those at DS1 ($p > 0.05$), but were slightly lower to DS2 ($p < 0.05$) during the initial water level rise prior to the managed inundation period (Table 3-2). CR rates at DS2 increased significantly during the rising phase of the hydrograph of the managed inundation period as compared to the rates observed at RS and DS1 sites ($p < 0.05$). However, CR at DS1 increased significantly compared to RS ($p < 0.05$) later, during the peak of the hydrograph, and this increase of CR at DS1 and a slowly decreasing of CR at DS2 led to no significant differences between the two downstream sites ($p > 0.05$) after the peak. Similar to the pattern observed with GPP, the rates at both downstream sites slowly dropped back to the level prior to the inundation period during the late falling phase of the hydrograph (Figure 3-5).

The greater increase in GPP relative to CR led to positive NEP values at DS1 and switched the metabolic balance from near zero at the RS to strongly autotrophic (Figure 3-5). This mainly occurred during the initial water level rise prior to the managed inundation period and during the rising phase of the hydrograph of the managed inundation period (Table 3-2). In contrast, at DS2, the greater change in CR relative to GPP led to negative NEP values and thus the switch the metabolic balance to strongly heterotrophic conditions. This large switch in metabolic balance at DS2 was observed once prior to the initial unplanned water level rise and during the rising phase of the hydrograph of the managed inundation period (Figure 3-5; Table 3-3). NEP at the RS, remained close to zero ($p > 0.05$) throughout the study, but was significantly positive [$M = 0.16$, $t(31) = 10.80$, $p <$

0.05] (Table 3-3) during the period prior to the initial water level rise before any substantial increase in the water level.

Table 3-3: Average NEP values during different phases of the hydrograph at three study sites; RS- Reference Site, DS1- Immediate Downstream Site, and DS2- Site 40 km Downstream, where * denotes $p \leq 0.05$, ** denotes $p \leq 0.01$, and *** denotes $p \leq 0.001$ obtained through students t-test to test if the average NEP is statistically different from 0.

Site	Phases	Average NEP
RS	Pre- inundation	0.027
	Rising	0.003
	Peak	0.019
	Falling	-0.045
	Post- inundation	0.147
DS1	Pre- inundation	0.251***
	Rising	0.340***
	Peak	0.069
	Falling	-0.046
	Post- inundation	-0.084
DS2	Pre- inundation	0.097
	Rising	-0.402**
	Peak	-0.047
	Falling	-0.269*
	Post- inundation	0.235

DISCUSSION

The use of environmental flow regulators to deliver environmental flows has now become an important tool in the rehabilitation of regulated rivers (Baldwin et al. 2016, Wallace and Furst 2016). Consequently, assessing the influence of managed inundation events on riverine productivity, and understanding how to deliver environmental flows in the best possible way to maximise productivity that does not lead to severe unintended outcomes such as hypoxic blackwater events and problematic algal blooms, is crucial. In this study, we assessed the influence of return flows from a floodplain anabranch to the MRC after a managed inundation of the floodplain using an environmental flow regulator, and examined the response in terms of ecosystem productivity at two sites downstream of the inundated floodplain.

Contrary to expectations, we did not observe elevated concentrations of dissolved nutrients during the managed inundation period when compared with concentrations prior to the managed inundation. This was likely the result of high variability across sites, influenced in part by the unexpected initial water rise that occurred prior to the managed inundation. This small flow pulse transported nutrients from the upstream reaches of the Murray-Darling basin, as increased nutrient concentrations were observed across all three sites during the initial water level rise, including the RS. However, when comparing the responses between sites, higher TP and TN concentrations were observed at the two downstream sites compared with the concentration at RS during the period coinciding with the peak and the early falling phases of the managed inundation, indicating contributions of nutrients from the inundated floodplain. This was also the period when phytoplankton biomass became significantly elevated at the two downstream sites relative to the RS. Floodplain inundation has been associated with an increase in the concentrations of nutrients and phytoplankton in other studies. Nielsen et al. (2015) observed a substantial increase in the concentrations of nutrients and phytoplankton biomass at two sites downstream of an extensive floodplain of the River Murray following a major spring flood that inundated 80 % of the 66, 000 ha total floodplain area. During the same spring flood, Cook et al. (2015) observed almost 26 % increase in the TN and 80 % increase in the TP concentration when compared with the concentration prior to any substantial flooding at a site further downstream to the site chosen by Nielsen et al. (2015).

Similar to the patterns observed with total nutrients, the DOC concentrations increased at the two downstream sites relative to the RS. This occurred during the peak and the falling phases of the hydrograph, as also reported for the immediate river monitoring locations by Wallace and Furst (2016). DOC concentrations declined to the level observed prior to the inundation period during the late falling and post-inundation phases, as the majority of flow was diverted back within the MRC after the managed inundation event (Wallace and Furst (2016). Significant higher concentrations of both total nutrients and DOC between RS and the two downstream sites during the managed inundation period indicates that return flows from the Chowilla anabranch increased the concentration of resources available to the riverine food-web for at least 40 km downstream of the return flows, and possibly beyond.

Where large increases in GPP and CR switched the metabolic balance to strongly autotrophic and heterotrophic states at the immediate and further downstream sites respectively, the metabolic rates at RS remained balanced with near zero net production throughout the study. Similar balanced responses in the MRC of the River Murray were also observed by Oliver and Merrick (2006) and by Cook et al. (2015) in the mid-Murray. Oliver and Merrick (2006) hypothesized that such observations resulted from full heterotrophic utilisation of the available food resources, suggesting restriction in food-web production by energy supply. Regulated rivers like the River Murray often tend to exhibit light and nutrient limitations (Baker et al. 2000), thereby reducing the primary production by in-stream autotrophs (Oliver et al. 1999). Additional inputs from allochthonous sources subsidizing the carbon supplies to the system are therefore important to enhance secondary productivity (Polis et al. 1997, Dolbeth et al. 2012).

The large increase in GPP observed at DS1 occurred during the rising phase of the hydrograph of the managed inundation period. This high GPP observed at the immediate downstream site supports the findings of Wallace and Furst (2016), who also observed higher GPP at their monitored site during the same inundation event. Cook et al. (2015), similarly observed a large increase in GPP at a downstream sites compared to an upstream site during a natural flood in mid-Murray downstream of a large extensive floodplain. However, in our case the large increase in GPP, did not align with increases in nutrients or phytoplankton biomass. This interpretation is based on discrete weekly data for the water quality variables and therefore may not accurately capture the changes that occurred, but suggest there may be other reasons for the apparent increase in GPP. One possibility is that the large increase in GPP was a result of the oxygen rich water transported to the MRC from the inundated floodplain, and not a result of increased photosynthesis in the MRC itself. This phenomena has previously been reported by Oliver and Lorenz (2013). The lack of observation of elevated nutrients and phytoplankton biomass supports this notion.

The large respiratory reduction in dissolved oxygen concentration observed at DS2 led to the shift of the metabolic balance to a strongly heterotrophic state as compared to the two upstream sites. There are multiple possible explanations for this observation. It is possible that the substantially increased CR rates were due to respiratory metabolism of organic materials transported from the floodplain through the return flow, with some additional contribution from organic material formed at sites in between. Returning flood waters can transport a large biomass of microorganisms including bacteria, phytoplankton and zooplankton to the main river channel (Furst et al. 2014, Cook et al. 2015, Nielsen et al. 2015). These are expected to increase respiration rates after a period of travel down the MRC. It is suspected that this is the reason for the increased CR rates at the downstream site. It is also possible that some of the respiration was associated with the utilization of the organic material accumulated in the benthic zone. The large change in CR observed at the site furthest downstream did not align with increased DOC concentrations, which occurred during the peak and the early falling phase of the hydrograph of the managed inundation period. This suggests that DOC is not the major driver of the large change in CR. Conducting more adequate and frequent spatio-temporal samplings for the water quality variables in designing future studies may enable a better understanding of the drivers of such large change in the metabolic rates (Marcé et al. 2016).

Some of the observed differences in the metabolic response at two downstream sites could also be attributed to their network positioning in relation to Lock 5 of the River Murray. DS1 lies in the upper reach of the weir pool of Lock 5 whereas DS2 is in the lower reach, and the differences associated with the hydraulic characteristics (such as depth, velocity of water), channel morphology, and in-channel processes could have a large influence on how an individual site responds to flow and influences the ecosystem productivity (Thomaz et al. 2007). Spatial variability in the measurements of ecosystem metabolism are common, and has been observed in River Murray (Wallace and Furst 2016), tropical river (Hunt et al. 2012) in Northern Australia, and in lakes in North Wisconsin (Van de Bogert et al. 2012), but received much less attention.

The metabolic rates at two downstream sites decreased to the levels observed prior to inundation during the late falling phase and the post inundation phase of the hydrograph, and were comparable to the rates observed at RS. This reflects the dilution occurring as a result of the increasing proportion of flow being delivered down the MRC during the falling phase of the hydrograph, and the progressive lowering of Lock 6 from the peak height required to achieve the inundation back to the operation level, which is 19.25 m AHD (Wallace and Furst 2016). Furthermore, the lack of increased GPP and CR rates at two downstream sites during the late falling phase could also be due to the closure of the large wetland regulators in the floodplain to facilitate increased likelihood of successful breeding by biota that responded to the inundation (Wallace and Furst 2016).

There is a growing interest in the construction of environmental flow regulators throughout the Murray-Darling Basin (Wallace and Furst 2016). Although the primary focus of the management of floodplain systems is often targeted for ecological benefits of floodplain habitats, our results show that the return flows from the inundated floodplain to the MRC have the potential to have a positive influence on riverine productivity at larger spatial scale, by providing terrestrial subsidies of organic carbon and nutrients to the MRC consumers. The potential for such benefits should be considered in the future design and management of floodplain inundation events. While our continuously monitored oxygen data made it possible to determine how river metabolism at two downstream sites were influenced by the return flows from the inundated floodplain, discretely monitored water quality variables made it difficult to attribute changes in metabolism to particular physio-chemical parameters. More adequate spatio-temporal sampling in the future studies may enable to better understand the drivers of such large changes in the river metabolism as observed in this study. This information will be important in supporting improved ecosystem productivity in large and regulated floodplain rivers where environmental water provisions are managed by the operation of floodplain regulators.

REFERENCES

Arthington, A. H. 2012. Environmental flows: saving rivers in the third millennium. Univ of California Press.

Arthington, Á. H., R. J. Naiman, M. E. McClain, and C. Nilsson. 2010. Preserving the biodiversity and ecological services of rivers: new challenges and research opportunities. Freshwater Biology **55**:1-16.

Atkinson, C. L., S. W. Golladay, S. P. Opsahl, and A. P. Covich. 2009. Stream discharge and floodplain connections affect seston quality and stable isotopic signatures in a coastal plain stream. Journal of the North American Benthological Society **28**:360-370.

Baker, P. D., J. D. Brookes, M. D. Burch, H. R. Maier, and G. G. Ganf. 2000. Advection, growth and nutrient status of phytoplankton populations in the lower River Murray, South Australia. Regulated Rivers: Research & Management **16**:327-344.

Baldwin, D. S. 1999. Dissolved organic matter and phosphorus leached from fresh and 'terrestrially'aged river red gum leaves: implications for assessing river–floodplain interactions. Freshwater Biology **41**:675-685.

Baldwin, D. S., M. J. Colloff, S. M. Mitrovic, N. R. Bond, and B. Wolfenden. 2016. Restoring dissolved organic carbon subsidies from floodplains to lowland river food webs: a role for environmental flows? Marine and Freshwater Research.

Baldwin, D. S., W. L. Paul, J. S. Wilson, T. Pitman, G. N. Rees, and A. R. Klein. 2015. Changes in soil carbon in response to flooding of the floodplain of a semi-arid lowland river. Changes **34**.

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

Cook, R. A., B. Gawne, R. Petrie, D. S. Baldwin, G. N. Rees, D. L. Nielsen, and N. S. Ning. 2015. River metabolism and carbon dynamics in response to flooding in a lowland river. Marine and Freshwater Research.

Cross, W. F., C. V. Baxter, K. C. Donner, E. J. Rosi-Marshall, T. A. Kennedy, R. O. Hall, H. A. W. Kelly, and R. S. Rogers. 2011. Ecosystem ecology meets adaptive management: food web response to a controlled flood on the Colorado River, Glen Canyon. Ecological Applications **21**:2016-2033.

Dolbeth, M., M. Cusson, R. Sousa, and M. A. Pardal. 2012. Secondary production as a tool for better understanding of aquatic ecosystems. Canadian journal of fisheries and aquatic sciences **69**:1230-1253.

Furst, D. J., K. T. Aldridge, R. J. Shiel, G. G. Ganf, S. Mills, and J. D. Brookes. 2014. Floodplain connectivity facilitates significant export of zooplankton to the main River Murray channel during a flood event.

Hunt, R. J., T. D. Jardine, S. K. Hamilton, and S. E. Bunn. 2012. Temporal and spatial variation in ecosystem metabolism and food web carbon transfer in a wet-dry tropical river. Freshwater Biology **57**:435-450.

Jolly, I. D., G. R. Walker, and K. A. Narayan. 1994. Floodwater recharge processes in the Chowilla anabranch system, South Australia. Soil Research **32**:417-435.

Junk, W. J., P. B. Bayley, and R. E. Sparks. 1989. The flood pulse concept in river-floodplain systems. Canadian special publication of fisheries and aquatic sciences **106**:110-127.

Mackay, N. 1990. Understanding the Murray. In N. MacKay & D. Eastburn (Eds.), The Murray. Canberra: Murray Darling Basin Commission.

Marcé, R., G. George, P. Buscarinu, M. Deidda, J. Dunalska, E. de Eyto, G. Flaim, H.-P. Grossart, V. Istvanovics, and M. Lenhardt. 2016. Automatic high frequency monitoring for improved lake and reservoir management. Environmental Science & Technology **50**:10780-10794.

MDBA. 2012. Chowilla Floodplain Environmental Water Management Plan 2012. Australian Government: Canberra, ACT.

MDBA. 2014. Preliminary Overview of Constraints to Environmental Water Delivery in the Murray–Darling Basin. Retrieved 1/04/2014, 2014, from http://www. mdba. gov. au/what-we-do/water-planning/managingconstraints/constraints-overview/nsw.

Nielsen, D. L., R. A. Cook, N. Ning, B. Gawne, and R. Petrie. 2015. Carbon and nutrient subsidies to a lowland river following floodplain inundation. Marine and Freshwater Research.

Odum, H. T. 1956. Primary production in flowing waters. Limnology and Oceanography:102-117.

Oliver, R., B. Hart, J. Olley, M. Grace, C. Rees, and G. Caitcheon. 1999. The Darling River: Algal growth and the cycling and sources of nutrients.

Oliver, R. L. and Z. Lorenz. 2013. Changes in metabolic activity in the South Australian section of the Murray River during the 2010/11 flood that followed a ten year drought. Goyder Institute for Water Research Technical Report Series.

Oliver, R. L. and C. J. Merrick. 2006. Partitioning of river metabolism identifies phytoplankton as a major contributor in the regulated Murray River (Australia). Freshwater Biology **51**:1131-1148.

Opperman, J. J., G. E. Galloway, J. Fargione, J. F. Mount, B. D. Richter, and S. Secchi. 2009. Sustainable floodplains through large-scale reconnection to rivers. Science **326**:1487-1488.

Pittock, J. and C. M. Finlayson. 2011. Australia's Murray–Darling Basin: freshwater ecosystem conservation options in an era of climate change. Marine and Freshwater Research **62**:232-243.

Polis, G. A., W. B. Anderson, and R. D. Holt. 1997. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. Annual review of ecology and systematics:289-316.

Robertson, A., S. Bunn, P. Boon, and K. Walker. 1999. Sources, sinks and transformations of organic carbon in Australian floodplain rivers. Marine and Freshwater Research **50**:813-829.

Robertson, A., A. Burns, and T. Hillman. 2016. Scale dependent lateral exchanges of organic carbon in a dryland river during a high flow experiment. Marine and Freshwater Research.

Roseman, E. F. and R. L. DeBruyne. 2015. The renaissance of ecosystem integrity in North American large rivers. Restoration Ecology **23**:43-45.

Saintilan, N. and I. Overton. 2010. Ecosystem response modelling in the Murray-Darling Basin. CSIRO Publishing.

Taylor, P. J., G. R. Walker, G. Hodgson, T. J. Hatton, and R. L. Correll. 1996. Testing of a GIS model ofEucalyptus Iargiflorens health on a semiarid, saline floodplain. Environmental management **20**:553-564.

Thomaz, S. M., L. M. Bini, and R. L. Bozelli. 2007. Floods increase similarity among aquatic habitats in river-floodplain systems. Hydrobiologia **579**:1-13.

Tockner, K., D. Pennetzdorfer, N. Reiner, F. Schiemer, and J. Ward. 1999. Hydrological connectivity, and the exchange of organic matter and nutrients in a dynamic river–floodplain system (Danube, Austria). Freshwater Biology **41**:521-535.

Valett, H., M. Baker, J. Morrice, C. Crawford, M. Molles Jr, C. Dahm, D. Moyer, J. Thibault, and L. M. Ellis. 2005. Biogeochemical and metabolic responses to the flood pulse in a semiarid floodplain. Ecology **86**:220-234.

Van de Bogert, M. C., D. L. Bade, S. R. Carpenter, J. J. Cole, M. L. Pace, P. C. Hanson, and O. C. Langman. 2012. Spatial heterogeneity strongly affects estimates of ecosystem metabolism in two north temperate lakes. Limnology and Oceanography **57**:1689.

Wallace, T. A. and D. Furst. 2016. Open water metabolism and dissolved organic carbon in response to environmental watering in a lowland river–floodplain complex. Marine and Freshwater Research **67**:1346-1361.

Watts, R., B. Richter, J. Opperman, and K. Bowmer. 2011. Dam reoperation in an era of climate change. Marine and Freshwater Research **62**:321-327.

Young, R. G. and A. D. Huryn. 1996. Interannual variation in discharge controls ecosystem metabolism along a grassland river continuum. Canadian journal of fisheries and aquatic sciences **53**:2199-2211.

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Overall percentage (%)	80 %		
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By signing the Statement of Authorship, each author certifies that:

i. the candidate's stated contribution to the publication is accurate (as detailed above);

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Name of Co-author	Roderick Oliver		
Contribution to the paper	Provided input in conceiving the study and design of experiments; supervised data analysis and interpretation; reviewed the manuscript		
Signature		Date	25 May 2017

Name of Co-author	Kane Aldridge		
Contribution to the paper	Provided input in conceiving the study and design of experiments; participated in and supervised field work; supervised data analysis and interpretation; reviewed the manuscript		
Signature		Date	25 May 2017

Name of Co-author	Justin Brookes		
Contribution to the paper	Provided input in conceiving the study and design of experiments; participated in and supervised field work; supervised data analysis and interpretation; reviewed the manuscript		
Signature		Date	25 May 2017

CHAPTER 4

LOW METABOLIC CONTRIBUTION BY HIGHER ORDER ORGANISMS REDUCES THE UTILITY OF ECOSYSTEM ASSESSMENTS BASED ON RIVER METABOLISM MEASUREMENTS

ABSTRACT

The perceived importance of metabolic activity as an indicator of aquatic ecosystem 'health' is based on the view that measurements of metabolism reflect energy sources and carbon fluxes in aquatic food webs. However, remarkably little effort has been dedicated to understanding the relative contributions made by different biotic components to the total metabolic activity. We estimated metabolic rates of various riverine organisms and compared with the estimates of whole ecosystem metabolism under different flow conditions during a managed floodplain inundation event in the lower River Murray, South Australia.Whole ecosystem metabolism was dominated by planktonic microorganisms (production: 60 – 75 % and respiration: 77 – 90 %), followed by benthic organisms (production: 6.45 – 11.30 % and respiration: 6.70 – 14.45 %); while zooplankton (0.70 – 1.65 %), invertebrates (0.007 – 0.04 %) and fish (0.07 – 0.35 %) contributed significantly less to ecosystem respiration.Although higher trophic levels of the aquatic food webs are critical for the ecological conditions of riverine systems, our findings revealthat this may not be reflected in their contribution to overall carbon fluxes, and as such, changes in metabolic activity primarily reflect the condition of lower trophic levels and not the ecosystem more broadly.

KEY WORDS: Ecosystem metabolism, primary production, community respiration, metabolic rates, food web

INTRODUCTION

Ecosystem metabolism, which incorporates photosynthesis by autotrophs and respiration by autotrophs and heterotrophs, encompasses major processes associated with the production and utilisation of basal food resources that supports upper-level consumers in riverine ecosystems (Odum 1956, Pomeroy 1974). Since photosynthesis and respiration are primary drivers of dissolved oxygen dynamics in rivers, tracking changes in dissolved oxygen concentrations provides an effective measure of metabolism at the ecosystem scale (Cole et al. 2000, Hanson et al. 2003, Staehr and Sand-Jensen 2007, Staehr et al. 2010). In-stream primary production by autotrophs, such as algae and macrophytes, provides a source of energy to grazing invertebrates and subsequently to higher order organisms (Odum and Barrett 1971), and therefore, estimates of gross primary production (GPP) provide measures of the rate at which this energy is made available to the food web. Conversely, community respiration (CR) reflects the in-stream use of energy by autotrophs and heterotrophs (Odum and Barrett 1971, Pomeroy 1974), and estimates the rate at which energy supplies are used (Woodwell and Whittaker 1968, Pomeroy 1974). Net ecosystem production (NEP) is the difference between GPP and CR, and can be used to describe the metabolic status of an ecosystem (Odum 1956, Woodwell and Whittaker 1968, Howarth et al. 1996, Staehr and Sand-Jensen 2007). Thus, ecosystem metabolism rates are considered to provide measures of food web energy sources andcarbon flows, and offer a foundation for the quantification of trophic structures in aquatic systems (Kemp and Boynton 2004).

Measurements of river metabolism are often used to gain insights into river ecosystem health (Fellows et al. 2006, Young et al. 2008), based on the relative contributions of autotrophs and heterotrophs to the balance between primary production and respiration as reflected in whole system NEP (Cremona et al. 2014).Although increasingly included in routine monitoring programs to inform the management of rivers in many regions of the world (Young et al. 2008), how information obtained from such measurements provide an understanding of the overall health of rivers is not well understood.

Different organisms in a system contribute distinctly to the measured metabolism, as they have differing metabolic rates, controlled primarily by their body sizes and temperature (Gillooly et al. 2001). The influence of particular groups of organisms on ecosystem metabolism depends also on their relative biomass (Oliver and Merrick 2006, Gawne et al. 2007, Cremona et al. 2014), in addition to their specific metabolic rates. Microbes and bacteria are known to be metabolically the most active components of the ecosystem, with higher metabolic rates per unit biomass compared to metazoans (Del Giorgio et al. 1997). It is estimated that anywhere between 30 to 60 % of the phytoplankton production in marine and freshwater systems is processed by planktonic bacteria (Cole et al. 1988, Del Giorgio et al. 1997). Moreover, aquatic systems dominated by microbes are considered to be more heterotrophic (CR > GPP) compared to those where larger metazoans are the primary consumers (Del Giorgio et al. 1997).

Studies on partitioning metabolism in aquatic ecosystems have primarily focussed on the metabolism of pelagic and benthic microorganisms such as phytoplankton, benthic algae, bacteria and fungi (Bunn et al. 2003, Oliver and Merrick 2006,); with little consideration on the role that higher order organisms play in the overall metabolic variability. This reflects the complexities involved with estimating the metabolic activity of different components of the ecosystems, as the analysis not only requires estimates of the metabolic activity of different biotic groups but also their biomasses, an often-difficult task for the patchily distributed larger organisms. So, despite a long history of study, our understanding of the contribution that higher order organisms make to the measurements of ecosystem metabolism is limited (Cremona et al. 2014, Benjamin et al. 2016).

In this study, we measured the whole ecosystem metabolism before, during and after managed inundation of the Chowilla Floodplain in the lower Murray River in South Australia. The objective was to estimate the metabolism of different aquatic biota and assess their contribution to the overall metabolic variability, and the three differing flow conditions were expected to provide different abundance of the aquatic biota considered, as floodplain inundation has often been associated with significant increases in the abundance of autotrophs and heterotrophs in aquatic systems. The functional groups of aquatic biota considered were: phytoplankton, zooplankton, macroinvertebrates (*Cherax destructor* and shrimps) and fish. We hypothesized that micro-planktons, mainly phytoplankton, small zooplankton and bacteria would be responsible for the majority of the measured metabolism, owing to their higher metabolic rates per unit biomass as compared to other metazoans.

MATERIALS AND METHODS

Study Site Description

Chowilla Floodplain (33°57′ S, 140°56′ E) is one of the major floodplains adjoining the River Murray. Covering an area of 17,700 hectares, it comprises a mixture of wetlands, lentic and lotic habitats, including anabranches and shallow depressions. The boundary of the floodplain is defined by the 1956 flood extent (Overton and Doody 2008). Water diverted from the River Murray channel upstream in the New South Wales section enters into a network of streams and then converges to form the main anabranch of the floodplain, Chowilla Creek, which runs for 100 km and flows back into the river channel approximately 8 km below Lock 6 in the South Australian section of the River Murray (Jolly et al. 1994) (Figure 4-1). Lock 6 controls the hydraulics of the Chowilla anabranch systems. More details on the Chowilla Floodplain can be obtained from Cale (2009).

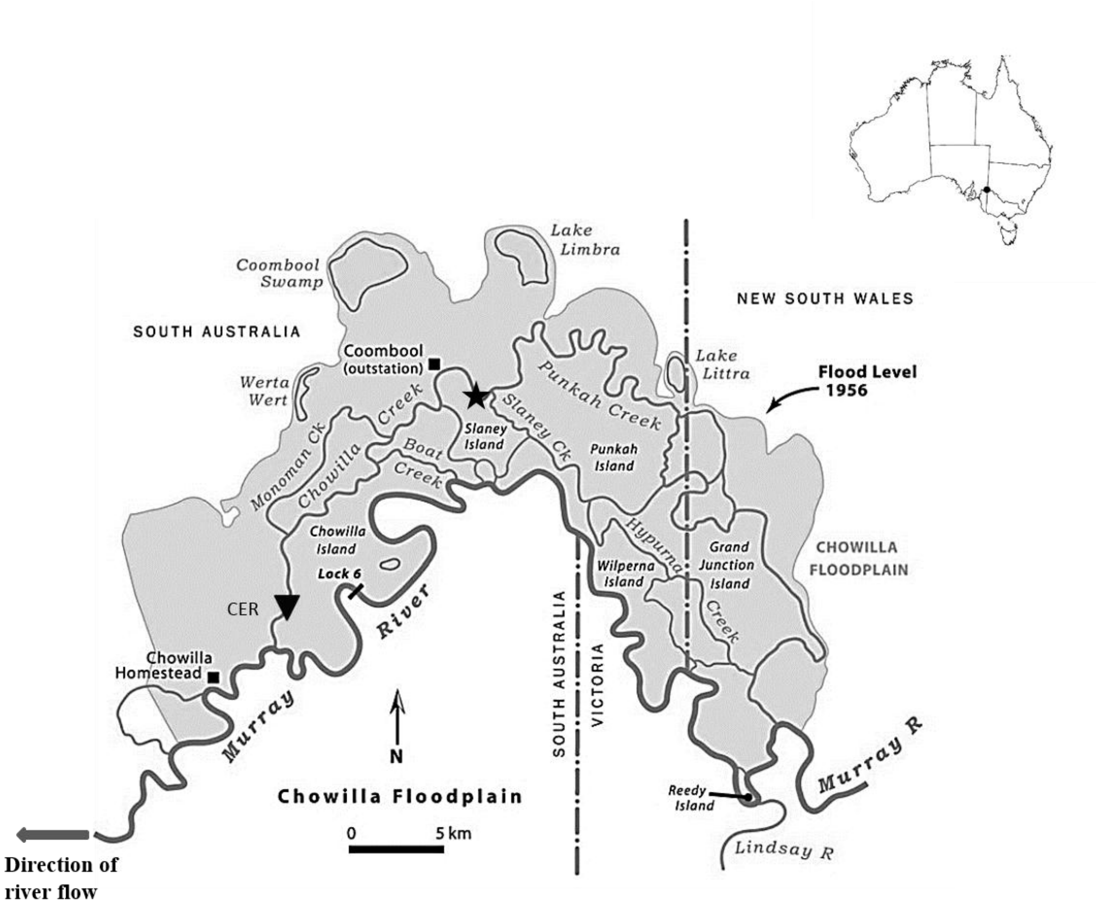

Figure 4-1. The River Murray and adjacent Chowilla Floodplain (modified from MDBA 2012). Water leaves the main channel of the River Murray and enters the floodplain via numerous creeks upstream of Lock 6 (see arrow denoting direction of river flow).Black star on the Chowilla Creek represents the sampling site, and the black inverted triangle represents the location of Chowilla Environmental Regulator (CER).

A 100 m reach of the permanently flowing Chowilla Creek was chosen as an experimental site (33°56′ S, 140°55′ E). Three samplings were conducted at three different flow conditions where flooding was controlled using a newly constructed Chowilla Environmental Regulator (CER). Sampling period I, II and III occurred in May 2014, November 2014, and March 2015; during the periods of low flow prior to floodplain inundation, managed inundation, and post-inundation low flow, respectively.

Chowilla Environmental Regulator Operations

CER was constructed on Chowilla Creek, approximately 1.45 km upstream of where it re-enters the Murray River, with the purpose of improving the ecological conditions of the floodplain by increasing the frequency, duration and extent of floodplain inundation. The water level at the CER is typically 16.3 m Australian Height Datum (AHD) under normal river operation conditions. The managed inundation of the floodplain commenced on 10 September 2014, and during the testing period of the CER, discharge in the River Murray upstream of the Chowilla inlet was in the range of 5,000 to 10,000 ML day^{-1}. The maximum achievable operating height for the CER is 19.87 m AHD, but for this inundation event, the maximum height of the regulator was set to 19.10 m AHD. Accordingly, water level at the CER was raised gradually from 16.90 m AHD to 19.10 m AHD between 10 September and 14 October 2014, which inundated a floodplain area of approximately 23 km^2. Water was then held at the level of about 19.10 m AHD for two weeks, between 15 October and 28 October 2014. Water level decreased from 29 October to 03 December 2014, and returned to the level prior to the inundation. Average water depth at the experimental site was about 1.40 m prior to and following the inundation period, and 1.96 m during the managed inundation.

Meteorology and Underwater Irradiance

Measurements of solar radiation, wind speed and barometric pressure were made at 10 min intervals with an Automated Weather Station established on Chowilla Island in February 2014. Light profiles of photosynthetically active irradiance (PAR; 400-700nm) were measured using an underwater quantum sensor (LI-COR LI-193) and the vertical attenuation coefficient (k_d) was estimated by linear regression of natural log transformed irradiance values against depth.

Field Sampling – Biomass Estimation

Phytoplankton (Chlorophyll a)

During each sampling occasion, three independent water samples were collected from spatially separated (>10 m) locations for the analysis of chlorophyll *a*(chl *a*) concentration. Samples were filtered through Whatman GF/C glass fibre filters in the field, stored in the dark in an ice-filled insulated box and transported back to the laboratory for further analysis. Filters were extracted in 10 mL methanol, centrifuged for 8 min at 3,500 rpm and read spectrophotometrically at 665 nm and 750 nm (Biochrom Libra S22), and the chl*a* concentration was calculated using a specific absorption coefficient for methanol of 13.9 in the equation by Parsons and Strickland (1963).

Fish

Four small fyke nets of size 9 m × 0.6 m × 0.6 m and two larger fyke nets of size 12.6 m × 1 m × 1 m were used in the experimental site, in order to obtain a representative sample of fish populations. The nets were placed overnight and removed the next morning. Fish were identified to the species level, and length and body mass were recorded. A small number of individuals that could not be identified in the field were stored in an ice filled insulated box and transported back to the laboratory for further identification within 24 hrs of the collection. Wet weight of fish was converted to carbon, assuming 10 % of fish wet weight consisted of carbon, following Nixon et al. (1986).

Shrimp and Cherax destructor

Long handled dip nets were used to sample shrimp populations across the shallow littoral zone to obtain a representative sample from the experimental site. Two 5 m wide strips on each side of the creek that represented approximately 20 % of the total experimental area were sampled to obtain the estimate of the shrimp population. Captured shrimps were patted dry and weighed, and then used for the respiration measurements.

Seven replicate baited traps were used to capture *C. destructor* in the experimental site, and length and body mass of the captured *C. destructor* were recorded. *C. destructor* of different sizes were selected for respiration measurements.

Zooplankton

Three independent composite samples were collected from spatially separated (>10 m) locations for enumeration and identification of zooplankton. Composite samples were generated by using a 4 L Haney trap and transferring a 'grab' from the top, middle and bottom of the water column respectively, to a pre-rinsed 20 L drum to produce a sample volume of 12 L. The total volume was concentrated to approximately 50 mL by filtering through a 35 µm net. The concentrated sample was transferred to a 200 mL PET jar and preserved with 70 % ethanol in the field, and returned to the laboratory for identification. Zooplankton species were identified and enumerated in the laboratory using the method by Shiel (1995) and expressed as number of individuals per litre (individuals L^{-1}). Zooplankton biomass was estimated using length-weight regressions, following Dumont et al. (1975), Maia-Barbosa and Bozelli (2005) and Michaloudi (2005).

Field measurement of metabolism

Whole Ecosystem Metabolism

On each sampling occasion, two D'Opto fluorescence oxygen probes with loggers (Zebratech, New Zealand) were suspended approximately 75 cm below the water surface from buoys at the upstream and downstream sections of the reach. Deployments lasted for about 96 hrs and provided a minimum of three sonde days for the whole ecosystem metabolism estimates. Three RBR thermistors (Ontario, Canada) were attached to the chains anchoring the buoys at depths of 0 m, 1 m and 2 m to monitor water temperature (°C) at 10 min intervals. Whole ecosystem metabolism was estimated from analyses of the daily time series of DO concentrations and light intensities (Odum 1956, Young and Huryn 1996, Oliver and Merrick 2006). The rate of change in DO concentration ($\frac{dO}{dt}$) in the whole ecosystem is a function of photosynthesis, respiration and the oxygen exchange at the air-water interface:

$$\frac{dO}{dt} = AE_t^p + kD + CR \quad (Equation\ 1)$$

where, E_t^p describes the dependence of integral gross primary production (GPP) on irradiance intensity (Kosinski 1984, Young and Huryn 1996, Oliver and Merrick 2006), E_t is theincident photosynthetically active solar radiation (PAR, µmol photons m^{-2} s^{-1}) at time t, p is the possibility that the integrated GPP shows a saturating response to irradiance through the day (Kosinski 1984), kD is theatmospheric gas exchange, where, k = re-aeration coefficient (time^{-1}) *and* D is the oxygen deficit, which is the difference between the saturation oxygen concentration and the measured oxygen concentration in the water (Odum 1956, McCutchan Jr et al. 1998), and CR is the community respiration rate, which is assumed to be constant over the incubation period.

Saturated oxygen concentrations were calculated from the measured water temperatures using formulae from the International Oceanographic Tables (1973) without salinity correction. Using the DO data and the respective calculated saturated oxygen concentrations at the given water temperature $\frac{dO}{dt}$ *and* D were estimated over 10 min intervals. E_t was obtained from the automated weather station at Chowilla Island. A three dimensional, non-linear regression curve was fitted to *Equation 1* using the time series data to estimate average values for A, p, k *and* CR. *Equation 1* was then used to calculate *GPP* (AE_t^p), and values were calculated for 10 min time intervals and summed over the day (Oliver and Merrick 2006, Oliver and Lorenz 2013).

Planktonic Metabolism

The metabolism of planktonic organisms was determined by enclosing water samples in 300 mL clear and opaque biological oxygen demand (BOD) bottles, and measuring the oxygen concentration change after an incubation period of 5 hrs. Triplicate sets of clear BOD bottles were suspended at seven depths extending over the euphotic zone to assess planktonic photosynthesis, while single opaque bottles were incubated at three depths to determine planktonic respiration rates. Initial and final oxygen concentrations were measured using a Witrox-1 fibre optic oxygen sensor (Loligo Systems, Tjele, Denmark). The calculations of planktonic GPP, CR and the planktonic net production ($NP_{planktonic}$) were performed according to Oliver and Merrick (2006).

Benthic Metabolism

Benthic production was determined using re-circulating benthic chambers. Chambers consisted of a clear Perspex dome with an internal base diameter of 29 cm and volume of approximately 12.76 L. Three domes were pushed into the sediment to a depth of approximately 0.1 m with an enclosed substrate surface area of 0.07 m^2. One of the domes was sealed on the bottom and isolated from the sediment to act as a control for planktonic metabolism in the contained water sample. All the chambers were placed at a water depth of 0.4 m and the measurements of dissolved oxygen concentration and temperature were recorded at 10 min intervals over 24 hrs using D'Opto oxygen loggers (Zebratech, New Zealand). A 12 V pump re-circulated water through the chamber and gently mixed the overlying water.

Deploying sufficient numbers of benthic chambers to account for the depth distribution of benthic photosynthesis was not possible, and several assumptions were made to depth integrate the benthic chamber photosynthesis measurements and to scale them to the reach area. From the photosynthetic rates measured within the chambers every 10 min, a photosynthesis-irradiance (P-I) curve was plotted based on the average irradiance encountered by the chambers within each measurement period. Night time measurements were used to estimate an average respiration rate. A maximum photosynthetic rate ($P_{\max}$), the saturation onset irradiance intensity (I_k) and the initial slope of the light curve before the onset of light saturation (α), the parameters required for the depth and time integration, were then estimated from the P-I plots. The P-I parameters, together with the vertical attenuation coefficient value, were used to estimate the productivity (P) at different depths using the equation from Jassby and Platt (1976) and Ralph and Gademann (2005) as:

$$P = P_m \left(1 - e^{-\left(\frac{\alpha \, E_d}{P_m} \right)} \right) \qquad (\textit{Equation 2})$$

where P_m is the photosynthetic capacity at saturating light, α is the initial slope of the light curve before the onset of saturation, and E_d is the downwelling irradiance (PAR).

The daily integral metabolic rates for each depth were scaled up to a reach estimate by multiplying by the area of reach bed for the given depth, estimated from a bathymetric survey. Caution is warranted in using this approach, as it may over-estimate the benthic production since benthic chl *a* concentrations are expected to decrease with depth, but it does account for the reduction in the photosynthetic rate as a result of the decreasing light intensity. The sediments were mainly composed of silty clay loam, which were identified using Thien (1979), and was the dominant sediment type within the 100 m reach of the creek where the sampling was performed.

Laboratory Measurement of Metabolism

Fish Metabolism

Three different species of fish were chosen for metabolism measurements according to their predominance in the experimental site. These were common carp (*Cyprinus carpio*), golden perch (*Macquaria ambigua*) and bony bream (*Nematalosa erebi*). Metabolic measurements were performed in two different sizes of respirometer depending on the size of the fish: a 30 L swim tunnel (Loligo Systems, Tjele, Denmark) with a rectangular chamber of internal dimensions 0.55 m × 0.14 m × 0.14 m, and a 1.5 L cylindrical chamber respirometer with internal diameter of 0.14 m and 0.1 m length. Oxygen levels in the chambers were monitored and recorded with a Witrox-1 fibre optic oxygen sensor (Loligo Systems, Tjele, Denmark). Flow in the working section of the swim tunnel was calibrated using a handheld digital TAD W30 flow-meter (Höntzsch, Germany). Solid blocking effects of the fish in the working section were corrected by the respirometry software (AutoResp, Loligo Systems) following Bell et al. (1970), to account for the increased water speed caused by the profile of the fish being tested. The velocity of the water inside the swim chamber was set in the range of 0.15 – 0.20 m s^{-1}, as the water velocity within the Chowilla creek during samplings was in this range.We then calculated the oxygen consumption rates (MO_2) by taking the mean of the lowest 10 % of the oxygen consumption measurements over the 24 hrs measurement period (Norin and Malte 2011, Clark et al. 2013, Roche et al. 2013).

Shrimp and Cherax destructor Metabolism

Depending on the size of shrimps, the respiration rates were measured with two different sizes of respirometer. A Rank Brother's Clark type oxygen electrode with chamber capacity of 5 mL was used for small shrimps of weight ≤ 1 g, while a chamber of 1.5 L (chamber dimension: 0.13 m x 0.13 m x 0.08 m) was used for shrimps > 1 g in weight. In each case, measurements were also made to account for the background respiration due to the microbial load in the water.

To measure the respiration of *C. destructor* in the laboratory, a single *C. destructor* at a time (n = 16) was placed in a 6 L chamber (chamber dimensions: 0.3 m × 0.2 m × 0.1 m) filled with water, and sealed after removing air bubbles. The respiration rate was measured using a D'Opto oxygen logger over a period of an hour. One of the chambers was set up as a control that contained river water only, to correct for background respiration due to the microbial load in the water.

Zooplankton Metabolism

A Rank Brother's Clark type oxygen electrode with chamber capacity of 5 mL was used to measure the oxygen consumption rate of zooplankton. Measurements were also made on water, without zooplankton, to correct for the background respiration by the microbial load. A total of 100 individuals of similar size were randomly selected with a pipette under an Olympus (VMZ 1X–4X) microscope into a 5 mL measuring cylinder, and transferred to the oxygen electrode chamber. To overcome the handling stress, the organisms were acclimatized in the chamber for 10 min prior to measurements. After the experiment, the length and width of the individual species were measured with the graduated scale of a Wild Heerbrugg microscope (Switzerland, M5-21732).

Estimation of Metabolic Contributions by Metazoans

Scaling Arguments – Higher Order Organisms

The contributions of different functional groups of organisms to the whole system metabolism were estimated by scaling-up metabolic rates obtained from the laboratory experiments to biomass estimates obtained from field samplings. The numbers and the biomass of respective organisms were standardized per unit catch area, before being scaled up to the overall experimental area. Although our techniques may not have sampled the organisms to exhaustion, comparison of our data with the few studies that have tried to estimate the abundance of organisms at these sites indicated that our catch data provided comparable estimates of the overall population sizes.

Because the approaches adopted may not have sampled the total number of organisms, alternative scenarios were tested, using biomasses reported in the literature in order to assess the maximum possible contribution higher order organisms might have made to the observed metabolism.

Shrimp and Cherax destructor

Richardson and Cook (2006) captured about 30 % of *Macrobrachium australiense* (which was also the dominant shrimp species in our study site) from the still littoral zone of the three different habitats they sampled based on the velocity of water (still littoral, slow-current-velocity littoral, and moderate-current-velocity channel), in the southern Murray-Darling Basin. Using this estimation, we scaled up shrimp numbers based on the assumption that we sampled the entire still littoral zone as classified in their study, and determined the total shrimp numbers at our study site accordingly. We then estimated the contribution they would make to the overall system metabolism, applying the laboratory estimates of the metabolic rates for different size classes of the shrimps.

Because of the lack of literature data on *C. destructor*, we scaled up the population of *C. destructor* based on the field observations and the catch effort, assuming that each baited trap attracted *C. destructor* from at least 2 m distance on each side, forming a rectangular area of 4 m^2.

Fish

Catch data obtained from this study were compared with results from a fish abundance study conducted by Zampatti et al. (2008) in the Murray River, in which they sampled 16 sites annually, from 2005 to 2008, using a boat mounted electrofishing system. One of their 16 study sites (Site # 3; Chowilla Creek downstream of Slaney Creek) was in close vicinity of the site used for this study. We assumed their catch number to be the maximum possible in the site, given their use of an electrofishing system, and accordingly, estimated the total contribution of fish to the whole system respiration by using the weight-respiration regression equation obtained in this study. As the sampling by Zampatti et al. (2008) was conducted during the period that corresponds to the prior to inundation low flow period in this study, we used the corresponding whole system respiration rate in making these estimates.

RESULTS

Phytoplankton Biomass

Phytoplankton biomass ranged from 11-35 mg chl *a* m^{-3} with mean values (±SE) of 13.35 (± 1.01), 31.10 (± 2.73), and 24.40 (± 0.39) mg chl *a* m^{-3} during the first, second and third samplings, respectively. The chl *a* concentration varied significantly between the sampling events with the lowest concentration during the prior low flow period and the highest concentration during the managed inundation period.

Whole Ecosystem Metabolism

Whole system GPP ranged from 2.39 g O_2 m^{-2} d^{-1} to 3.65 g O_2 m^{-2} d^{-1}, with mean values of 2.50 ± 0.10, 2.95 ± 0.02 and 3.55 ± 0.10 g O_2 m^{-2} d^{-1} in the first, second and third samplings respectively, and varied significantly between the sampling events. Areal CR ranged from -2.24 to -2.99 g O_2 m^{-2} d^{-1} with mean values of -2.25 ± 0.02, -2.85 ± 0.15 and -2.70 ± 0.15 g O_2 m^{-2} d^{-1} in the first, second and third samplings respectively, but did not vary significantly between the sampling events. NEP ranged from -0.06 to 0.95 g O_2 m^{-2} d^{-1} with mean values of 0.25 (±0.15), 0.10 (±0.15) and 0.70 (±0.20) g O_2 m^{-2} d^{-1} in the first, second and third samplings, respectively, but did not vary significantly between the sampling events(Table 4-1; Figure 4-2).

Planktonic Metabolism

Planktonic GPP during the post-inundation period differed significantly compared to the first two sampling periods, with a mean difference of 2.01 g O_2 m^{-2} d^{-1}

Table 4-1. Whole System, Planktonic and Benthic Areal Estimates of Metabolism Measurements

	Metabolic Component	S I	S II	S III	S I & S II	S I & S III	S II & S III
Whole system	GPP	2.50 (±0.10)	2.95 (±0.02)	3.55 (±0.10)	**	**	**
	CR	-2.25 (±0.02)	-2.85 (±0.15)	-2.70 (±0.15)	ns	ns	ns
	NEP	0.25 (±0.15)	0.10 (±0.15)	0.70 (±0.20)	ns	ns	ns
Planktonic	GPP	1.87 (±0.01)	1.72 (±0.26)	3.73 (±0.15)	ns	***	***
	CR	-2.80 (±1.67)	-2.50 (±0.80)	-2.20 (±0.80)	ns	ns	ns
	$NP_{planktonic}$	-0.92 (±1.65)	-0.90 (±0.40)	1.55 (±0.60)	ns	*	***
Benthic	GPP	0.16 (±0.01)	0.22 (±0.00)	0.39 (±0.01)	**	**	**
	CR	-0.15 (±0.01)	-0.19 (±0.07)	-0.40 (±0.02)	ns	*	ns
	$NP_{benthic}$	0.01 (±0.02)	0.03 (±0.07)	-0.004 (±0.02)	ns	ns	ns

Results on the left are whole system, planktonic and benthic areal estimates of GPP (±SE), CR (±SE) and Net Production (±SE) measured on three sampling events (I, II and III); S I: pre-inundation period, S II: during inundation, and S III: post inundation period. Results on the right denote statistical significance of the comparisons of metabolic rates using the Students T-test between the three sampling events, where ns denotes non-significant values, * denotes $p \leq 0.05$, ** denotes $p \leq 0.01$, and *** denotes $p \leq 0.001$.

between the second and third samplings (Table 4-1; Figure 4-2). Planktonic CR was highest during the low flow period prior to inundation (-2.80 ± 1.67 g O_2 m^{-2} d^{-1}) and lowest during the post-inundation period (-2.20 ± 0.80 g O_2 m^{-2} d^{-1}), however, there was no significant difference in planktonic CR between the sampling events. Planktonic net production ($NP_{planktonic} = GPP_{planktonic} - R_{planktonic}$), varied significantly between the sampling events, and was significantly different from zero in the third sampling. However, $NP_{planktonic}$ was not significantly different from zero in the first two samplings, suggesting that planktonic GPP and CR rates were balanced before and during the inundation event.

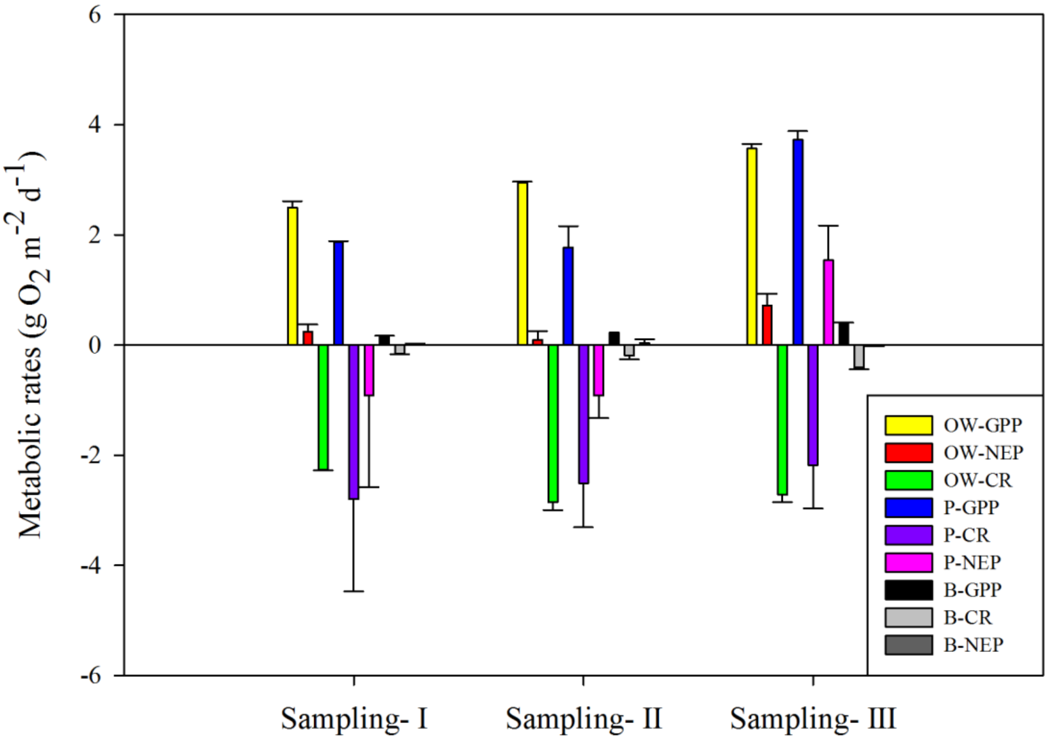

Figure 4-2: Areal estimates of GPP, CR and NEP for the open water (OW), planktonic (P) and benthic (B) compartments measured on each sampling occasion; Sampling I: pre-inundation period, Sampling II: during inundation, and Sampling III: post inundation period. Error bars are ± standard errors.

Organic matter production through photosynthesis was largely dominated by phytoplankton, which on average accounted for 75 % of the whole system areal GPP in the low flow period prior to inundation, and 60 % during the managed inundation. Similarly, planktonic organisms were mainly responsible for respiring organic material, with their respiration accounting for 90 % and 77 % of the whole system respiration during the inundation and post-inundation periods, respectively.

Benthic Metabolism

Areal benthic GPP ranged from 0.15 to 0.40 g O_2 m^{-2} d^{-1}, with mean values of 0.16 ± 0.01, 0.22 ± 0.00 and 0.39 ± 0.01 in the first, second and third samplings respectively, and varied significantly between sampling events (Table 4-1; Figure 4-2). Benthic respiration rates ranged between -0.45 to -0.12 g O_2 m^{-2} d^{-1}, with mean values of -0.15 ± 0.01, -0.19 ± 0.07 and -0.40 ± 0.02 g O_2 m^{-2} d^{-1} in the first, second and third samplings, respectively. Benthic net production ($NP_{benthic}$) was not significantly different from zero in all three samplings, and was not significantly different between the samplings (Table 4-1).

Benthic organisms accounted for only a small proportion of the whole system metabolism. For whole system production, benthic photoautotrophs contributed about 8.70 % (±1.40 %) on average, with 6.45 %, 8.30 % and 11.30 % contribution in the first, second and third samplings, respectively. Similarly, respiration rates by benthic organisms accounted for 9.70 % (±2.40 %) of the whole system respiration on average, with 6.70 %, 8.00 % and 14.45 % in the first, second and third samplings, respectively. The highest contribution from the benthos was during the post-inundation period, and the lowest prior to the inundation period.

Functional Group Specific Metabolism Based on Laboratory Estimates

Laboratory experiments were performed to discriminate the contribution from four groups of organisms (zooplankton, *C. destructor*, shrimps and fish) to the overall metabolic rates. From the respiration rates obtained through the laboratory experiment for various size classes of fish, *C. destructor*, shrimps and zooplankton (Table 4-2), the relationships between body mass and respiration rate were established (Figure4-3). As the respiratory metabolic rate is commonly found to be a power function of the body weight (Kleiber 1947, Ikeda 1966, Glazier 2008), power functions were fitted to data for the four organisms to obtain relationships of respiration rates against their body masses (Figure 4-3).

Table 4-2. Body Masses and Respiration Rates of Various Group of Organisms

Functional Group	Body Mass		Respiration Rate	
	Min	Max	Min	Max
Fish	10	250	0.0010	0.04
Cherax destructor	5	200	0.0003	0.0175
Shrimp	0.01	9	0.0110	1.85
Zooplankton	50	120	0.0400	0.1

Range of body masses, and respiration rates of various functional groups of organisms as estimated from laboratory experiments. Body masses and respiration rates of fish, *C. destructor* and shrimp are in g and g O_2 h^{-1} respectively; while corresponding measurements for zooplankton are in μg and μg O_2 h^{-1}.

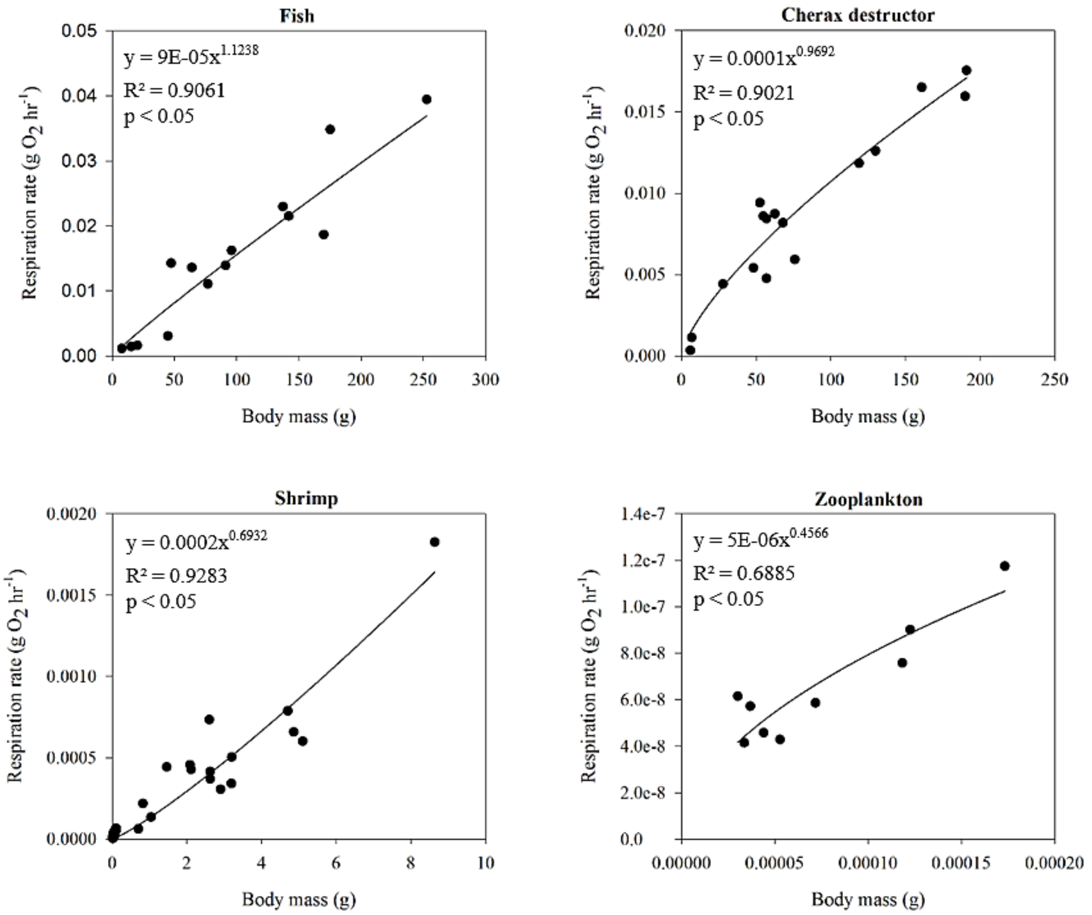

Figure 4-3. Relationships between respiration rates (g O_2 hr^{-1}) and body mass (g) for four riverine organisms: fish, *C. destructor*, shrimps and zooplankton based on laboratory experiments. For fish, *C. destructor* and shrimp, each individual is represented by a single data point; for zooplankton, a single data point represents 100 individuals.

Zooplankton Metabolism

Zooplankton abundance varied between the sampling events, with a total of 995, 555 and 2184 individuals L^{-1} sampled in the first, second and third samplings, respectively. *Polyarthra dolichoptera*, *Trichocerca pusilla* and *Keratella cochlearis* were the most dominant species during the pre-inundation, inundation and post-inundation periods, respectively. Based on the total biomass derived from the abundance and bio-volume measurements, zooplankton respiration was estimated to be 0.02 g O_2 m^{-2} d^{-1}, 0.02 g O_2 m^{-2} d^{-1} and 0.04 g O_2 m^{-2} d^{-1} in the first, second and third samplings, respectively; which represented 0.75 %, 0.70 % and 1.65 % of the whole system respiration rate.

Shrimp and Cherax destructor Metabolism

Macrobrachium australiense was the only shrimp species obtained during all three sampling occasions. A total of 182, 407 and 870 individuals of shrimps were sampled in the first, second and third samplings, respectively, with corresponding wet weights totalling 150, 679 and 1021 g respectively. Standardizing this catch data showed that shrimps contributed about 0.0002 g O_2 m^{-2} d^{-1}, 0.0004 g O_2 m^{-2} d^{-1}, and 0.0010 g O_2 m^{-2} d^{-1} in the first, second and third samplings, which represented 0.007 %, 0.014 % and 0.037 % of the whole system respiration, respectively.
C. destructor was the only species obtained by sampling on each occasion. The number of *C. destructor* sampled varied largely between the sampling events, with a total of 7, 46 and 20 individuals captured in the first, second and third samplings, respectively, with corresponding wet weights totalling 620, 1777 and 820 g. Standardizing this catch data showed that *C. destructor* contributed about 0.0003 g O_2 m^{-2} d^{-1}, 0.0006 g O_2 m^{-2} d^{-1}, and 0.0004 g O_2 m^{-2} d^{-1} in the first, second and third samplings, representing 0.01 %, 0.02 % and 0.02 % of the whole system respiration, respectively.

Fish Metabolism

A total of 238 (7.24 kg wet weight; 0.72 kg C), 926 (17.71 kg wet weight; 1.77 kg C), and 174 (2.26 kg wet weight; 0.23 kg C) fish of six species were sampled respectively in the first, second and third sampling events. Bony bream (*Nematalosa erebi*), a native Australian fish was the most abundant species sampled in all three sampling events (Table 4-3), as also observed previously in a study within the Chowilla Floodplain by Zampatti et al. (2008).

Standardizing the numbers of fish captured showed that fish contributed about 0.0062 g O_2 m^{-2} d^{-1}, 0.0102 g O_2 m^{-2} d^{-1} and 0.0020 g O_2 m^{-2} d^{-1} in the first, second and third samplings, which respectively represented 0.30 %, 0.35 % and 0.07 % of the whole system respiration. The highest contribution was during the managed inundation period while the lowest was during the post-inundation period.

Table 4-3. Fish Catch Data, Corresponding Wet/Dry Weights and Estimated Respiration Rates

Common Name	Total Catch Count			Total Wet Weight (g)			Total Carbon Biomass (g C)			Respiration Rate (g O_2 d^{-1})		
	S I	S II	S III	S I	S II	S III	S I	S II	S III	S I	S II	S III
Bony Bream	207	332	117	1,231	2,919.1	537.1	123.1	291.91	53.71	3.47	8.5	1.46
Common Carp	2	231	1	143	12,689.9	380	14.3	1,268.99	38	0.49	45.25	1.55
Golden Perch	23	6	5	5,668	1,234.2	1,268.9	566.8	123.42	126.89	23.05	5.07	5.11
Australian Smelt	3	5	34	50	6.9	71.6	5	0.69	7.16	0.16	0.02	0.17
Carp Gudgeon	3	153	17	147	60.5	8.9	14.7	6.05	0.89	0.48	0.12	0.02
Flathead Gudgeon	-	199	-	-	805	-	-	80.5	-	-	2.23	-

Fish catch data, corresponding wet and dry biomasses, and respiration rates for three sampling events, calculated using laboratory estimates of fish body mass – respiration rate relationships.

Scaling Arguments – Higher Order Organisms

Shrimp and Cherax destructor

Using the estimation from Richardson and Cook (2006), we scaled up the total number of shrimps and their potential total metabolic contributions, which are presented in Table 4-4.

Similarly, assuming a sampling area of 28 m^2 area for the 7 baited traps used within the experimental site, the estimated total number of *C. destructor* and their potential contribution to whole ecosystem metabolism is presented in Table 4-4.

Fish

The electrofishing by Zampatti et al. (2008) yielded fish counts from a low of 263 individuals in 2007 to a high of 1,107 individuals in 2006. The 926 fish we sampled during the managed inundation period was comparable to their sampling results in 2006, while our findings during the low flow period was similar to their lower end catch number. Based on the biomass estimate by Zampatti et al. (2008) corresponding to 1,107 individuals in 2006 during the low flow period, the maximum fish contribution to the whole system respiration during the low flow period prior to inundation during this study would have been 1.79 %.

DISCUSSION

Studies investigating direct measures of the contributions that higher order organisms make to aquatic ecosystem metabolism are limited. This is in part because of the challenges involved in estimating the biomasses and metabolic rates of the many functional groups of aquatic organisms. Despite the uncertainties and complexities, we nevertheless attempted to partition the ecosystem metabolism between different major biota in the Chowilla Floodplain of the lower River Murray.

Our results showed that planktonic organisms dominated the measured metabolism, and were therefore, primarily responsible for energy turnover and carbon flux within the river system. This finding supports the observations of Oliver and Merrick (2006) in the main river channel (MRC) of the River Murray and Cremona et al. (2014) in an eutrophic lake in Central Estonia, where both of

Table 4-4. Metabolic Contributions by Shrimps and *Cherax destructor* Based on Scaling Arguments

Functional Group	Number of Individuals Sampled (Total Weight in g)			Number of Individuals Scaled Up (Total Weight in g)			Relative Contribution to Whole Ecosystem Metabolism Based on the Scaled Up Numbers (%)		
	S I	S II	S III	S I	S II	S III	S I	S II	S III
Shrimps	182 (150)	407 (679)	870 (1,021)	606 (500)	1,356 (2,262)	2,900 (3,403)	0.29	0.46	0.12
Cherax destructor	7 (620)	46 (1,777)	20 (820)	1,125 (99,643)	9,857 (385, 709)	2,857 (117, 137)	2.12	4.48	2.09

Total numbers and corresponding total biomass (within the parentheses) of shrimps and *C. destructor* sampled during three sampling occasions; S I: pre-inundation period, S II: during inundation, and S III: post inundation period, scaled up total numbers and corresponding estimate of biomass (within the parentheses) based on the assumptions made for shrimps and *C. destructor*; and their relative contribution to whole system metabolism based on scaled up numbers.

Table 4-5. Relative Contribution from Different Functional Groups to Whole Ecosystem Metabolism

	GPP (g O_2 m^{-2} d^{-1})			CR (g O_2 m^{-2} d^{-1})			Relative Contribution to Whole Ecosystem Production (%)			Relative Contribution to Whole Ecosystem Respiration (%)		
	S I	S II	S III	S I	S II	S III	S I	S II	S III	S I	S II	S III
Whole System	2.50	2.95	3.55	-2.25	-2.85	-2.70						
Planktonic	1.87	1.72	3.73	-2.80	-2.50	-2.20	75	60	104	123	90	77
Benthic	0.16	0.22	0.39	-0.15	-0.19	-0.40	6.45	8.30	11.30	6.70	8	14.45
Zooplankton				0.02	0.02	0.04				0.75	0.70	1.65
Shrimps				0.0002	0.0004	0.0010				0.007	0.014	0.037
Cherax destructor				0.0003	0.0006	0.0004				0.01	0.02	0.02
Fish				0.0062	0.0102	0.0020				0.30	0.35	0.07

Estimated GPP and CR rates, with relative contribution from different functional groups to the whole ecosystem metabolism during three sampling events.

the studies implicated phytoplankton as the largest contributor to the whole ecosystem metabolism. Although we did not partition the respiratory contribution between the planktonic microorganisms, Cremona et al. (2014) reported that out of 75 % contribution from the planktonic microorganisms to the whole system CR; phytoplankton made the largest contribution (43 %) , and the bacteria and protists contributed about 20% and 12 %, respectively.

Some unexpected discrepancies were, however, observed between planktonic and whole system CR during the period prior to inundation, when the measured planktonic CR was higher than whole system CR measured through whole ecosystem changes in DO. A similar discrepancy occurred between planktonic and whole system GPP during the post-inundation period, when the planktonic GPP was higher than the total GPP (Table 4-5). Such observations are not uncommon, and reflect the difficulties of capturing the complexities of these environments using enclosed incubations (Staehr et al. 2012). For example, vertical mixing influences phytoplankton production (Gawne et al. (2007), as it affects both the physiological state (Ferris and Christian 1991) and the rate of photosynthesis (Nicklisch and Fietz 2001) by altering the light environment (Oliver et al. 2003). This is not accounted for in the bottle experiments used for the planktonic metabolism measurements in this study, and therefore may overestimate the production rates.

Floodplain inundation has often been associated with significant increases in the abundance of metazoans, with such increases being linked to higher levels of primary production by phytoplankton and bacteria (Neckles et al. 1990, Tan and Shiel 1993, Basu and Pick 1997, Poff 1997, Nielsen et al. 2002, Obertegger et al. 2007, Balcombe and Arthington 2009, Ning et al. 2010). We observed an increased abundance of all autotrophic and heterotrophic organisms considered in this study during the managed inundation period. However, despite the increase in the number of higher trophic organisms during this period, the contribution by the planktonic functional group dominated the metabolism signal, while the larger organisms, i.e. *C. destructor*, shrimps and fish, contributed to less than 0.5 % of the whole ecosystem metabolic estimate (Table 4-5). Meta-zooplankton contributed less than 2 % to the overall metabolic estimate in each sampling, which is similar to results reported by Cremona et al. (2014), who found meta-zooplankton contributing less than 2 % to their overall lake metabolism of about 3.03 g O_2 m^{-2} d^{-1} (estimated using the conversion factor of 0.375 to convert from the unit of oxygen to carbon), while micro-organisms like bacteria and protists contributed about 30 %.

Benthic organisms made a relatively small contribution compared to planktonic organisms but higher than the overall contribution from higher order organisms (Table 4-5). The benthic contribution observed in this study is in similar proportion to that observed by Oliver and Merrick (2006) in two of their three study sites within the River Murray. A slightly higher contribution observed at our site during the post-inundation period could be attributed to the smaller water volume to sediment area ratio of the creek compared to the MRC. Our findings are comparable to other ecosystem productivity studies, where planktonic organisms were the major contributors, followed by benthic organisms (Oliver and Merrick 2006, Cremona et al. 2014). This could be possibly due to the lower metabolic rates of benthos per unit biomass as well as their lower biomass compared to planktonic organisms (Cremona et al. 2014), but we are unable to conclude this with reasonable confidence for our study because of lack of data on biomass of benthic organisms.

Due to concerns that we may not have sampled higher order organisms (shrimps, *C. destructor* and fish) exhaustively, and that our estimates may have underestimated the contributions from these organisms to the whole ecosystem metabolism, we further assessed the contributions by these organisms to the observed metabolism, by testing alternative scenarios based on available literature. However, these estimates did not alter the key findings. Therefore, despite the large uncertainties associated with biomass estimates of various functional groups of organisms, we conclude that the higher order organisms made small contributions to the whole ecosystem metabolism when compared to the microorganisms, and that this would be the outcome even with substantial increase in biomass of the higher order organisms (Table 4-4) for shrimps and *C. destructor*; for fish, refer to scaling arguments for higher order organisms in results section).It is difficult to estimate individual errors and their effect on cumulative propagated errors, but the close accounting of the whole system metabolism by summing of the measured functional group contributions suggests that the errors that may have been associated with these uncertainties are not sufficient to alter our interpretations of the results. Moreover, it is well established in ecology that biomass decreases as one ascends the food chain due to the lesser energy available at the succeeding level compared to the trophic level below, based on the generalised 10 % energy transfer efficiency (Lindeman 1942, Brown et al. 2004). Accordingly, it can be inferred that biomass of microorganisms far exceed the biomassesof organisms in the higher trophic levels, and this interplay, explains their dominance of metabolism signal in comparison to larger organisms.

Because of the limited research on the contributions of higher order organisms to ecosystem metabolism in aquatic ecosystems, it is difficult to compare our findings to other studies. However, a recent lake study by Cremona et al. (2014) estimated that fish contributed nearly 20 % to the measurement of the whole system metabolism, compared to 0.35 % observed in this study. This discrepancy may be a result of the differences in fish biomass. Cremona et al. (2014) calculated overall fish biomass of 1.83 g C m^{-2}, whereas, the estimated maximum fish biomass observed in our study was 0.39 g C m^{-2}. Structural heterogeneity of food webs in lotic and lentic systems may possibly explain such differences, as it is an important factor mediating predatory interactions among ecosystem communities (Diehl 1992). For example, zooplankton biomass and composition is positively correlated with water residence time (Bum and Pick 1996), and because of shorter water residence time compared to lakes, the zooplankton community in rivers is typically dominated by rotifers (Shiel et al. 1982, Akopian et al. 1999), tend to avoid predation by fish (Brooks and Dodson 1965).

The fluxes of the oxygen concentrations in the whole ecosystem field metabolism measurements are assumed to represent the summed contribution of primary production and respiration of photoautotrophic and heterotrophic organisms such as phytoplankton, bacteria, zooplankton, macroinvertebrates and fish (Cremona et al. 2014). Our results suggest that the field measurements of metabolism mainly reflects the contribution from the planktonic groups, whereas the higher order organisms tend to have such small contribution to the measurement of metabolism that their signal is not large enough to be discernible. Although relative river health is often assessed by using the measurements of the ecosystem metabolism(Fellows et al. 2006, Young et al. 2008), our findings warrant caution when interpreting the ecosystem metabolism rates as an indicator of the overall river health. This is because metabolism measurements may only reflect changes in metabolic activity associated with planktonic communities and not the ecosystem more broadly. In our study, despite a large increase in the biomass of higher order organisms during the managed inundation event, which would otherwise be considered an improvement in the condition of the ecosystem, this was not observed in the total metabolic activity observations. The lack of sensitivity to substantial changes in the biomass of larger organisms thus casts doubt on the suitability of metabolism measurements as an indicator of system condition, and therefore challenges the application of metabolism measurements as holistic indicators of river health.

REFERENCES

Akopian, M., J. Garnier, and R. Pourriot. 1999. A large reservoir as a source of zooplankton for the river: structure of the populations and influence of fish predation. Journal of Plankton Research **21**:285-297.

Balcombe, S. R. and A. H. Arthington. 2009. Temporal changes in fish abundance in response to hydrological variability in a dryland floodplain river. Marine and Freshwater Research **60**:146-159.

Basu, B. and F. Pick. 1997. Phytoplankton and zooplankton development in a lowland, temperate river. Journal of Plankton Research **19**:237-253.

Bell, W., F. R. B. o. Canada, F. R. B. o. C. B. Station, and L. Terhune. 1970. Water tunnel design for fisheries research. Ottawa: Queen's printer.

Benjamin, J. R., J. R. Bellmore, and G. A. Watson. 2016. Response of ecosystem metabolism to low densities of spawning Chinook Salmon. Freshwater Science **35**:810-825.

Brooks, J. L. and S. I. Dodson. 1965. Predation, body size, and composition of plankton. Science **150**:28-35.

Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage, and G. B. West. 2004. Toward a metabolic theory of ecology. Ecology **85**:1771-1789.

Bum, B. K. and F. R. Pick. 1996. Factors regulating phytoplankton and zooplankton biomass in temperate rivers. Limnology and Oceanography **41**:1572-1577.

Bunn, S. E., P. M. Davies, and M. Winning. 2003. Sources of organic carbon supporting the food web of an arid zone floodplain river. Freshwater Biology **48**:619-635.

Cale, B. 2009. Literature review of the current and historic flooding regime and required hydrological regime of ecological assets on the Chowilla Floodplain. Murray Bridge, South Australia.

Clark, T. D., E. Sandblom, and F. Jutfelt. 2013. Aerobic scope measurements of fishes in an era of climate change: respirometry, relevance and recommendations. The Journal of experimental biology **216**:2771-2782.

Cole, J. J., S. Findlay, and M. L. Pace. 1988. Bacterial production in fresh and saltwater ecosystems: a cross-system overview. Marine ecology progress series. Oldendorf **43**:1-10.

Cole, J. J., M. L. Pace, S. R. Carpenter, and J. F. Kitchell. 2000. Persistence of net heterotrophy in lakes during nutrient addition and food web manipulations. Limnology and Oceanography **45**:1718-1730.

Cremona, F., T. Kõiv, V. Kisand, A. Laas, P. Zingel, H. Agasild, T. Feldmann, A. Järvalt, P. Nõges, and T. Nõges. 2014. From bacteria to piscivorous fish: estimates of whole-lake and component-specific metabolism with an ecosystem approach. PloS One **9**:e101845.

Del Giorgio, P. A., J. J. Cole, and A. Cimbleris. 1997. Respiration rates in bacteria exceed phytoplankton production in unproductive aquatic systems. Nature **385**:148-151.

Diehl, S. 1992. Fish predation and benthic community structure: the role of omnivory and habitat complexity. Ecology **73**:1646-1661.

Dumont, H. J., I. Velde, and S. Dumont. 1975. The dry weight estimate of biomass in a selection of Cladocera, Copepoda and Rotifera from the plankton, periphyton and benthos of continental waters. Oecologia **19**:75-97.

Fellows, C. S., J. E. Clapcott, J. W. Udy, S. E. Bunn, B. D. Harch, M. J. Smith, and P. M. Davies. 2006. Benthic metabolism as an indicator of stream ecosystem health. Hydrobiologia **572**:71-87.

Ferris, J. and R. Christian. 1991. Aquatic primary production in relation to microalgal responses to changing light: a review. Aquatic Sciences **53**:187-217.

Gawne, B., C. Merrick, D. G. Williams, G. Rees, R. Oliver, P. M. Bowen, S. Treadwell, G. Beattie, I. Ellis, and J. Frankenberg. 2007. Patterns of primary and heterotrophic productivity in an arid lowland river. River Research and Applications **23**:1070-1087.

Gillooly, J. F., J. H. Brown, G. B. West, V. M. Savage, and E. L. Charnov. 2001. Effects of size and temperature on metabolic rate. Science **293**:2248-2251.

Glazier, D. S. 2008. Effects of metabolic level on the body size scaling of metabolic rate in birds and mammals. Proceedings of the Royal Society of London B: Biological Sciences **275**:1405-1410.

Hanson, P. C., D. L. Bade, S. R. Carpenter, and T. K. Kratz. 2003. Lake metabolism: Relationships with dissolved organic carbon and phosphorus. Limnology and Oceanography **48**:1112-1119.

Howarth, R., R. Schneider, and D. Swaney. 1996. Metabolism and organic carbon fluxes in the tidal freshwater Hudson River. Estuaries and Coasts **19**:848-865.

Ikeda, T. 1966. Relationship between respiration rate and body size in marine plankton animals as a function of the temperature of habitat. Bulletin of Faculty of Fisheries, Hokkaido University**21**:91-112.

Jassby, A. D. and T. Platt. 1976. Mathematical formulation of the relationship between photosynthesis and light for phytoplankton.

Jolly, I. D., G. R. Walker, and K. A. Narayan. 1994. Floodwater recharge processes in the Chowilla anabranch system, South Australia. Soil Research **32**:417-435.

Kemp, W. and W. Boynton. 2004. Productivity, trophic structure, and energy flow in the steady-state ecosystems of Silver Springs, Florida. Ecological Modelling **178**:43-49.

Kleiber, M. 1947. Body size and metabolic rate. Physiol. rev **27**:511-541.

Kosinski, R. J. 1984. A comparison of the accuracy and precision of several open-water oxygen productivity techniques. Hydrobiologia **119**:139-148.

Lindeman, R. L. 1942. The trophic-dynamic aspect of ecology. Ecology **23**:399-417.

Maia-Barbosa, P. M. and R. L. Bozelli. 2005. Length-weight relationships for five cladoceran species in an Amazonian lake. Brazilian Archives of Biology and Technology **48**:303-308.

McCutchan Jr, J. H., W. M. Lewis Jr, and J. Saunders III. 1998. Uncertainty in the estimation of stream metabolism from open-channel oxygen concentrations. Journal of the North American Benthological Society:155-164.

Michaloudi, E. 2005. Dry weights of the zooplankton of Lake Mikri Prespa (Macedonia, Greece). Belgian journal of zoology **135**:223.

Neckles, H. A., H. R. Murkin, and J. A. Cooper. 1990. Influences of seasonal flooding on macroinvertebrate abundance in wetland habitats. Freshwater Biology **23**:311-322.

Nicklisch, A. and S. Fietz. 2001. The influence of light fluctuations on growth and photosynthesis of Stephanodiscus neoastraea (diatom) and Planktothrix agardhii (cyanobacterium). Archiv für Hydrobiologie **151**:141-156.

Nielsen, D., T. Hillman, F. Smith, and R. Shiel. 2002. The influence of seasonality and duration of flooding on zooplankton in experimental billabongs. River Research and Applications **18**:227-237.

Ning, N. S., D. L. Nielsen, W. L. Paul, T. J. Hillman, and P. J. Suter. 2010. Microinvertebrate dynamics in riverine slackwater and mid-channel habitats in relation to physico-chemical parameters and food availability. River Research and Applications **26**:279-296.

Nixon, S., C. Oviatt, J. Frithsen, and B. Sullivan. 1986. Nutrients and the productivity of estuarine and coastal marine ecosystems. Journal of the Limnological Society of Southern Africa **12**:43-71.

Norin, T. and H. Malte. 2011. Repeatability of standard metabolic rate, active metabolic rate and aerobic scope in young brown trout during a period of moderate food availability. The Journal of experimental biology **214**:1668-1675.

Obertegger, U., G. Flaim, M. G. Braioni, R. Sommaruga, F. Corradini, and A. Borsato. 2007. Water residence time as a driving force of zooplankton structure and succession. Aquatic Sciences **69**:575-583.

Odum, E. P. and G. W. Barrett. 1971. Fundamentals of ecology. Saunders Philadelphia.

Odum, H. T. 1956. Primary production in flowing waters. Limnology and Oceanography:102-117.

Oliver, R. L. and Z. Lorenz. 2013. Changes in metabolic activity in the South Australian section of the Murray River during the 2010/11 flood that followed a ten year drought. Goyder Institute for Water Research Technical Report Series.

Oliver, R. L. and C. J. Merrick. 2006. Partitioning of river metabolism identifies phytoplankton as a major contributor in the regulated Murray River (Australia). Freshwater Biology **51**:1131-1148.

Oliver, R. L., J. Whittington, Z. Lorenz, and I. T. Webster. 2003. The influence of vertical mixing on the photoinhibition of variable chlorophyll a fluorescence and its inclusion in a model of phytoplankton photosynthesis. Journal of Plankton Research **25**:1107-1129.

Overton, I. and T. Doody. 2008. Groundwater, surface water, salinity and vegetation response to a proposed regulator on Chowilla Creek. CSIRO, Glen Osmond, South Australia.

Parsons, T. R. and J. D. Strickland. 1963. Discussion of spectrophotometric determination of marine-plant pigments, with revised equations for ascertaining chlorophylls and carotenoids. Journal of Marine Research **21**:155-163.

Poff, N. L. 1997. Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. Journal of the North American Benthological Society:391-409.

Pomeroy, L. R. 1974. The ocean's food web, a changing paradigm. BioScience **24**:499-504.

Ralph, P. J. and R. Gademann. 2005. Rapid light curves: a powerful tool to assess photosynthetic activity. Aquatic Botany **82**:222-237.

Richardson, A. and R. Cook. 2006. Habitat use by caridean shrimps in lowland rivers. Marine and Freshwater Research **57**:695-701.

Roche, D. G., S. A. Binning, Y. Bosiger, J. L. Johansen, and J. L. Rummer. 2013. Finding the best estimates of metabolic rates in a coral reef fish. The Journal of experimental biology **216**:2103-2110.

Shiel, R., K. Walker, and W. Williams. 1982. Plankton of the lower River Murray, South Australia. Marine and Freshwater Research **33**:301-327.

Shiel, R. J. 1995. A guide to identification of rotifers, cladocerans and copepods from Australian inland waters. Co-operative Research Centre for Freshwater Ecology Canberra.

Staehr, P. A., D. Bade, M. C. Van de Bogert, G. R. Koch, C. Williamson, P. Hanson, J. J. Cole, and T. Kratz. 2010. Lake metabolism and the diel oxygen technique: state of the science. Limnology and Oceanography: Methods **8**:628-644.

Staehr, P. A. and K. Sand-Jensen. 2007. Temporal dynamics and regulation of lake metabolism. Limnology and Oceanography **52**:108-120.

Staehr, P. A., J. M. Testa, W. M. Kemp, J. J. Cole, K. Sand-Jensen, and S. V. Smith. 2012. The metabolism of aquatic ecosystems: history, applications, and future challenges. Aquatic Sciences **74**:15-29.

Tan, L.-W. and R. J. Shiel. 1993. Responses of billabong rotifer communities to inundation. Hydrobiologia **255**:361-369.

Thien, S. J. 1979. A flow diagram for teaching texture-by-feel analysis. Journal of Agronomic Education **8**.

Woodwell, G. M. and R. H. Whittaker. 1968. Primary production in terrestrial ecosystems. American Zoologist **8**:19-30.

Young, R. G. and A. D. Huryn. 1996. Interannual variation in discharge controls ecosystem metabolism along a grassland river continuum. Canadian journal of fisheries and aquatic sciences **53**:2199-2211.

Young, R. G., C. D. Matthaei, and C. R. Townsend. 2008. Organic matter breakdown and ecosystem metabolism: functional indicators for assessing river ecosystem health. Journal of the North American Benthological Society **27**:605-625.

Zampatti, B., S. Leigh, and J. Nicol. 2008. Chowilla Icon Site–Fish Assemblage Condition Monitoring 2005-2008. SARDI Publication.

CHAPTER 5

GENERAL DISCUSSION

This thesis examined two important topics on river-floodplain ecosystems management and assessment: (1) the role of managed floodplain inundation in achieving effective lateral hydrological connectivity between anabranch channels and peripheral floodplain habitats to improve riverine productivity by mobilizing floodplain dissolved organic carbon (DOC) and nutrients; and (2) the contribution of different functional group of riverine organisms to the measurements of ecosystem metabolism,to better understand the utility of aquatic ecosystem metabolism measurements as an indicator of riverine ecosystem health.

Ecosystem metabolism rates were measured and compared between anabranch habitats with distinct spatialpositions during periods of lateral hydrological connection and disconnection to the adjacent floodplain, resulting from the operation of a newly constructed environmental flow regulator. Whole ecosystem metabolism rates were also measured in the river channel downstream of the inundated floodplain, at two distinct sites separated by a considerable longitudinal distance. The metabolic rates observed at theanabranch and river channel sites were compared with a reference site located on the river channel, upstream of the outlet of the floodplain into the river. This site acted as an indicator of ambient water quality and productivity under non-inundated conditions. Additionally, the whole ecosystem metabolism was partitioned across the major biotic groups to assess their contribution to the community respiration.Acombination of field and laboratory experiments were performed to estimate the size specific respiration rates for the various groups oforganisms, and thebiomass of the organisms were estimated using a combination of approaches during the field samplings.

The effects of the managed inundation event in mobilizing floodplain dissolved organic carbon (DOC) and nutrients,and its impact on ecosystem productivity inanabranch habitats were examined in Chapter 2 of the thesis.Building on the findings from Chapter 2, the impact of return flows from the inundated floodplain in themain river channel (MRC) downstream of the inundated areaon ecosystem productivity was investigated in Chapter 3. Results from these chapters supported the hypothesis that managed inundation events can positively influence riverine productivity, even during periods of low water availability. This was demonstrated by: (1) increased metabolic rates (gross primary production (GPP) and community respiration (CR)) at two anabranch sites during the managed inundation period; and (2) increased metabolic rates (GPP and CR) at two river sites downstream of the confluence of the inundated floodplain with the MRC.

Natural floods are often largerin magnitude than managed inundation, and can homogenise hydrological conditions across larger spatial extents of the floodplain (Thomaz et al. 2007), facilitatingsignificant mixing and exchange of resources between the complex habitats patchesand reducing the spatial variability (Agostinho and Zalewski 1995, Agostinho et al. 2000, Neiff et al. 2001, Thomaz et al. 2007).Since managed floods generally tend to be smaller in comparison to a range of natural floods, it is less likely that such homogenisation could be achieved. This was supported by the findings that ecosystem productivity at two anabranch sitestended to be influenced strongly by the floodplain mosaic,withpossible input of resources from different habitat sources constituting distinct physical and chemical characteristics. This further suggeststhat in complex river-floodplain ecosystems, the interaction between hydrological connectivity and physicalheterogeneity is a key determinant of ecosystem productivity over space and time. Such observations reflect the need for usingmultiple sites to measure and evaluate the ecological responses that can be achieved throughmanaged inundation events.In addition, these findings support the need for measurements of ecosystem metabolism that capture the greater spatio-temporal heterogeneity to account for site variability as well as differences in source water chemistry.

This study also demonstrated how the episodic nature of flood pulses in degraded dryland river-floodplain ecosystems tend to exhibit ‘boom and bust’ ecological dynamics. An initial modest water level rise that occurred prior to the managed inundation period resulted in an unexpectedly large stimulation of ecosystem productivity rates at the anabranch sites. The elevated ecosystem productivity rates resulted froma significant increase in water flow through the main channel of the River Murray thatraised the water level in Lock 5.This in turn created backwater curve and increased the water level in the floodplain anabranch, prior to the managed inundation. In alignment with sampling plan, water quality parameters were sampled only twice prior to the managed inundation period; asthis was expected to be sufficient to characterize the baseline water quality conditions. However, these samplings only provided data once before the initial water level rise, and once during the increased flow.The episodic nature of the flow pulse made it difficult to assess its influence on some of the important water quality indicators, such as phytoplankton biomass, DOC and nutrients. As the automated high frequency measurement of dissolved oxygen was already underway,it was possible todetermine how ecosystem productivity was influenced bythe initial flow pulse.

Highly elevated rates of GPP and CR were observed both during the unexpected initial water level rise and the managed inundation period, and indicates the high sensitivity of anabranch habitatsto even a small change in water level. Intriguingly, the rates of GPP and CR were higher during the initial water level rise compared to the rates observed during the rising phase of the hydrograph of the managed inundation period, despite the size and lateral extent of the overbank flow associated with the latter being larger. This was interpreted to be the result of the release of available nutrients and labile carbon from the floodplain surfaces during the flow pulse that resulted from the initial water level rise. This further provides evidence that the rate of carbon cycling in river-floodplain ecosystems is not only a function of the extent of the flooding, but also the duration of period between the drying and wetting cycle.

Findingsfrom this study support the importance of more frequently monitored data for water quality variables in assessing the ecosystem metabolism responses in complex river-floodplain ecosystems with highly variable flow pattern. Such datawill greatly improve our ability to understand and identify the drivers of large changesin the metabolic rates(Marcé et al. 2016). This is also important in the context of uncertainties associated with global climate change. More frequentlymonitored water quality variables and dissolved oxygen data will help determine if river ecosystemsare shifting towards heterotrophyin association with theincrease in temperature and predicted increase in precipitation in many regions of the world,which may lead to transport of higher allochthonous DOC into the aquatic systems (Jennings et al. 2012, Jones and Lennon 2015). These global changes may particularly be important in rivers like the River Murray,which exhibit high variability in flow, and unexpected episodic events.

In summary, Chapter 2highlights that managed floods are less likely to homogenise the hydrological conditions across the floodplain, and therefore, tend to show high variability in water quality and productivity. Although managed inundation events have the potential to improve the riverine productivity, spatial variability in the metabolic activity should be considered in the planning of future managed inundation events. Further studies on the importance of the drivers of the spatial and temporal variability are required to fully understand the broader impacts of managed floods, and to enable optimal management of floodplain inundationto maximize the ecological benefits. This information will be particularly important in supporting improved ecosystem productivity in large and regulated floodplain rivers where environmental water provisions and floodplain regulators are used in tandem.

In Chapter 3,the influence of return flows fromthe floodplain anabranch on whole ecosystem metabolism rates at two sites in the MRC downstream of the inundated floodplainwas investigated. There was a strongly autotrophic (net ecosystem productivity (NEP)>>1) response at the immediate downstream site, and strongly heterotrophic (NEP<<1) response at a site located approximately 40 km downstream of confluence of the anabranch with the MRC.These observations support the findings of Wallace and Furst (2016), who also observed higher GPP at their monitored impact site during the same managed inundation event. This also supports the observations made by Cook et al. (2015), where a large increase in GPP and CR rates were observed during a natural flood in the mid-River Murray, downstream of a large extensive floodplain.Despite the smaller extent of the inundation during this study, which inundated only 2,300 ha of the floodplain, impacts were observed in the MRC beyond the immediate vicinity of the anabranch confluence, as elevated concentrations of nutrients and DOC and subsequent changes in GPP, CR and NEP were observed at a site 40 km downstream of the inundated floodplain, and could possibly extend beyond that. This indicates that managed inundation events potentiallyhave an important rolein stimulating riverine productivity, and could play a vital role in improving degraded ecological conditions as well as delivering important external energy resources to support energy limited aquatic food webs.

Although the rates of GPP and CR were significantly elevated at sites downstream of the floodplain, these increases did not align with increased nutrients or DOC at either site. However, this interpretation is based on discrete weekly data for the water quality variables and therefore may not accurately capture the changes that have occurred, making it difficult to ascribe changes in metabolism to particular physio-chemical changes. It is possible that the large increase in GPP was a result of the oxygen rich water transported to the MRC from the shallower inundated floodplain, and not a result of increased photosynthesis in the MRC itself. This phenomena has previously been observed by Oliver and Lorenz (2013). The lack of observation of elevated nutrients and phytoplankton biomass supports this notion further.

The larger change in CR at the site furthest downstream in the MRC was interpreted to be the result of respiratory metabolism of organic materials transported from the floodplain through the return flow, with some additional contribution from organic materials formed at sites in between.Returning flood waters can transport a large biomassof microorganisms including bacteria, phytoplankton and zooplankton to the main river channel (Furst et al. 2014, Cook et al. 2015, Nielsen et al. 2015). These are expected to increase respiration rates after a period of travel down the MRC. It is suspected that this is the reason for the increased CR rates at the downstream site.More frequently monitored water quality variables and the oxygen data in the future events may help to improve our ability to understand and identify the drivers of large changes in the metabolic rates (Marcé et al. 2016). Nevertheless, it is evident that managed inundation events using environmental regulatorshave a large spatial impact on the river metabolism, even during periods of low water availability when river systems may otherwise be energy limited. Better understanding of whether the detrital or newly derived organic material from the floodplain passes up through the food-web and influences the biomass of organisms at higher trophic level in the rivers will not only depend upon the quantity of the organic material delivered by the flood, but also upon its quality and bio-availability. This requires further assessment, involving sampling at more adequate temporal and spatial scales. Further, combining ecosystem metabolism measurements with stable isotopes analysis of food web carbon and nitrogen in the future would provide a better understanding of the sources of the organic carbon available for food-webs (Hunt et al. 2012).

In Chapter 4, the relative importance of the contribution to river metabolism made by different biotic components was examined. In this study, the production and respiration rates of a range of biotic components were estimated, and scaled to a reach where the whole ecosystem metabolism was measured. The findings on biomass specific respiration were then used to partition the whole ecosystem respiration measurements. It was evident thatmicroorganisms, such as phytoplankton, small zooplankton and bacteriacontributed the dominant fraction to the whole ecosystem CR. This indicates there ishigh carbon flux through smaller ecosystem components. The contribution by larger zooplankton, invertebrates and fish was less significant and this appeared to be the case even with the large increase in their biomasses during the managed inundation period. The lack of sensitivity to substantial changes in the biomass of larger organisms, which would otherwise be considered an improvement in the condition of the ecosystem, casts doubt on the suitability of metabolism measurements as an indicator of ecosystem condition.

Because of the limited number of studies assessing the contributions of higher order organisms to the ecosystem metabolism in aquatic ecosystems, it is difficult to make broader comparisons with literature to build a consensus on this important area of research. However, comparing with a recent study (Cremona et al. 2014), we found a considerably lower contribution of fish to the overall rates of ecosystem respiration. This was interpreted to be a result of differences in the trophic structure of the food web in the two systems; lotic (creek in this study) and lentic (lake in their study), habitat being an important factor mediating predatory interactions among ecosystem communities (Diehl 1992). Although higher trophic levels of the aquatic food webs are critical for the functioning and ecological conditions of riverine systems, this may not always be reflected in their contribution to overall carbon fluxes.

The higher contribution from fish as observed in theCremona et al. (2014) study suggests that the contribution by higher organisms depends on the characteristics of the ecosystem. The intensified river regulation in the River Murray has changed the dominance of fish species; from native fish to non-native Carp, with the reduction of almost 90% of the native fish population since European settlement(Lintermans 2007). It is possible that if fish populations in the river were at the levels that are thought to have existed originally, they would perhaps make a larger contribution to the systemmetabolism. The findings thus highlight that for any given open water metabolism measurements there is uncertainty about what components of the biota are included. This study therefore cautions against interpreting the measurements of metabolism as a holistic functional indicator of river ecosystem health, mainly because metabolism measurements may not reflect the ecosystem more broadly.

The concepts and knowledge developed in this study will contribute to a more comprehensive understanding of the ecological mechanisms linking environmental flows and the biotic processes in riverine ecosystems. This research demonstrates considerable scope for carbon and nutrient cycling in the river-floodplain ecosystems to be actively managed through environmental water delivery using environmental flow regulators. It provides empirical evidence to support our understanding of the role of anabranches and floodplains in supporting riverine food-webs during managed floods. Managed floods can stimulate the riverine productivity if careful consideration of the sites to be inundated is undertaken. This is because managed floods tend to be influenced by local driving forces associated with habitat heterogeneity of the floodplain. Inundating a range of habitat types should be considered to promote physico-chemical diversity that will help in promoting high biodiversity through heterogeneous floodplain habitats. Consequently, recognition of the role of anabranch channels and the importance of good hydrological connectivity with the main river channel will produce more effective and targeted management solutions with long-term benefits to river-floodplain ecosystems as a whole. One important concern this study raises is in using and interpreting whole ecosystem metabolism measurements as an indicator of overall health of the ecosystem. This is because of the uncertainties associated with components of the biota that are included in such measurements, as ecosystem metabolism measurements may only reflect the activity of microorganisms, but not the ecosystem broadly. Nevertheless, ecosystem metabolism measurements do provide powerful tools for assessing the metabolic activity of plankton, such as how phytoplankton and carbon are utilized within the system, as an indicator of carbon and nutrient cycling. This in itself is a useful metric to complement bio-monitoring of higher order organisms, and to develop a reliable picture of riverine ecosystem health.

REFERENCES

Agostinho, A., S. Thomaz, C. Minte-Vera, and K. Winemiller. 2000. Biodiversity in the high Paraná River floodplain. Biodiversity in wetlands: assessment, function and conservation **1**:89-118.

Agostinho, A. A. and M. Zalewski. 1995. The dependence of fish community structure and dynamics on floodplain and riparian ecotone zone in Parana River, Brazil. Pages 141-148 The Importance of Aquatic-Terrestrial Ecotones for Freshwater Fish. Springer.

Cook, R. A., B. Gawne, R. Petrie, D. S. Baldwin, G. N. Rees, D. L. Nielsen, and N. S. Ning. 2015. River metabolism and carbon dynamics in response to flooding in a lowland river. Marine and Freshwater Research.

Cremona, F., T. Kõiv, V. Kisand, A. Laas, P. Zingel, H. Agasild, T. Feldmann, A. Järvalt, P. Nõges, and T. Nõges. 2014. From bacteria to piscivorous fish: estimates of whole-lake and component-specific metabolism with an ecosystem approach. PloS One **9**:e101845.

Diehl, S. 1992. Fish predation and benthic community structure: the role of omnivory and habitat complexity. Ecology **73**:1646-1661.

Furst, D. J., K. T. Aldridge, R. J. Shiel, G. G. Ganf, S. Mills, and J. D. Brookes. 2014. Floodplain connectivity facilitates significant export of zooplankton to the main River Murray channel during a flood event.

Hunt, R. J., T. D. Jardine, S. K. Hamilton, and S. E. Bunn. 2012. Temporal and spatial variation in ecosystem metabolism and food web carbon transfer in a wet-dry tropical river. Freshwater Biology **57**:435-450.

Jennings, E., S. Jones, L. Arvola, P. A. Staehr, E. Gaiser, I. D. Jones, K. C. Weathers, G. A. Weyhenmeyer, C. Y. CHIU, and E. De Eyto. 2012. Effects of weather-related episodic events in lakes: an analysis based on high-frequency data. Freshwater Biology **57**:589-601.

Jones, S. E. and J. T. Lennon. 2015. A test of the subsidy–stability hypothesis: the effects of terrestrial carbon in aquatic ecosystems. Ecology **96**:1550-1560.

Lintermans, M. 2007. Fishes of the Murray-Darling Basin: an introductory guide.

Marcé, R., G. George, P. Buscarinu, M. Deidda, J. Dunalska, E. de Eyto, G. Flaim, H.-P. Grossart, V. Istvanovics, and M. Lenhardt. 2016. Automatic high frequency monitoring for improved lake and reservoir management. Environmental Science & Technology **50**:10780-10794.

Neiff, J., B. Gopal, and W. Junk. 2001. Diversity in some tropical wetland systems of South America. Biodiversity in wetlands: assessment, function and conservation **2**:157-186.

Nielsen, D. L., R. A. Cook, N. Ning, B. Gawne, and R. Petrie. 2015. Carbon and nutrient subsidies to a lowland river following floodplain inundation. Marine and Freshwater Research**67:**1302-1312.

Oliver, R. L. and Z. Lorenz. 2013. Changes in metabolic activity in the South Australian section of the Murray River during the 2010/11 flood that followed a ten year drought. Goyder Institute for Water Research Technical Report Series.

Thomaz, S. M., L. M. Bini, and R. L. Bozelli. 2007. Floods increase similarity among aquatic habitats in river-floodplain systems. Hydrobiologia **579**:1-13.

Wallace, T. A. and D. Furst. 2016. Open water metabolism and dissolved organic carbon in response to environmental watering in a lowland river–floodplain complex. Marine and Freshwater Research.