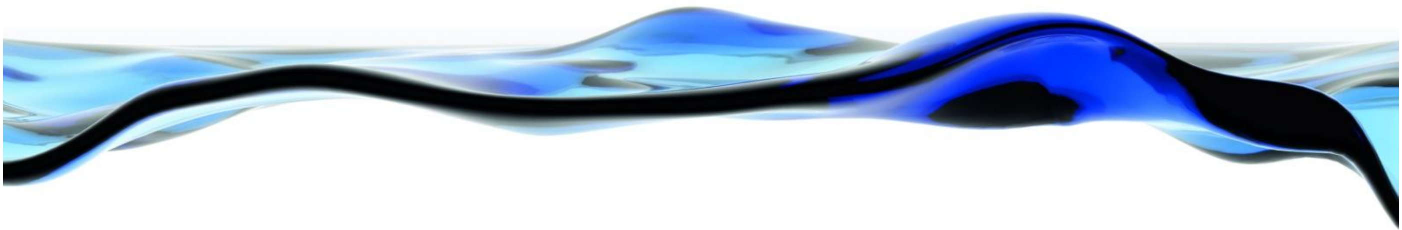
Ecological Responses to Flooding in the Lower River Murray Following an Extended Drought

Synthesis Report of the Murray Flood Ecology Project

Qifeng Ye, George C. Giatas, Kane T. Aldridge, Simon N. Benger, Chris M. Bice, Justin D. Brookes, Luciana B. Bucater, Katherine J. M. Cheshire, Courtney R. Cummings, Tanya M. Doody, Peter G. Fairweather, Kate A. Frahn, Josh F. Fredberg, Susan L. Gehrig, Kate L. Holland, Sandra J. Leigh, Rebecca E. Lester, Zygmunt Lorenz, Kelly B. Marsland, Jason M. Nicol, Roderick L. Oliver, Ian C. Overton, Jodie L. Pritchard, Arron D. Strawbridge, Leigh A. Thwaites, Chris J. Turnadge, Phillipa K. Wilson, Brenton P. Zampatti.



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The following Associate organisation led the preparation of this report:

Enquires should be addressed to: Goyder Institute for Water Research
Level 1, Torrens Building
220 Victoria Square, Adelaide, SA, 5000
tel: 08-8303 8952
e-mail: enquiries@goyderinstitute.org

Citation

Ye Q[1*], Giatas GC[1], Aldridge KT[2], Benger SN[3], Bice CM[1], Brookes JD[2], Bucater LB[1], Cheshire KJM[1], Cummings CR[3], Doody TM[4], Fairweather PG[3], Frahn KA[1], Fredberg JF[1], Gehrig SL[1], Holland KL[4], Leigh SL[1], Lester RE[3], Lorenz Z[4], Marsland KB[1], Nicol JM[1], Oliver RL[4], Overton IC[4], Pritchard JL[4], Strawbridge AD[1], Thwaites LA[1], Turnadge CJ[4], Wilson PK[1], Zampatti BP[1](2014) Ecological responses to flooding in the lower River Murray following an extended drought. Synthesis Report of the Murray Flood Ecology Project. Goyder Institute for Water Research Technical Report Series No. 14/6.

*Corresponding author: qifeng.ye@sa.gov.au
[1]SARDI Aquatic Sciences, PO Box 120, Henley Beach, SA 5022, Australia
[2]School of Earth and Environmental Sciences, the University of Adelaide, Adelaide, SA 5005, Australia
[3]Flinders University, GPO Box 2100, Adelaide, SA 5001, Australia
[4]CSIRO Land and Water, PMB 2, Urrbrae, SA 5064, Australia

Table of contents

List of figures

List of tables

Acknowledgements

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Executive summary

Background

The Murray–Darling Basin (MDB) is a large drainage system (1 million km^2) of south-eastern Australia, which supports a diverse range of flora and fauna. The MDB is comprised of numerous rivers and catchments including the Darling, Murray and Murrumbidgee rivers. The River Murray is the primary river in the South Australian section of the MDB, which is of high economic, social, cultural and ecological significance. The 'lower River Murray' (LRM), in South Australia (SA) is highly regulated; the upstream water diversion and extraction and the construction of a series of low-level weirs during the 1920s and 1930s have dramatically altered the natural flow regimes in this region. There have been significant flow reductions, and the main channel is now characterised by a series of cascading lentic weir pools under low within-channel flows (<30,000 ML day^{-1}).

Between 1997 and 2009 the MDB experienced its most severe drought on record. Over this period, low and stable within-channel flows (<15,000 ML day^{-1}) predominated in the LRM and were insufficient to inundate floodplains. Concurrently, water levels downstream of Lock 1 fell below sea level for the first time in recorded history. Consequently, floodplain and fringing wetlands became disconnected and desiccated, and large areas of acid sulphate soils were exposed in the Lower Lakes. In mid-late 2010, above average rainfalls throughout most of the upper-catchment of the MDB resulted in widespread flooding in the LRM. River flow at the SA border increased substantially from September 2010 to a peak of approximately 93,800 ML day^{-1} in February 2011. These overbank flows provided longitudinal and lateral hydrological connectivity and returned hydraulic complexity to the weir pools of the LRM.

Whilst the River Murray is recognised as a significant ecological asset to be targeted by environmental flows, current knowledge of environmental water requirements in the LRM is limited. To achieve the greatest ecological benefits from available environmental water, it is important to understand ecological responses to different flow scenarios, including floods. The 2010/11 flood ended a 10 year period of drought and provided a unique opportunity to investigate the impacts of increased flow on the ecology and resilience of the key populations and communities in LRM.

Murray Flood Ecology project and research aim

The Murray Flood Ecology (MFE) project was a collaborative research project developed in response to the 2010/11 overbank flood in the LRM. The aim of the MFE project was to investigate key ecological responses to flooding following an extended drought in the LRM. The project included a series of sub-projects undertaken to test hypotheses that were based on a conceptual understanding of the life histories of relevant biota and ecological processes, and the responses that might be expected from floods. The flow ecology research through this project aimed to develop critical knowledge to underpin the prediction of future responses to environmental watering, particularly in the context of overbank flows. Data collected will aid in the development of models for assessing ecosystem response to various flow events, helping to create a framework of future management tools for the LRM.

The MFE project involved investigations that targeted the main channel, wetland and floodplain environments, covering both abiotic (water quality and nutrients) and biotic (primary productivity, plants and fish) responses to flooding. Research sub-projects were grouped under three themes investigating the effects of flood on 1) nutrients, primary production and metabolic activity; 2) fish ecology; and 3) aquatic and floodplain vegetation. Data were integrated to develop a conceptual model of the ecosystem response to flooding in the LRM.

Key findings and outputs

Effects of flooding on nutrients, primary production and metabolic activity

- Flooding in the LRM led to an increase in nutrient concentrations, which was associated with an increase in phytoplankton biomass. Phytoplankton communities changed from a Cyanophyta dominated community during the low-flow period (<7,000 ML day^{-1}) between June 2008 and August 2009 to a mixed community during the high-flow period in 2010/11. This community was dominated by diatoms on the rising and falling limbs of the hydrograph during October 2010 and mid-2011, and Chlorophyta during peak flow (~80,000 ML day^{-1}) in February 2011. High diatom abundance was observed at the completion of the study in August 2011 when flows were approximately 35,000 ML day^{-1}.

- The shift in phytoplankton communities from Cyanophyta to diatom dominated is associated with reduced risk of Cyanophyta blooms and nutritional benefits for the aquatic foodwebs.

- The Chowilla and Barmera floodplains were major sites for phytoplankton photosynthetic production and sources of organic matter during the high-flow period. This highlights the importance of lateral connectivity between the main channel and off-channel habitats, and the significance of specific floodplain areas. A large proportion of respiration in the main channel was attributed to unidentified sources and is believed to be associated with these two influential floodplains. It has not been determined if this was due to planktonic organisms in floodwaters on the floodplain, or due to benthic activity associated with the flooded soils, but it suggests that significant processing of organic material occurs on the floodplain prior to waters returning to the channel.

Fish ecological responses to flooding

- The larval fish assemblage during flooding in 2010 differed significantly from the assemblages during the drought (flows <7,000 ML day^{-1}) in 2006, 2007 and 2008, and appeared to be more similar to the assemblage during 2005 with small within-channel flows of ~13,500 ML day^{-1} in the LRM. This was mainly attributed to the presence of flow-cued spawners (golden perch and silver perch) and higher relative abundances of Murray cod larvae during 2005 and 2010.

- Following flooding in 2011, abundance of golden perch was significantly greater (5–6 times) than during low-flow years. Age structures indicated that increased abundance was predominantly due to recruitment of fish spawned during the flood in 2010/11 and during the previous year (2009/10), which was characterised by low within-channel flows in the LRM.

- Radio-tagged Murray cod movements ranged from localised small-scale (<2 km) movement to large-scale (>50 km) upstream riverine movement. Murray cod exhibited high fidelity to perennial anabranch habitat of Chowilla but also moved extensively between anabranches and the main channel, highlighting the importance of connectivity between these two habitats. Mortality of radio-tagged Murray cod was considerable (25%) across a broad geographic range (>100 km) in association with a hypoxic blackwater event during the flood.

- Flooding was integral in structuring fish assemblages in the main channel of the LRM. Flooding indirectly resulted in the absence or reduced abundance of small-bodied fish species, by re-structuring macrophyte cover (i.e. loss of submerged macrophytes). In contrast, large-bodied species (i.e. golden perch and common carp) exhibited flexible microhabitat use and increases in abundance following flooding were related to the direct influence of flow on critical life history processes (i.e. spawning and recruitment).

- Flooding was associated with significant changes in wetland fish assemblages. There was an overall reduction in abundances of native fish following the flood. In general, differences in assemblage structure were driven by decreases in the abundance of carp gudgeon, flathead gudgeon, dwarf flathead gudgeon and eastern gambusia, and an increase in the abundance of common carp.

Aquatic and floodplain vegetation response to flooding

- The response of aquatic plant communities below Lock 1 to the reinstatement of water levels (return to normal pool level) varied among floodplain wetlands between Mannum and Blanchetown and the Lower Lakes. Emergent plants generally persisted throughout the study area during low-flow conditions and increased in abundance after flows were re-instated, demonstrating resistance to disturbance. Submergent plants were extirpated from the Lower Lakes during the drought but recruited in shallow water habitats (shorelines and wetlands) after water levels were reinstated, demonstrating resilience. Between Mannum and Blanchetown, however, the submergent plant community did not exhibit a positive response, either due to lack of resilience and/or other non-biotic factors such as turbidity. However they are expected to recover and recruit after normal pool levels return and be maintained post-flooding. Terrestrial and floodplain plants which recruited onto exposed wetland beds and lakeshores during the drought became extirpated after flows returned, but recruited between Mannum and Blanchetown at higher elevations once overbank flows receded.

- Lateral bank recharge is an important mechanism in the maintenance and improvement of river red gum condition along the LRM. A lateral recharge zone of influence 30 to 90 m from the LRM main channel and feeder creeks was identified as important in maintaining river red gums in better condition. Higher within-channel irrigation water delivery during summer months was critical to tree survival adjacent to the channel during the drought. River red gum response to flooding was greatest when inundated between 7 and 60 days on the Chowilla floodplain.

- Tree water availability, indicated by the extent and degree of soil and groundwater freshening, was significantly greater after the flood than after artificial watering and groundwater management. However, the persistent high water tables caused by elevated river levels appear to have suppressed or delayed the expected tree canopy response to the flood. Understory vegetation species richness at Pike (24 taxa before, 68 taxa after) and Chowilla (43 taxa before, 66 taxa after) floodplains increased after natural flooding, but the response was not consistent. This was due to the large number of floodplain and amphibious species that were present on the Chowilla floodplain prior to the 2010/11 flood due to artificial watering.

Conceptual river–ecosystem model

- A high-flow/flood ecosystem model was developed for the LRM using data collected from the sub-projects of the MFE (based on the 2010/11 flooding event) and some data during the drought. For most ecological components, flooding was thought to have an overall positive impact.

- As this model is based on a single natural flood (2010/11) following an extended drought, there is a need to broaden our knowledge over multiple flood events, which will strengthen the conclusions drawn from the MFE project and ensure a comprehensive understanding of ecological responses to flooding in the LRM.

Conclusions and recommendations

Natural flooding in 2010/11 facilitated important ecological processes including increased primary production, improved lateral and longitudinal connectivity, lateral bank recharge, re-structuring of aquatic plant communities, plant recruitment and fish spawning, recruitment and movement, leading to increased abundances, improved condition and recovery of key communities after drought. The research outcomes highlight that flooding, as an integral part of the natural flow regime, is important in maintaining the ecological integrity of floodplain rivers.

Overall, research sub-projects had a high level of concurrence in findings. For instance,

- Flood and increased within-channel flows facilitated spawning and recruitment of golden perch, a flow-cued spawning species in the LRM, while floods also led to increased recruitment and abundance of common carp, a flood opportunistic invasive species, in the main channel and most wetlands. This implies that careful management of flow is required in order to minimise benefits for carp, while maximising benefits for native species.

- In the main channel, both larval and adult fish assemblages showed a structure shift from drought to flood mainly due to reduced relative abundances of small-bodied fish and increased abundances of large-bodied fish during the flood. This was linked to the alteration of microhabitats (i.e. reduction of submerged aquatic macrophytes with which small-bodied fish are associated) and enhanced spawning, recruitment and abundance of large-bodied fish (e.g. golden perch and carp).

- The vegetation communities of the floodplains and their wetlands in the LRM demonstrated ecological resistance and resilience in their response to the flood following an extended drought. While artificial watering maintained the diversity of floodplain and amphibious vegetation species during the drought in selected areas, it was spatially limited. Riparian tree communities benefited from lateral bank recharge caused by fluctuations in river levels, artificial watering, groundwater management and the flood.

- Both water quality and golden perch studies suggest that maintaining flow integrity and continuity (e.g. Darling or upper-, mid-Murray to the LRM) are important to facilitate nutrient transport, larval drift and juvenile fish dispersion. This also supports the notion that environmental flow management needs to consider appropriate spatio-temporal scales (e.g. river scale).

- River metabolism and Murray cod movement studies have both highlighted the importance of maintaining connectivity between the main channel and key off-channel habitats to facilitate carbon/nutrient and biotic movements.

The conceptual model developed based on findings from sub-projects captures our understanding of the ecological responses to flow. This model has the potential to be used as a basis for the future development of tools to assist in the flow management of the LRM. Investigation of ecological responses to further floods and within-channel flows in the LRM will allow for more reliable predictions of flow response, which will better inform environmental water planning and management.

Management considerations were identified for each MFE sub-project and general recommendations are provided as follows:

- The LRM is an integrated floodplain riverine system; complementary management actions are needed to achieve ecosystem outcomes.

- Environmental water management should consider appropriate scale (e.g. river scale) concordant with ecological process and life history of targeted biota, and should not be limited to the site or reach scale.

- Flow delivery to facilitate large scale connectivity (river or basin level) is important for maintaining a healthy and diverse river. Maintaining lateral connectivity is also critical between the river main channel and productive off-channel wetland and floodplain habitats.

- Returning a more natural flow regime that includes a mix of flooding, low- and medium-level flows where various species and functional groups can meet their specific life-history requirements is suggested to restore and maintain aquatic ecosystems of the LRM.

- Currently, environmental flows are delivered to the LRM typically to create spring/summer flow pulses, aiming to increase flow variability and achieve ecological outcomes. Within-channel flows (e.g. 15,000–50,000 ML day^{-1}) could be restored within the current constraints of system operation.

- In contrast, using engineering to mimic natural floods is more challenging and has clear limitations as manipulated flood events are unlikely to serve the complete ecological function of a natural flood and could create risks by disconnecting riverine processes and functions.

In order to further understand the role of flow in the ecology of the LRM, ongoing investigations during various flow scenarios are required. The MFE project has improved our conceptual understanding of flow-related ecology in LRM, which can be used to guide flow restoration and develop hypothesis driven monitoring to adaptively manage environmental flows. Integral to this are rigorous and robust long-term monitoring programs.

Introduction

Murray Flood Ecology

The Murray Flood Ecology (MFE) project was developed in 2010 to investigate ecological responses to an overbank flow in the lower River Murray, South Australia (SA). Funded predominantly by the Goyder Institute for Water Research, research was undertaken by scientists from a number of organisations including the South Australian Research and Development Institute (SARDI), Commonwealth Scientific and Industrial Research Organisation (CSIRO), University of Adelaide and Flinders University.

Murray–Darling Basin and lower River Murray

The Murray–Darling Basin (MDB) is a large, regulated drainage system that covers an area of more than 1 million km^2 of south-eastern Australia and supports a diverse range of flora, fish, waterbirds, reptiles, amphibians, mammals and macroinvertebrates (MDBA 2014). The MDB is comprised of numerous rivers and catchments including the Darling (~2,800 km long), Murray (~2,300 km long) and Murrumbidgee (~1,600 km long) rivers. The River Murray flows along the NSW–Victoria border into SA and discharges into the Southern Ocean.

The 'lower River Murray' (LRM) is classified as the reach of the River Murray downstream of the Darling River junction, differentiated by hydraulic, hydrologic and geomorphic properties (Walker 2006). This MFE project focuses on the SA section of the LRM as most projects were confined within the SA border. From herein, the 'LRM' will be defined as the section of the River within SA unless specified. The LRM is an area of high economic, social, cultural and ecological significance. It is the major source of domestic drinking water for the SA population and an important supply of water for irrigated agriculture. Within the LRM three sites are listed as wetlands of international importance under the Ramsar Convention ('the Riverland', 'Banrock Station Wetland Complex' and 'the Coorong and Lakes Alexandrina and Albert') and three as Murray–Darling Basin Authority Icon sites ('Chowilla Floodplain', 'the River Murray Channel' and 'the Coorong and Lakes Alexandrina and Albert') (MDBA 2014), which have been identified as areas of high ecological importance. The LRM can be divided into four distinct geomorphic regions: the floodplain, gorge, swamplands and lakes (Figure 1). Within SA, the floodplain geomorphic region extends from the SA–NSW border to Overland Corner and is characterised by an extensive floodplain (up to 10 km wide) and a complex network of anabranch systems. The gorge geomorphic region extends from Overland Corner downstream to Mannum and is characterised by vertical limestone cliffs and a relatively narrow floodplain (1–2 km wide), with large permanent wetlands. The swamplands region comprises the reach between Mannum and Wellington, which is characterised by reclaimed swamplands used for agriculture (primarily dairy). The lakes region begins at Wellington and is comprised of two large, shallow freshwater lakes: Lake Alexandrina and Lake Albert. The river enters the top of Lake Alexandrina, the larger of the two lakes, with water flowing into Lake Albert from Lake Alexandrina through a narrow channel. The Murray estuary and Coorong receive water through a series of channels that drain from Lake Alexandrina (Phillips and Muller 2006).

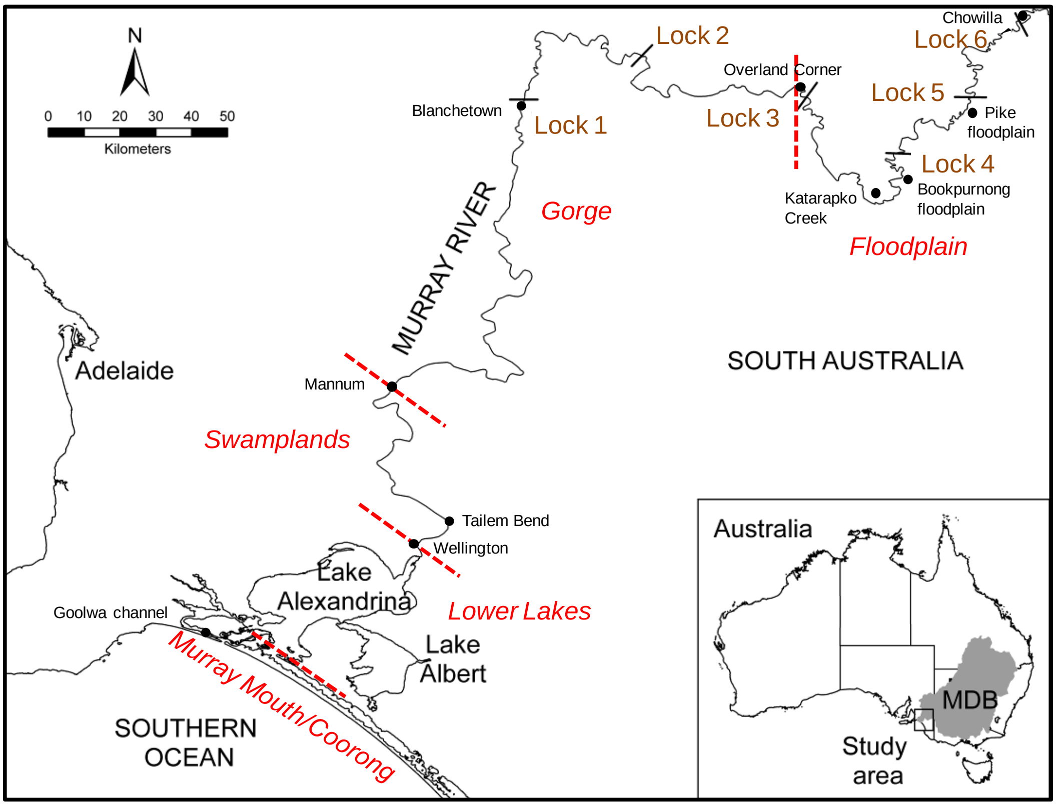

Figure 1. The lower River Murray, South Australia showing four geomorphic regions and six locks and weirs.

Hydrology

The LRM is highly regulated by upstream diversions and a series of low-level (~3 m) weirs that were constructed during the 1920s and 1930s for the purpose of irrigation and navigation (Walker 2001). Additionally, a series of tidal barrages were constructed between Lake Alexandrina and the Murray estuary to prevent saltwater intrusion. River regulation and water abstraction have altered the natural flow regime of the LRM, dramatically reducing flow volumes and hydrological variability (Maheshwari *et al.* 1995). Post-regulation, only ~40% (4,915 GL) of the natural mean annual discharge (12,300 GL) of the River Murray Basin reaches the Southern Ocean (Walker 2006). Under low-flow conditions, which predominate, the LRM is now characterised by series of lentic weir pool habitats, contrasting the rivers historically highly variable, lotic form (Walker 2006).

Since the late 1970s, flow into South Australia has been highly variable with peak flows of >100,000 ML day^{-1} experienced in 1981, 1990, 1993 (Figure 2). Between 1997 and 2009, the MDB experienced its most severe drought on record (Leblanc *et al.* 2012), characterised by low, stable within-channel flows (mostly <15,000 ML day^{-1}) after 2001 in the LRM (Figure 2). Concurrently, water levels downstream of Lock 1 (including lakes Alexandrina and Albert) fell below sea level in 2008 for the first time in recorded history (MDBA 2014). Consequently, floodplain and fringing wetlands became disconnected and desiccated (Nicol 2010), and large areas of acid sulphate soils were exposed in lower reaches of the Murray and in the lakes (Simpson *et al.* 2010).

In mid-late 2010 above average rainfalls throughout the upper-catchment of the MDB caused widespread flooding in the LRM. Flow over the SA border began to increase in September 2010 and peaked at 93,872 ML day^{-1} in February 2011 (Figure 2). Overbank flows, which occur at discharges of >35,000–50,000 ML day^{-1} in the LRM depending on location, occurred from November 2010 to February 2011. Large areas of floodplain were inundated (Nicol *et al.* 2013; Doody *et al.* 2014), temporarily restoring lateral connectivity and potentially providing a source of nutrients and other external inputs into the river (Robertson *et al.* 1999). Flows of this magnitude, and subsequent removal of the weirs, restore the lotic nature of the LRM (Walker 2006).

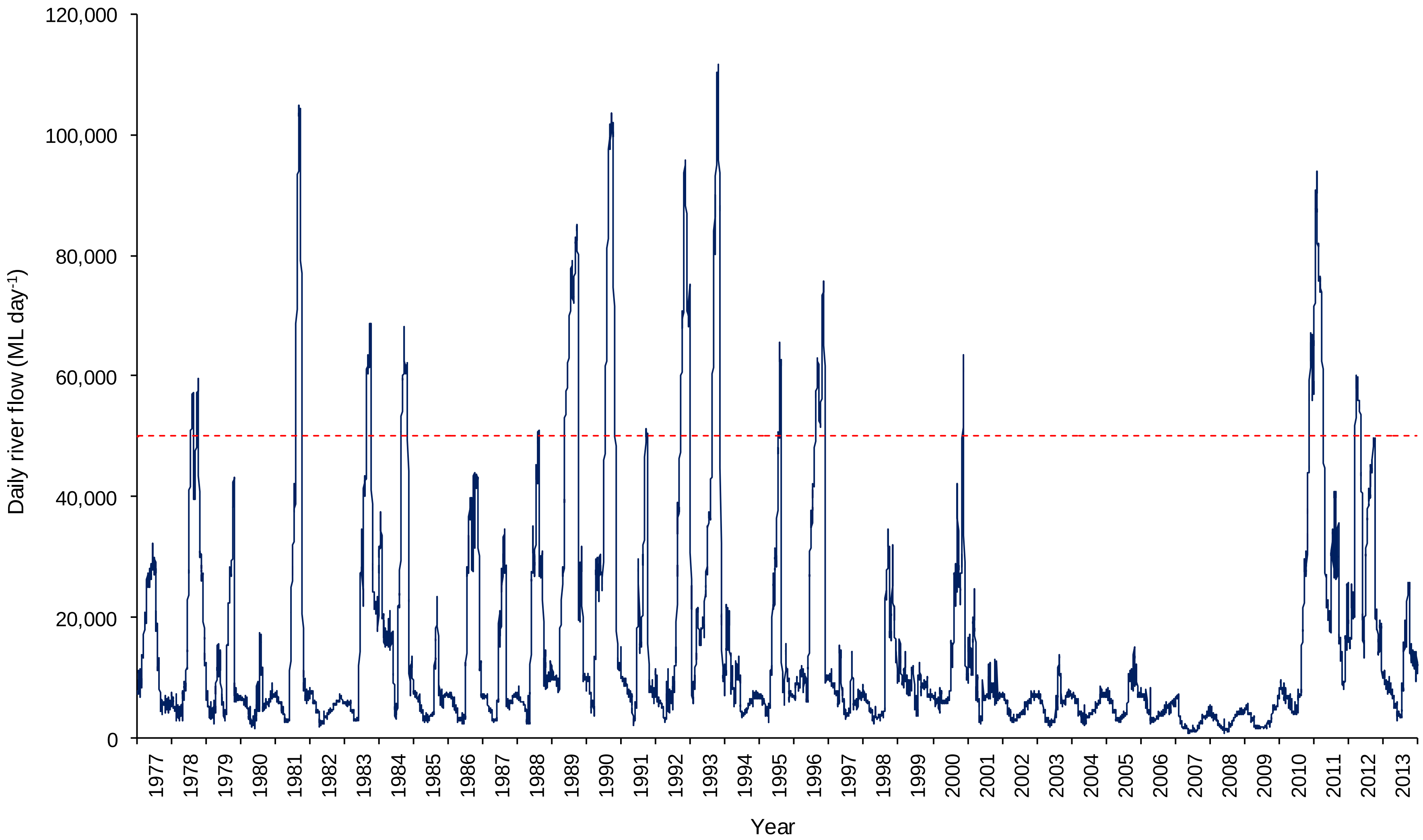

Figure 2. River Murray daily flow discharge rate (ML day $^{-1}$) over the SA–NSW border between 1977 and 2014 (Source: www.waterconnect.sa.gov.au). Dashed red line indicates approximate bank-full flow in the lower River Murray.

Knowledge gaps and aims

The main channel of the River Murray is recognised by the MDBA as a significant ecological asset to be targeted by environmental flows (DEWNR 2013). Despite this, the environmental water requirements of the LRM and flow-ecology relationships in this region are not well understood. To achieve the greatest ecological benefits from available environmental water in the River Murray, it is important to understand ecological responses to different flow scenarios, including flood. Significant ecological research and monitoring has occurred in the LRM in the past decade, predominantly investigated under low-flow conditions during drought. The 2010/11 flood provided a unique opportunity to investigate the influence of increased flow on the ecology and resilience of the ecosystem.

The overall aim of the MFE project was to investigate the response of key ecosystem components to flooding in the LRM following several years of extreme drought. The project also aimed to test several hypotheses (Table 1). These hypotheses will aid in the development of a framework and models for assessing the ecological response of the system to various flow events and provide future management tools for the system (e.g. regarding environmental flows).

MFE research components

The following conceptual diagram is a simplistic representation of the components and processes of river ecosystems that are influenced by changes in flow (Figure 3). This conceptual understanding formed the base design of the MFE project. Connections between the floodplains, wetlands and the main river channel are poorly understood, despite supporting important ecological components and underpinning important functions during periods of high flow. Therefore, this project involved studies that targeted the main channel, wetlands and floodplain. Both abiotic (water quality and nutrients) and biotic (primary productivity, plants and fish) responses to flooding were investigated.

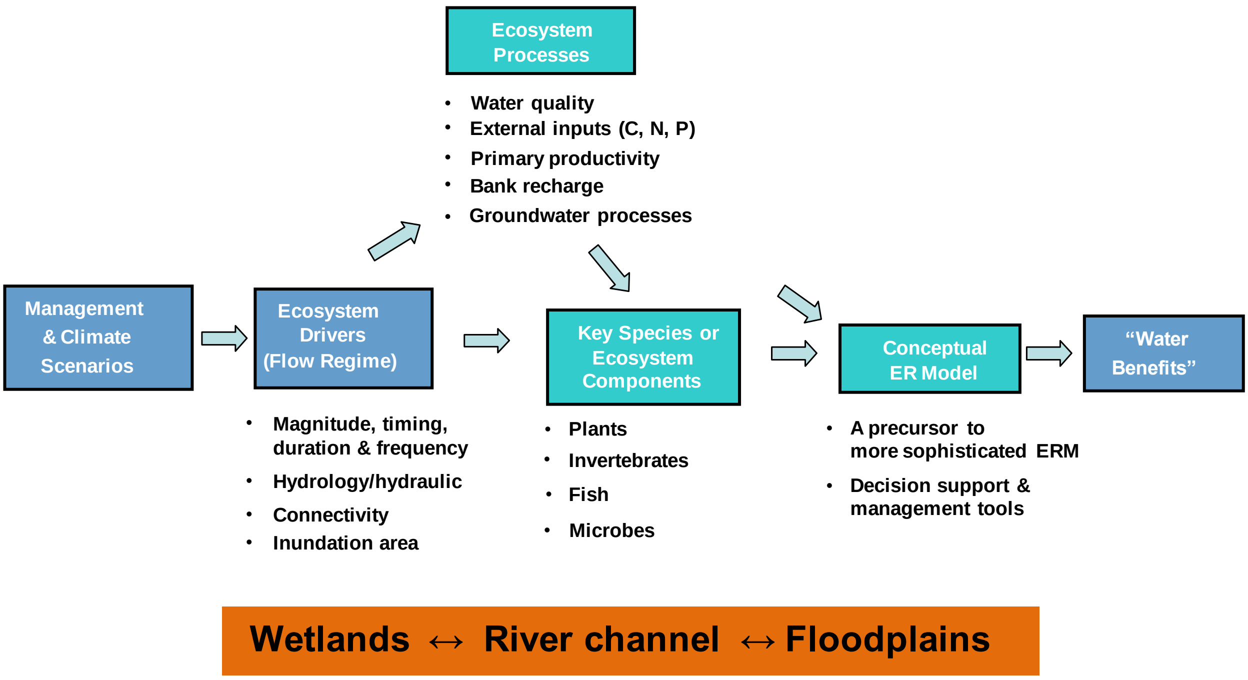

Figure 3. Conceptual representation of ecological components that can be influenced by changing flow for the lower River Murray. C=carbon, N=nitrogen, P=phosphorus, ER =ecosystem response , ERM = ecosystem response model.

The MFE project included a number of sub-projects designed to investigate key ecological responses to flow (Table 1). Data and knowledge developed from these studies were then used to create a conceptual model of the response of the LRM to flooding.

This synthesis report provides background on the MFE collaborative study, presents a summary of the key findings of each sub-project and provides general recommendations for flow management to achieve environmental outcomes in the LRM. More detailed information (e.g. methodology, statistics etc.) for sub-projects are available in Goyder technical reports or journal publications of research sub-projects (see Table 1). In this report, the findings from each research sub-project are presented under three main themes: effects of flooding on 1) nutrients, primary production and metabolism (Section two); 2) fish ecology (Section three); and 3) aquatic and floodplain vegetation (Section four) (Table 1). The conceptual model that was created based on findings from the sub-projects follows in Section five.

Table 1. Murray Flood Ecology (MFE) sub-projects and hypotheses/questions being addressed.

Main theme	Sub-project title	Hypothesis/Question	Publication
Nutrients, primary production and metabolic activity	The influence of flow on abiotic and biotic conditions in the River Murray channel.	The increase in flow will reduce underwater light availability leading to a reduction in phytoplankton and macrophyte biomass and a change in the phytoplankton community composition from Cyanophyta and green algae to diatoms.	Aldridge *et al. (*2012)
	Flow induced alterations in total river metabolism and changes in component contributions.	An increase in flow will increase the proportion of organic material (food) coming from external sources and decrease the proportion from in channel primary productivity (phytoplankton and macrophytes), thus re-balancing the form of food energy available to support invertebrates and fish.	Oliver and Lorenz (2013)
Fish ecology	Annual variation in larval fish assemblages in a heavily regulated lowland river.	Current high flow and flooding event will trigger fish spawning for flow-cued spawners in the main channel of the LRM; while conditions may not be optimal for low-flow spawner and circa-annual spawner species. Applicability of the flow related spawning/recruitment models will be tested by comparing the current fish spawning response to spawning during a within channel flow pulse and three low-flow years.	Cheshire *et al.* (2012)
	Effects of flooding on recruitment and abundance of golden perch in the LRM.	A large within-channel flow/flooding event (30,000–90,000 ML day^{-1}) will provide the hydrological and hydraulic conditions to facilitate the recruitment of golden perch in the LRM.	Zampatti and Leigh (2013b)
	Movement and mortality of Murray cod during overbank flows in the LRM.	A large within-channel flow/flooding event will promote large-scale exploratory movements of Murray cod and the potential establishment of new home ranges.	Leigh and Zampatti (2013)
	Flow induced alterations to aquatic macrophyte communities and fish assemblages in the River Murray channel.	Increases in water velocity will decrease the cover of aquatic macrophytes and in turn restructure fish assemblages by decreasing the abundance of generalist/wetland species in the main channel of the River Murray.	Bice *et al.* (2014)
	What is the response of wetland fish assemblages following flooding?	The response of fish communities in wetlands following flooding will be influenced by the resilience of fish species; therefore, post-flood communities may not immediately reflect pre-drying fish assemblages and are likely to be heavily dominated by opportunistic species.	Thwaites and Fredburg (2014)
Aquatic and floodplain vegetation	Resilience and resistance of aquatic plant communities downstream of Lock 1 in the River Murray.	Aquatic plant communities in the River Murray (including Lower Lakes) are resilient. Plant communities similar to those observed pre-2007 will recruit in response to the current flow events (using the River Murray downstream of Lock 1 as a model ecosystem).	Nicol *et al.* (2013)
	Investigate the response of river red gums to the current flow/flooding event.	The flow/flooding event will improve lateral hydrological connectivity between the river banks and riparian zones. This will have a positive impact on the health of river red gums (*Eucalyptus camaldulensis*) in those zones.	Doody *et al.* (2014)
	Floodplain response and recovery: comparison between natural and artificial floods.	Overbank flows will lead to salt leaching by vertical infiltration, groundwater freshening by bank recharge and an understorey vegetation and tree health response. Comparison of floodplain and vegetation responses to natural overbank floods with previous artificial floods will demonstrate the relative effectiveness of artificial floods.	Holland *et al.* (2013)
Conceptual river–ecosystem model	Conceptual river–ecosystem model.	To develop a preliminary conceptual model for the ecological responses measured in the LRM as a precursor to more sophisticated river management tools.	Lester *et al.* (2014)

Effects of flooding on nutrients, primary production and metabolic activity

Flows in rivers transport nutrients, organic matter and food resources and are a key driver of productivity in aquatic systems (Poff *et al.* 1997). These inputs can be from an allochthonous source (external supply from terrestrial origin) or an autochthonous source (internal supply from primary production by aquatic autotrophs) (Vannote *et al.* 1980). For a highly regulated arid/semi-arid river such as the LRM, autochthonous energy sources from the main river channel are the main contributor of energy (Oliver and Merrick 2006; Oliver and Lorenz 2010). However, overbank flooding events and associated inundation of floodplains can also deliver to the river large amounts of nutrients along with dissolved and particulate organic material of highly variable composition from allochthonous sources on the floodplain (Robertson *et al.* 1999). The frequency, duration and magnitude of droughts and floods can therefore shape river ecosystems, through large-scale changes in energy sources. Key findings by Aldridge *et al.* (2012) and Oliver and Lorenz (2013) for the changes in water quality, nutrients, primary production and metabolic activity from low-flow to high-flow/flood conditions are presented below.

Nutrients and phytoplankton communities

Aldridge *et al.* (2012) investigated changes in nutrient and phytoplankton communities in the River Murray, primarily from low-flow (2008/09) to high-flow (2010/11) conditions. This study was conducted from Lock 9 (see Aldridge *et al.* (2012) for map) to Tailem Bend, which included the swamplands, gorge and floodplain geomorphic regions of the LRM (Figure 1). Changes in salinity, dissolved organic carbon (DOC) and dissolved oxygen (DO) were also examined. See Aldridge *et al.* (2012) for a more detailed description of methodology.

There were clear differences in nutrient concentrations and phytoplankton communities between flow periods. Low nutrient concentrations occurred during the low-flow period, likely a result of low inputs from upstream areas and retention due to sedimentation of organic and inorganic material. Concurrently, Cyanophyta (cyanobacteria) dominated the phytoplankton community in the LRM (<10,000 ML day^{-1}) (Figure 4). Salinity and DOC concentrations were relatively constant during the low-flow period for most sites except the Darling River, where DOC and salinity were high in 2003 and 2007. Whilst elevated levels of nutrients, DOC concentrations, salinity and Cyanophyta (*Anabaena*) were observed in the Darling River during the low-flow period, these appeared to have minor influences on downstream sites in the LRM, due to the large dilution of Darling flows. During the low-flow period high electrical conductivities (>1,500 µS/cm) were observed in the river below Lock 1. These elevated salinities appeared to originate from Lake Alexandrina, resulting from evapotranspiration and seawater intrusions into the lake, and subsequent wind driven transport upstream.

The high-flow period resulted in the mobilisation of nutrients from the basin. The majority of these nutrients were attributed to the River Murray upstream of South Australia and the Darling River. However, the area between Lock 9 and Lock 1 was also a source of total phosphorus and total nitrogen, presumably through mobilisation from the floodplain (allochthonous source) and possibly from internal sources such as sediment resuspension. The phytoplankton community became dominated by diatoms/Bacillariophyceae (e.g. centric diatom, *Aulacoseira*) in place of Cyanophyta (Figure 4; Figure 5). Dissolved nutrient concentrations fell rapidly after peak flows, whereas phytoplankton biomass further increased after the flow peak passed (Figure 4). Chlorophyta were moderately abundant at all flows, but increased during the high-flow period. During the high-flow period heterotrophic productivity was also stimulated through mobilisation of organic carbon from the basin, largely from upstream sources. DOC concentrations were typically below 10 mg L^{-1} until the beginning of the high-flow period (20 mg L^{-1}), as floodplain and terrestrially-derived organic carbon entered the river. This shifted the river from a net autotrophic system to a net heterotrophic system.

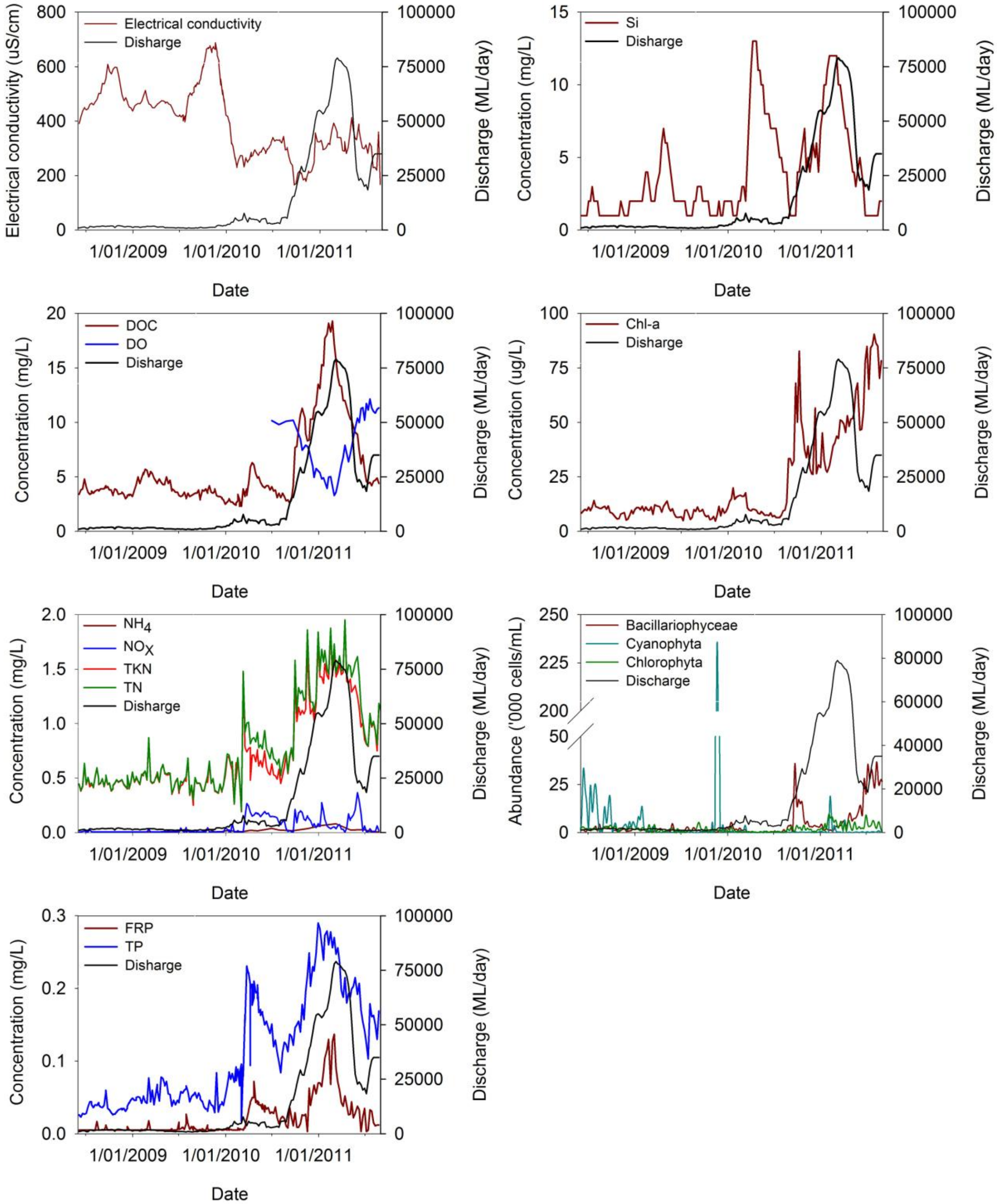

Figure 4. Changes in physico-chemical conditions and phytoplankton communities at Morgan (Figure 1), South Australia during the low-flow (June 2008 to August 2009) and high-flow period (June 2010 to August 2011). Shown are the changes in discharge, electrical conductivity, dissolved organic carbon (DOC), dissolved oxygen (DO) ammonia (NH4), oxidised nitrogen (NOx), total Kjeldahl nitrogen (TKN), total nitrogen (TN), filterable reactive phosphorus (FRP), total phosphorus (TP), chlorophyll a (Chl-a), silica (Si), and selected phytoplankton groups.

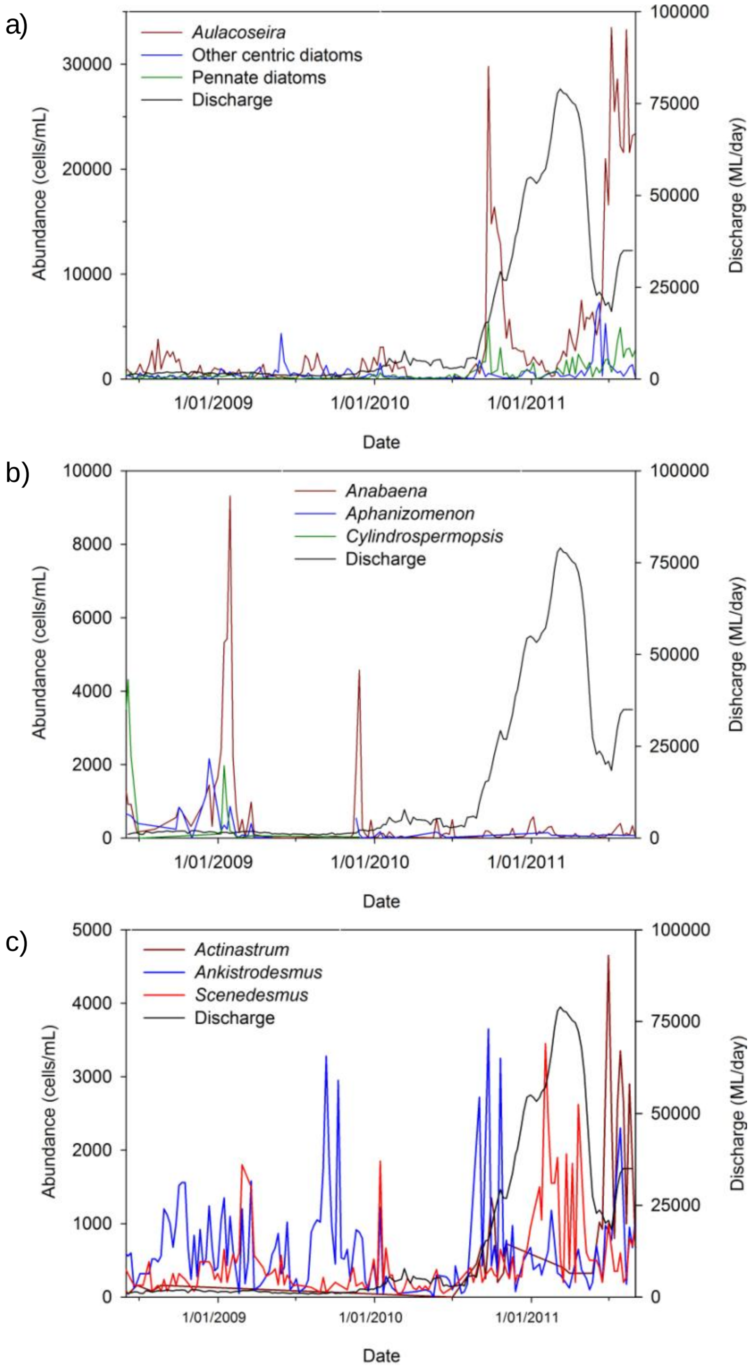

Figure 5. Changes in phytoplankton communities at Morgan (Figure 1), South Australia during the low flow (June 2008 to August 2009) and high-flow period (June 2010 to August 2011). Shown are dominant genera and groups from diatoms (a), Cyanophyta (b) and Chlorophyta (c).

It was clear that both low-flow and high-flow periods present different water quality risks. Extended periods of low flow increase the risk of salinisation, hypoxia and Cyanophyta blooms and the provision of dilution flows to the LRM is required to minimise these risks. Such conditions also result in the accumulation of carbon on the floodplain, increasing the potential for hypoxic conditions (i.e. 'blackwater') upon re-inundation. Reducing the interval between floodplain inundation events may reduce the risk of hypoxic events. Furthermore, given Cyanophyta tend to dominate at low flows, floodplain inundation should accompany 'high flow' because otherwise Cyanophyta may access increased nutrient loads following inundation and thus the risk of nuisance blooms would increase. Cyanophyta are often non-preferred food sources for zooplankton whereas diatoms are considered to be of high nutritional value for higher trophic levels. Provisions of water to the floodplain should be complemented with river flow rates that favour a phytoplankton community dominated by diatoms, particularly during periods of warm, calm conditions. These provisions would have environmental, social and economic benefits.

Organic matter and metabolic activity

Photosynthesis and respiration are the metabolic processes responsible for the formation and breakdown of organic material. The balance between photosynthesis and respiration within the river channel identifies the energy captured and utilised by the aquatic food webs. Environmental conditions can influence river metabolism across a wide range of time scales from sub-daily changes in incident irradiance to inter-annual variations in weather patterns. Less well recorded are the decadal changes in response to extreme environmental conditions such as droughts and floods.

Oliver and Lorenz (2013) measured the rates of photosynthesis in the River Murray channel in response to the 2010/11 flood. Estimates of production and respiration were based on day-night changes in oxygen concentration measured continuously over 24-36 hour periods in the river, and in plankton incubation chambers. Estimates were obtained of gross primary production (GP), community respiration (CR) and net ecosystem production (NP) for the whole channel and for the plankton. The difference between these two provides an estimate of the metabolism associated with non-planktonic sources. Results from the high-flow period were compared to measurements previously recorded periodically along the main channel during periods of within-channel, near bank-full irrigation flows (1998/99 and 2006/07) and during the very low-flow period of the drought (2008/09) (Oliver and Merrick 2006; Oliver and Lorenz 2010). This provided the opportunity to investigate the effects of flow conditions and especially flooding on metabolism (Figure 6).

Prior to the flood, the metabolic rates in the South Australian section of the River Murray were similar to those measured upstream at other sites along the river. In flowing sections the net primary production rates were close to zero. This indicated that systems were largely driven by phytoplankton photosynthesis and the respiratory breakdown of phytoplankton cells. Metabolism was more variable in weir pools in the South Australian section of the river compared to upstream flowing river reaches (Figure 6; Figure 7). Small to moderate negative net primary production values were common indicating that weir pool sites accumulated organic material either from upstream or from their local catchment.

Metabolism changed dramatically in response to the flood. Unexpectedly, planktonic photosynthesis remained similar throughout the flood despite the increased turbidity and water depth reducing the availability of light. In addition, open water gross primary production was larger than planktonic rates suggesting an additional source of photosynthetic production, although the conditions within the river channel were not supportive of photosynthesis (Figure 6). A detailed analysis showed that enhanced photosynthetic production occurred in the shallow waters on the floodplain and was associated with significant increases in phytoplankton biomass, indicated by chlorophyll-a measurements (MDBA) of river samples peaking at 85 mg m^{-3}. Evidently phytoplankton growing in the flood waters made a substantial contribution to the organic carbon load returning to the river. Further analyses indicated that in the South Australian section of the River Murray, the two large floodplain areas of Chowilla and Barmera were major sites for enhanced phytoplankton photosynthetic production, with little contribution from other surrounding floodplains (Figure 8).

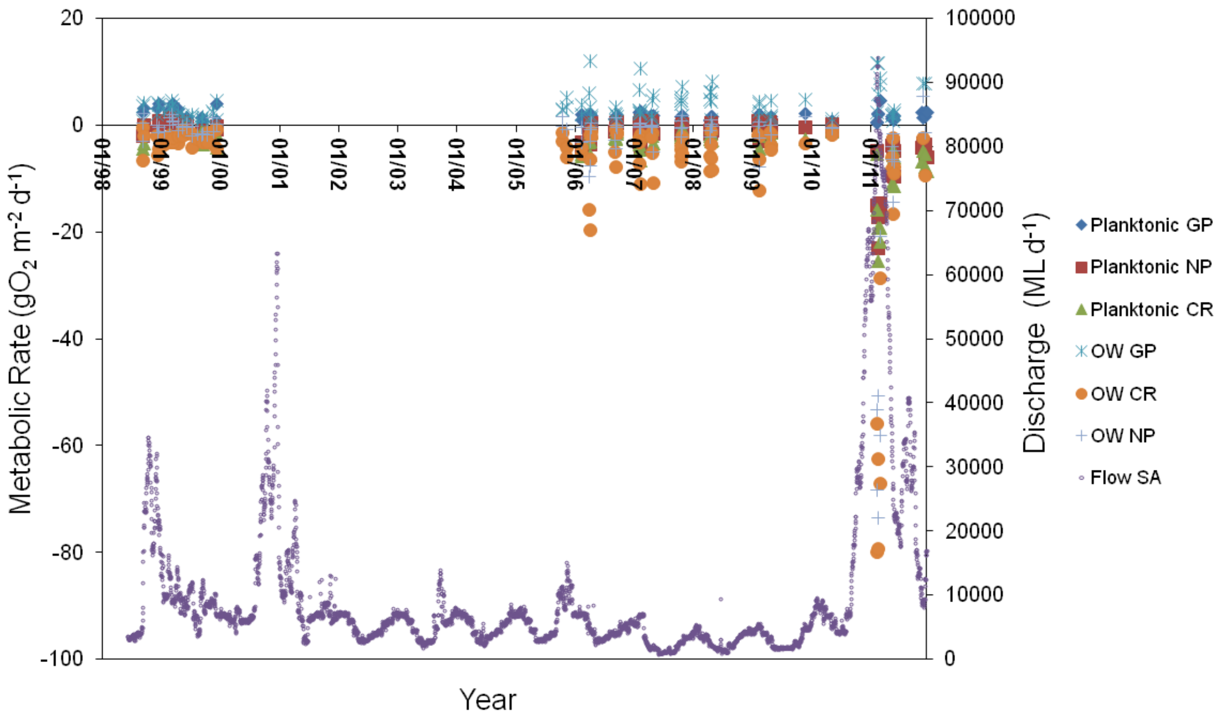

Figure 6. Areal rates of gross photosynthesis (GP), community respiration (CR) and net production (NP) for the open water (OW) of the river channel and for the plankton at all sampling sites and times along the River Murray measured during different hydrological conditions, indicated here by the flow to South Australia. Note: measurements for 1998/99 were only taken from sites upstream of the South Australian section of the river.

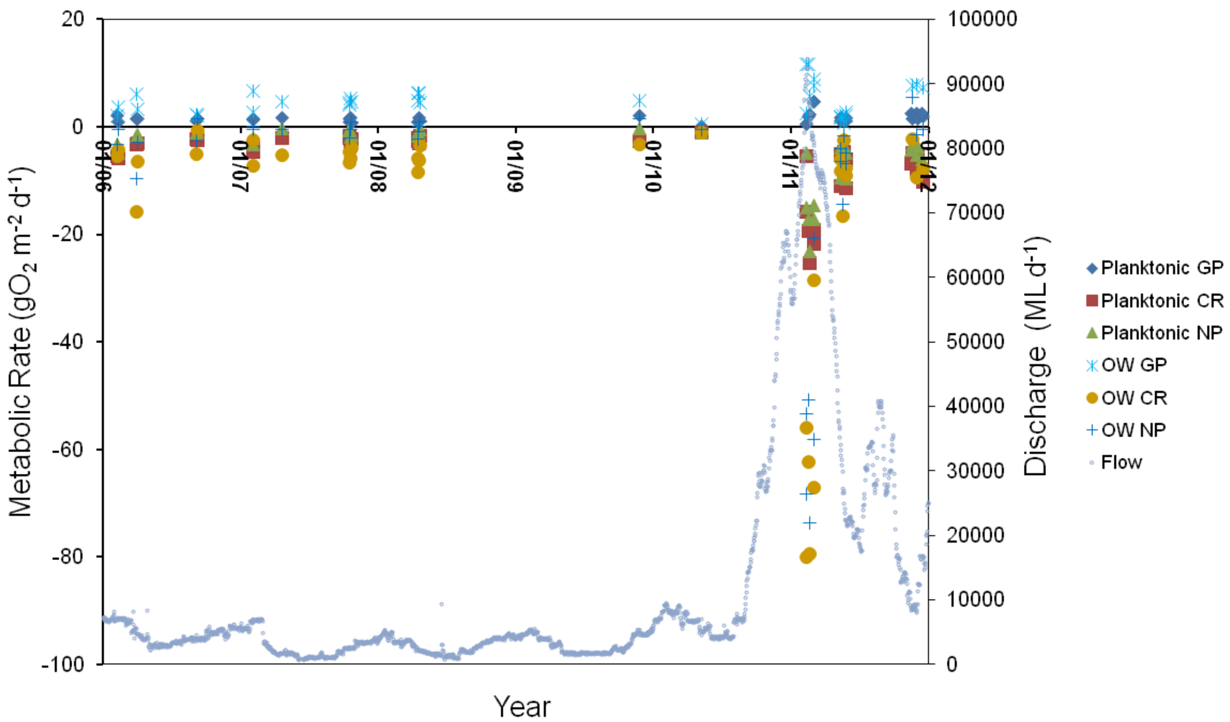

Figure 7. Areal rates of gross photosynthesis (GP), community respiration (CR) and net production (NP) for the open water (OW) of the river channel and for the plankton at sampling sites and times along the River Murray in South Australia extracted from Figure 6.

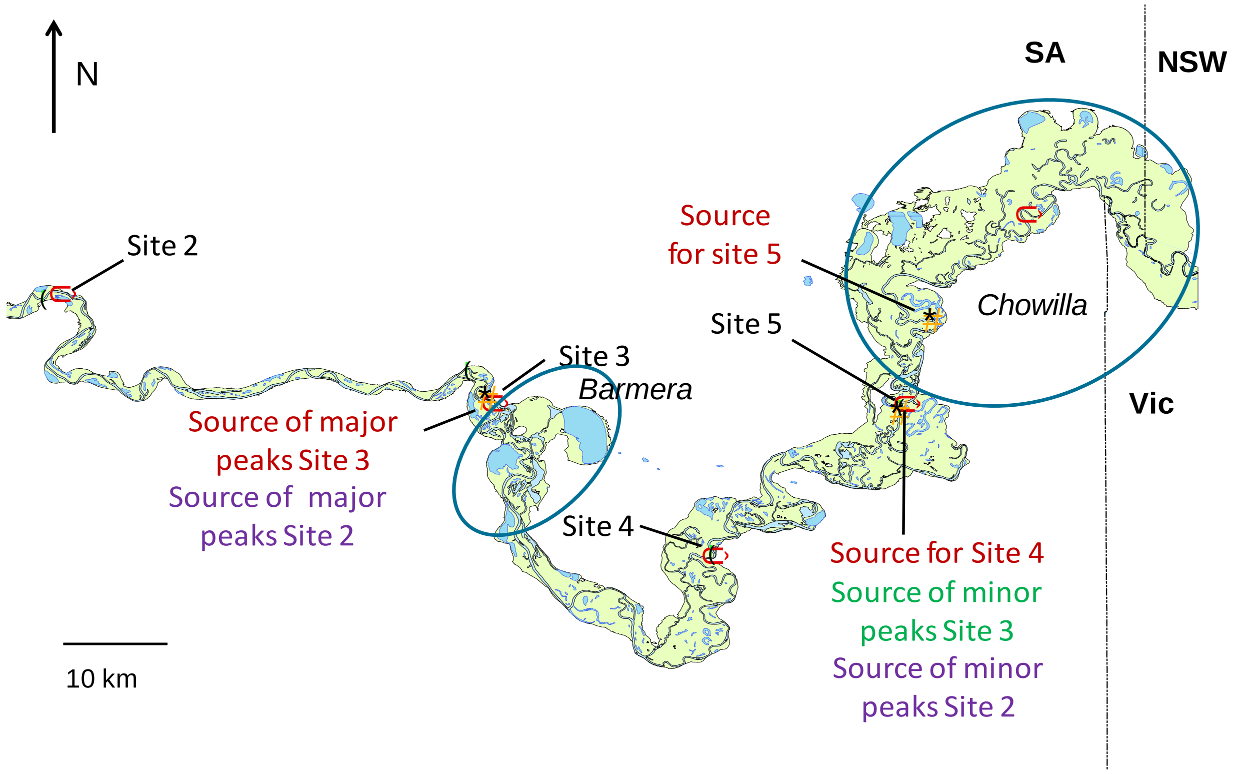

Figure 8. Floodplain areas responsible for major metabolic activity observed in the river channel during the 2010/11 flood. Shown are the source locations for major and minor production peaks observed travelling along the River Murray at sampling sites 2, 3, 4 and 5 during the flood. The floodplain area is depicted as the extent of the 1956 flood.

As expected, there were large increases in respiration rates associated with the flooding of terrestrial organic carbon reserves that had accumulated on the floodplain during the previous drought period (Howitt *et al.* 2007). Reduced oxygen concentrations that occur in rivers during floods are often attributed to the respiratory metabolism of organic material transported from the floodplain back into the channel. In this case the majority (70%) of the river channel respiration was attributed to non-planktonic sources suggesting two possible processes. Respiratory reduction in oxygen could have been due to the metabolism of organic material transported from the floodplain and sedimenting within the river channel, or alternatively due to a large, respiratory activity on the floodplain causing oxygen drawdown in water moving across the floodplain and returning to the river. Analyses of the oxygen time series again highlighted the important role of the Chowilla and Barmera floodplains. These appear to be major sites of oxygen depletion due to heterotrophic transformation of organic material into microbial biota, which in addition to the autotrophic phytoplankton production, further enhances food supplies to the river. This interpretation of floodplain heterotrophic activity is supported by observations of very large numbers of zooplankton growing in the floodplain waters (Deborah Furst, pers. comm.).

Following the major flood, the rates of metabolism declined to levels similar to those observed prior to the flood. There were slightly increased respiration rates that suggested a small store of residual organic carbon had been transported into the river by the flood, but this was not the substantive store that had been expected. It appears that the flood did not result in a long term reserve of organic carbon in the river channel. The results of this study confirm that floods are an important source of organic material to the river, some of this being of terrestrial origin and some generated within the flood waters by the growth of photosynthetic micro-organisms. Both of these sources of organic material provide food for heterotrophic micro-organisms through the microbial loop and through the classic food chain of herbivores, carnivores, and decomposers. It is considered that the mix of organic materials supplied and their utilisation within the food web play an important role in determining the total biomass of secondary producers that can be supported, and the characteristics of the trophic links that underpin community structure and diversity. Important to the management of these interactions, this study has shown that the Chowilla and Barmera floodplains are critical floodplain areas with major effects in the South Australian section of the River Murray. In part this influence is related to the area of floodplain inundated, but is also likely to be affected by the degree of connectivity to the river, and by the floodplain geomorphology which determines the flow routes and transit times of the flood waters. Critical to the growth of organisms in the flood waters is the characteristics of the flow patterns including flood duration and extent. These are also important characteristics for enabling access to the floodplain food resources by higher organisms. Understanding these interactions can help managers set flow and water quality targets for sustaining food webs of suitable composition to provide food resources to populations of fish and waterbirds that are of direct concern to the public. Overall the results highlight the importance of the dynamic connection between the river and floodplain and especially the role of particular floodplain areas.

Fish ecological responses to flooding

Flow is the overarching driver of riverine ecosystem structure and function (Poff and Allan 1995; Sparks *et al.* 1998), influencing the distribution and abundance of aquatic biota, including fish. In the MDB, there has been a significant decline in native fish populations, primarily attributed to the effects of river regulation and alteration of the natural flow regime (Cadwallader 1978; Gehrke *et al.* 1995; Thorncraft and Harris 2000; Humphries *et al.* 2002; MDBC 2004). Importantly, flow can directly and indirectly influence the distribution, abundance and population demographics of fish. Indeed, spawning of some native fish species (e.g. golden perch, *Macquaria ambigua ambigua*) is directly stimulated by changes in flow (Mackay 1973; King *et al.* 2009), whereas flow may indirectly influence the recruitment of others (e.g. Murray cod, *Maccullochella peelii*) (Ye and Zampatti 2007; King *et al.* 2009). Elevated flows may also facilitate fish movement (Reynolds 1983) and dispersal (Humphries *et al.* 1999; Dudley and Platania 2007). Changes in flow can lead to habitat modification, including changes in microhabitat structure, hydraulic conditions and water level (Bunn and Arthington 2003), and affect habitat availability through inundation and changes in longitudinal and lateral connectivity (Junk *et al.* 1989). Furthermore, flow-driven changes in productivity may influence food availability (Poff *et al.* 1997). All these factors influence the population dynamics of fish.

Understanding the response of fish (e.g. spawning, recruitment, abundance, movement, distribution and habitat use) to changes in flow regimes is vital to underpin the conservation and sustainable management of fish populations, particularly through environmental flow delivery. Summaries of the responses of fish to the direct and indirect effects of flooding in the LRM in 2010/11 from Cheshire *et al*. (2012), Zampatti and Leigh (2013b), Leigh and Zampatti (2013), Bice *et al.* (2014) and Thwaites and Fredberg (2014) are presented below.

Variations in larval fish assemblages

Larval abundances can be used as a useful indicator of spawning for fish species. Small-bodied fish species (e.g. Australian smelt, *Retropinna semoni*; carp gudgeon complex, *Hypseleotris spp*.; and flathead gudgeon, *Philypnodon grandiceps*) will spawn under a variety of flow conditions in the MDB (Humphries *et al.* 1999), while large-bodied flow-cued spawners (i.e. golden perch and silver perch, *Bidyanus bidyanus*) are considered to require increased discharge to initiate spawning (Humphries *et al.* 1999; King *et al.* 2009).

Cheshire *et al.* (2012) investigated assemblages of native and alien fish larvae (as an indicator of spawning) in the main channel of the LRM during the 2010 flood. Larval fish were sampled using plankton tows in spring/summer (peak spawning periods) in the gorge and floodplain geomorphic regions of the LRM, at Lock 1 and 6, respectively (Figure 1). Larval assemblages during over bank floods (~25,000–68,000 ML day^{-1}) in 2010 were compared to two other distinct hydrological periods: 1) in 2005 under a within-channel flow pulse (peak of ~13,500 ML day^{-1}) and water level rising; and 2) in 2006, 2007 and 2008 during a drought with very low regulated flows (<7,000 ML day^{-1}) and stable water levels. Data from low-flow periods were obtained from previous studies conducted by (Cheshire and Ye 2008; Bucater *et al.* 2009; Cheshire 2010). The aim of this study was to determine if there were annual differences in larval fish assemblages, and whether these differences could be correlated to changes in hydrology and other key environmental variables. Data were analysed for annual, spatial and seasonal variations and correlations were identified between changes in larval assemblages and the environmental variables of discharge, water level, conductivity and temperature.

The larvae of eleven fish species (nine native and two exotic) were collected in this study. Larvae of several small- to medium-bodied fish species: Australian smelt, bony herring (*Nematalosa erebi*), carp gudgeon, and flathead and dwarf flathead gudgeons (*Philypnodon spp.*) were abundant and collected in all years. Larvae of flow-cued spawners: golden perch and silver perch were only collected during a small within channel low pulse in 2005 (~13,500 ML day^{-1}) and the flood in 2010 (>50,000 ML day^{-1}).

Larval fish assemblages differed among years, sites and trips, but not in a uniform manner. The 2010 assemblage was most strongly characterised by golden perch, silver perch and Murray cod larvae and the presence of golden perch and/or silver perch eggs and newly hatched larvae ('hatchlings'). Assemblages in 2010 (flood year) and 2005 (within-channel flow pulse) were more similar due to the presence of golden perch, silver perch and higher relative abundances of Murray cod larvae, compared to low-flow years (2006, 2007 and 2008) (Figure 9; Figure 10). Changes in larval abundances were significantly correlated to hydrology and environmental variables, with most variation explained by water discharge and water level, conductivity (weak) and temperature (Figure 10). Temperature correlations likely reflected seasonal differences in spawning of individual species.

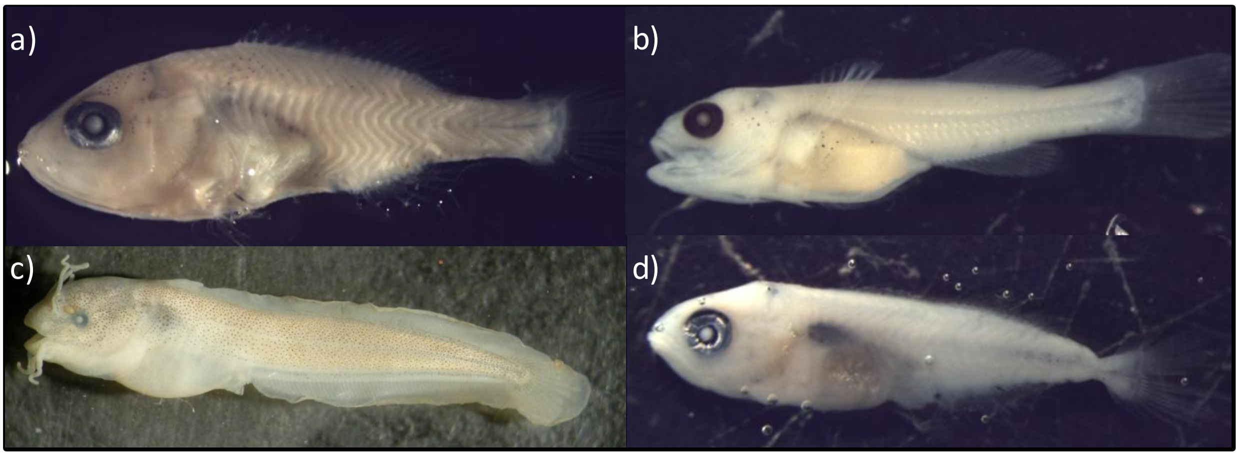

Figure 9. Large-bodied native fish larvae: (a) golden perch, (b) Murray cod, (c) freshwater catfish and (d) silver perch.

While a number of small- to medium-bodied fish species will spawn and their larvae develop during low-flows (<7,000 ML day^{-1}) in the weir pools of the LRM, for golden perch and silver perch, prolonged low-flow conditions will likely pose a significant threat to populations. Environmental water planning and flow management should aim to provide flow conditions that support the critical life history processes (spawning and recruitment) of these large-bodied species. Restoring a more natural flow regime and connectivity throughout the MDB is integral to maintain and rehabilitate native fish populations.

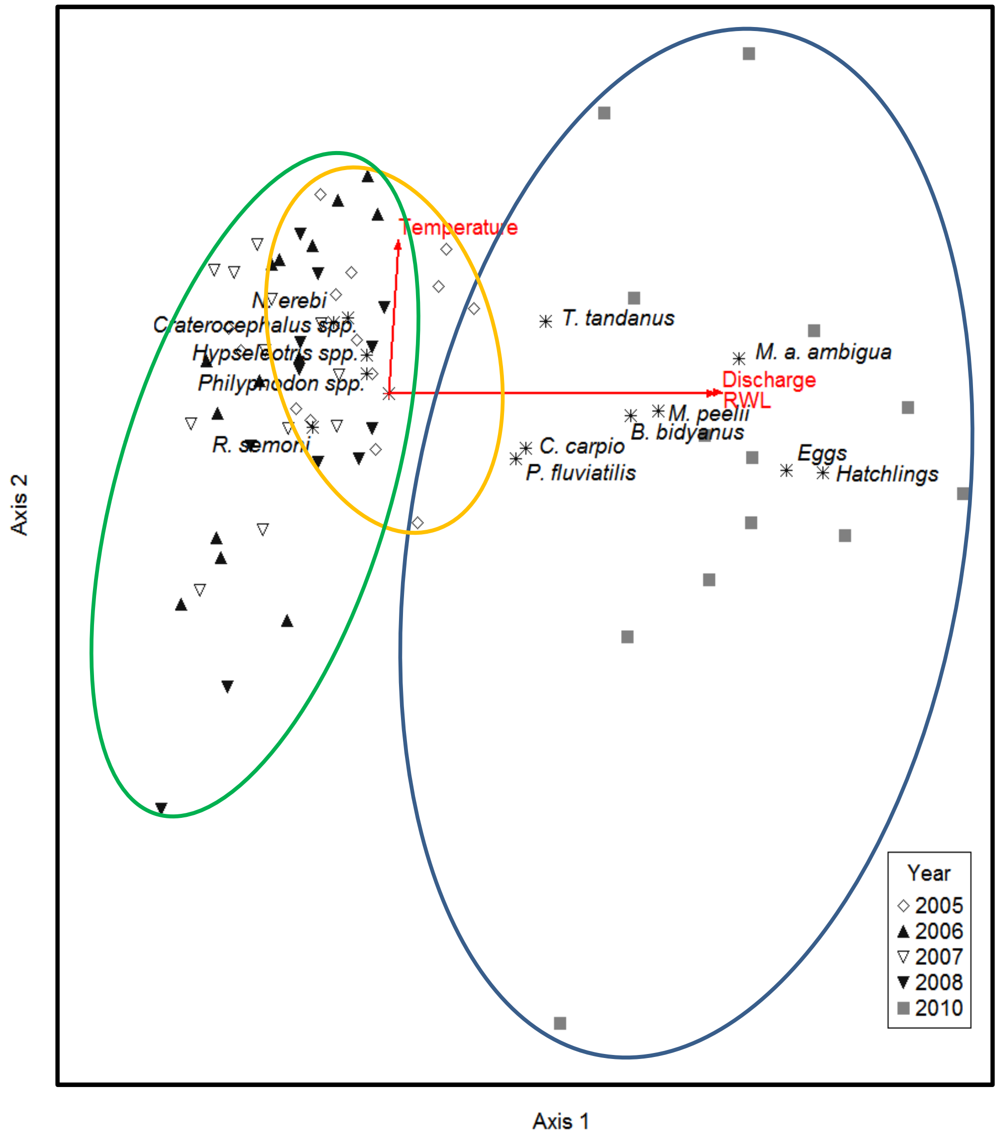

Figure 10. NMS ordination (stress 0.14) showing the annual separation of the larval assemblages, during 2010 from 2005, 2006, 2007 and 2008. Note that sites and trips are not distinguished. Correlations for species (*) and environmental variables (->) are overlaid; vectors indicate strength of correlation with axes. RWL = relative water level. Data from 2010 (>25,000 ML day^{-1}) are grouped by a blue band, 2005 (7,000–13,500 ML day^{-1}) by a yellow band and years 2006, 2007 and 2008 (<7,000 ML day^{-1}) are grouped by a green band. Fish species are *N. erebi* = bony herring, *Craterocephalus* spp. = Unspecked hardyhead and/or Murray hardyhead, *Hypseleotris* spp. = carp gudgeon complex, *Philypnodon spp.* = flathead gudgeon and/or dwarf flathead gudgeon, *R. semoni* = Australian smelt, *T. tandanus* = freshwater catfish, *M. a. ambigua* = golden perch, *M. peelii* = Murray cod, *B. bidyanus* = silver perch, *C. carpio* = common carp, *P. fluviatilis* = redfin perch. Hatchlings refer to newly-hatched golden perch and/or silver perch larvae. Eggs refer to golden perch and/or silver perch eggs.

Golden perch recruitment and abundance

Golden perch is a widespread, large-bodied potamodromous fish species that is of high recreational and commercial significance in the MDB. This species is one of only two native fish species in the MDB, along with silver perch, that is considered to require increased flow to initiate spawning (Humphries *et al.* 1999). Enhanced recruitment in golden perch has been linked to both within-channel increases in flow (Mallen-Cooper and Stuart 2003; King *et al.* 2005; Zampatti and Leigh 2013a) and flooding (King *et al.* 2009).

After extensive flooding (>90,000 ML day^{-1}) in the LRM during 2010/11, the recruitment response of golden perch, following 10 years of drought and floodplain isolation, was investigated by Zampatti and

Leigh (2013b). Golden perch was collected, using quantitative electrofishing surveys, from sites throughout the LRM (total of 128 sites) (see Zampatti and Leigh 2013b). Spatial variation in recruitment was investigated by comparing the age structure of golden perch in the swamplands/lakes, gorge and floodplain geomorphic regions (Figure 1). Furthermore, annual variation in golden perch abundance and recruitment were investigated in anabranch and main channel habitats at Chowilla in the floodplain geomorphic region over a 7-year period incorporating the flood and 6 years of in-channel flow.

Following extensive flooding in 2010/11, abundance of golden perch in the Chowilla region was significantly (5–6 times) greater during 2011 than all previous low-flow years (Figure 11); whilst there were no significant differences in abundance between low-flow years 2005–2010. Age structures indicated that increased abundance was due predominantly to fish spawned during the flood (2010/11) and the previous year (2009/10) (Figure 12), which was characterised by low in-channel flows (5,000–10,000 ML day^{-1}). It is possible that this 2009/10 cohort originated in the lower Darling River and was transported downstream to the LRM by larval drift or juvenile movement. Age structure was similar in the nearby Katarapko anabranch system indicating a uniform post-flood recruitment response in the floodplain geomorphic region.

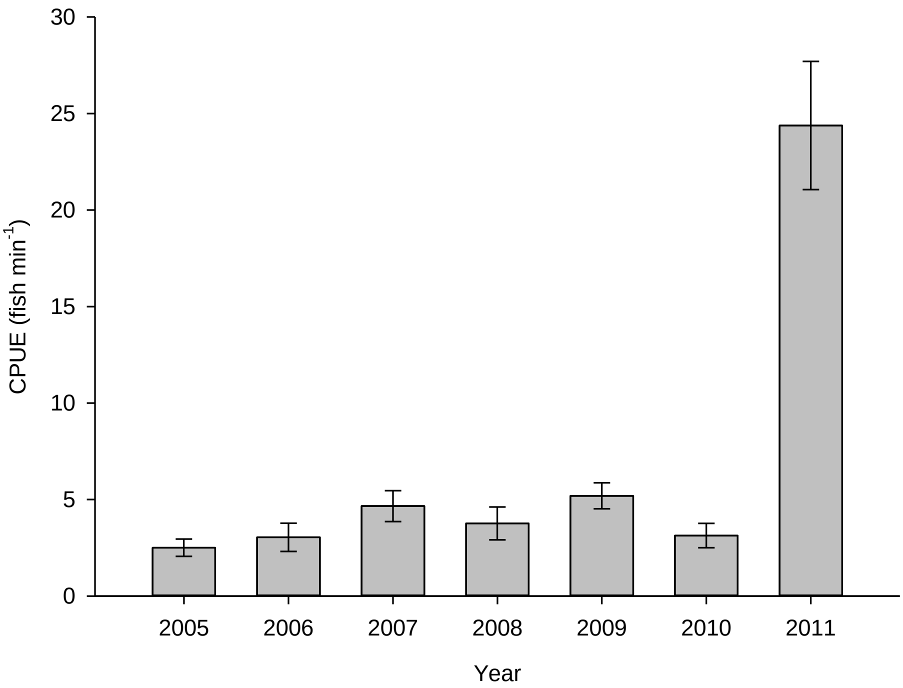

Figure 11. Mean (±S.E.) catch-per-unit-effort (fish min^{-1}) of golden perch collected annually from 2005–2011 at all sites in the Chowilla Anabranch system and adjacent River Murray.

Age structures collected prior to flooding (2005–2010) indicated episodic recruitment with strong cohorts spawned in 1996, 1998, 2000 and 2005 and little or no recruitment in intervening years. These dominant cohorts were spawned in association with overbank floods (1996 and 2000) or increases in flow contained within the river channel (1998 and 2005) (Zampatti and Leigh 2013a). Comparisons of size and age composition of golden perch between different geomorphic regions showed that the floodplain region was made up of younger fish (1+, 2+ and 6+ year olds) compared to the gorge and swampland/lakes regions, where 11- and 15-year old fish dominated age structures (Figure 12). Additionally, juvenile golden perch from the 2010/11 and 2009/10 cohorts were less apparent in the gorge and swamplands/lakes regions.

This study supports the notion that golden perch have flexible life histories and will spawn and recruit in conjunction with in-channel rises in flow and overbank flows, but significant increases in abundance in the LRM may result from overbank flooding. Contemporary approaches to flow restoration in the MDB emphasise overbank flows and floodplain processes. Zampatti and Leigh (2013b) suggest, however, that environmental flow management that incorporates floodplain and in-channel processes, at spatio-temporal scales concordant with life history processes (e.g. river scale), will result in more robust populations of golden perch.

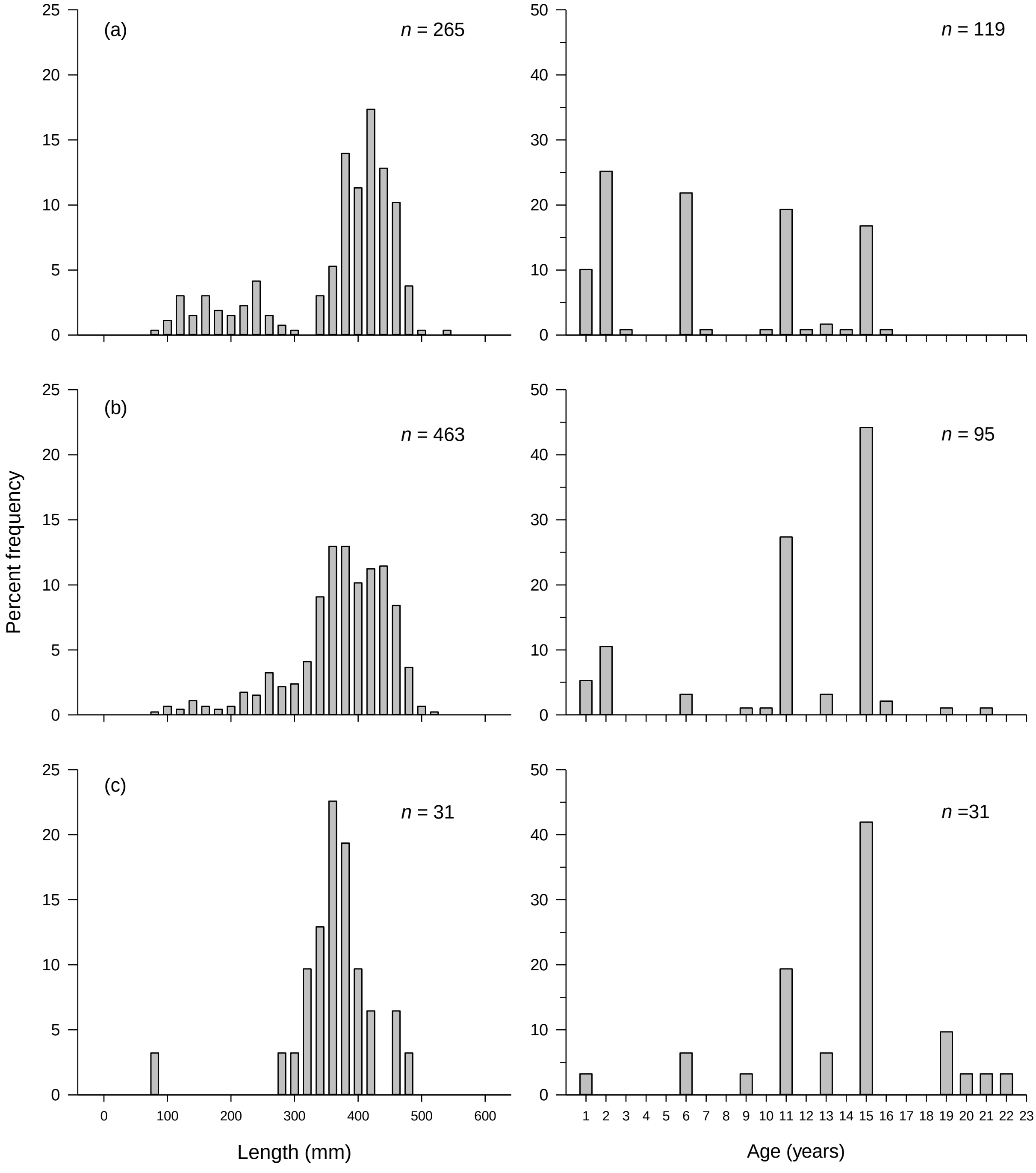

Figure 12. Length (left column) and age (right column) structure of golden perch collected from the lower River Murray in Nov/Dec 2011: a) floodplain section, b) gorge section, c) swamplands and lakes.

Movement and mortality of Murray cod

Murray cod is the largest freshwater fish in the MDB and is considered Critically Endangered by the International Union for the Conservation of Nature (IUCN). Conservation and restoration of Murray cod populations relies on a robust understanding of its life history, including movement patterns and habitat use.

Leigh and Zampatti (2013) used radio-transmitters and passive integrated transponder (PIT) tags to investigate the movement of 36 Murray cod during the 2010/11 flood and associated hypoxic blackwater event in the LRM, including the Chowilla Anabranch system. Murray cod (mean TL ± S.D. = 827 ± 206 mm) that were tagged between October 2007 and January 2009 were actively (manually by boat and aircraft) and passively (remote loggers and fishways) tracked between November 2010 and April 2011.

Fourteen radio-tagged Murray cod (~39%) exhibited high fidelity to the Chowilla system. Half of these fish undertook localised small-scale (<2 km) movements, whilst the other half undertook broader movements (2–10 km) within the Chowilla system. A large proportion of cod (45%, n=16) moved between the Chowilla system and the River Murray main channel (2–40 km) and six cod (17%) moved greater than 50 km, typically in an upstream direction. These large scale movements (>50 km) generally occurred prior to the peak of the flood in February 2011 (Figure 13). The greatest total linear range moved by a cod was 212.8 km by a 985 mm TL female from the Chowilla system to Lock 10 (Wentworth). Murray cod that undertook small-scale localised movements were significantly smaller (mean TL ± S.E: 674 ± 77 mm) than those undertaking broad-scale movements (1017 ± 54 mm TL). There were no significant differences in sizes for other movement types.

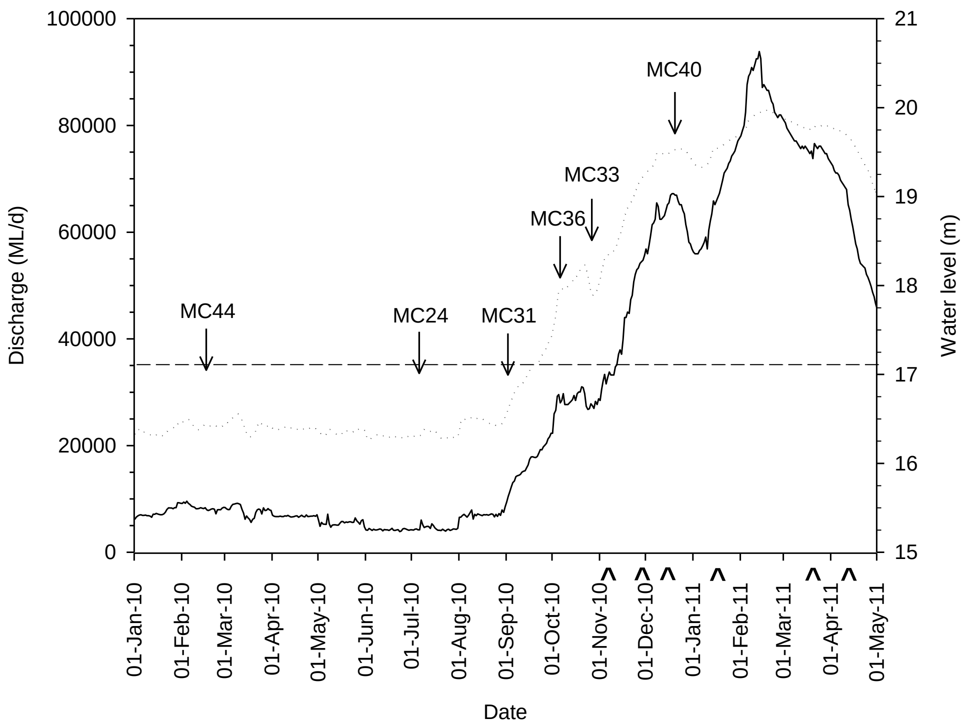

Figure 13. Timing of movement out of the Chowilla system for Murray cod undertaking large-scale movements (>50 km) plotted with River Murray discharge (ML day^{-1}) measured at the South Australian border (black line) and water level (m) in the River Murray main channel downstream Lock No. 6 (dotted line) from January 2010 – May 2011. Horizontal dashed line indicates approximate bankfull discharge in the vicinity of Chowilla of ~35,000 ML day^{-1}, ^ denotes timing of manual tracking events.

During the flood, flow peaked at ~93,000 ML day^{-1} and dissolved oxygen decreased to 1.2 mg L^{-1}. Mortality of radio-tagged Murray cod was considerable (25%) in association with low dissolved oxygen concentrations. This indicated that hypoxic blackwater may have had a substantial impact on Murray cod populations in the LRM. Radio tagged cod that emitted mortality signals were significantly larger (961 ± 54 mm TL) than those with active transmitters (783 ± 39 mm TL), suggesting a greater effect of hypoxic blackwater on larger cod, potentially due to higher oxygen demands.

This study incorporated the Murray cod spawning season, a flood following 10 years of low flows and a hypoxic blackwater event. Long-distance migrations may reflect movement in response to each of these stimuli, but further research is required to explain the specific purpose of long-distance migrations of cod in the LRM. The Chowilla system contains hydraulic and physical habitats similar to those in unregulated reaches of the River Murray. Cod undertaking movements in the Chowilla system generally followed the same route, moving between fast-flowing mesohabitats with abundant coarse woody debris. From a meso-habitat perspective throughout the study Murray cod were consistently located in the River Murray main channel or in permanent anabranches, suggesting use of floodplain habitats is limited and highlighting the importance of connectivity between perennial off-channel and main-channel habitats.

Fish–habitat associations in the main channel of the LRM

Flow variability is the overarching driver of riverine fish assemblage structure (Poff and Allan 1995). Flow variability affects fish assemblage structure directly, by influencing critical life history processes including migration, spawning and recruitment (Welcomme 1985; Junk *et al.* 1989; King *et al.* 2009), and indirectly, by influencing hydraulics and channel morphology, the distribution of aquatic vegetation and structural elements (e.g. in-stream wood), and subsequently habitat availability (Nestler *et al.* 2012). An understanding of the mechanistic influence of flow variability on fish assemblage structure is imperative to inform future environmental water delivery and ecologically sound operation of river infrastructure.

Bice *et al.* (2014) investigated spatio-temporal variation in fish assemblage structure, microhabitat cover and fish-habitat associations in the main channel (gorge and floodplain geomorphic regions) of the LRM (Figure 1) in 2008 during a prolonged period of low within-channel flows and in 2012 following the high-flow event and flood. See Bice *et al.* (2014) for a more detailed description of methodology.

In general, species richness and total abundances were greater in 2008 compared to 2012. Fish assemblages were significantly different between 2008 and 2012 for both floodplain and gorge geomorphic regions. This was primarily driven by the absence or reduced abundances of small-bodied species (e.g. unspecked hardyhead, *Craterocephalus stercusmuscarum fulvus* and Murray rainbowfish, *Melanotaenia fluviatilis*) in both regions and an increase in large-bodied species (e.g. golden perch) in the gorge region in 2012 (Figure 14).

Microhabitat cover differed between 2008 and 2012 for both floodplain and gorge regions. A greater number of microhabitats were present in both regions of the LRM in 2012, and the composition of microhabitat cover changed considerably. Notably, submerged vegetation (e.g. *Myriophyllum verrucosum*) was absent in 2012 and there were increases in the cover of emergent, amphibious (e.g. *Duma florulenta*), floodplain (e.g. *Eucalyptus camaldulensis*) and terrestrial taxa (e.g. *Stemodia florulenta*) (Figure 15). Changes in discharge and increases in water velocities, water level and potentially turbidity following high flow and flooding likely resulted in the loss of submerged macrophytes.

Whilst no fish–habitat associations (positive or negative) were found to be consistent between years in either region, several small-bodied species (e.g. carp gudgeon) were significantly associated with submerged macrophytes in 2008. Bice *et al.* (2014) suggest that a loss of submerged macrophytes and re-structuring of macrophyte cover and distribution following increased flow in part led to the absence or reduced abundance of small-bodied fish species in the main channel. Increased inundation and access to off-channel wetland and floodplain habitats may have resulted in lateral movement of small-bodied fish into these newly inundated habitats. Large-bodied species that are cued to spawn by increases in flow (e.g. golden perch) or spawn and recruit in inundated floodplain habitats (e.g. common carp, *Cyprinus carpio*), exhibited flexible microhabitat use. Increases in the abundance of these large-bodied species (e.g. golden perch and common carp) appeared largely dictated by the direct influence of flow on critical life history processes (i.e. spawning and recruitment) and not changes in microhabitat.

Microhabitat cover did not vary significantly between regions in 2012, unlike 2008. Whilst patterns in fish abundances were significantly different between regions for 2008 and 2012, they were more similar between regions in 2012; when abundances of small-bodied species decreased in abundance and large-bodied species increased across both regions. This highlights the large spatial scale at which the high-flow event in 2010/11 influenced biotic patterns in the LRM and suggests a level of longitudinal homogenisation following high flow. Contrastingly, under low-flow conditions and limited connectivity, microhabitat and fish assemblage structure within the two geomorphic regions of the LRM may be more influenced by local abiotic (e.g. turbidity and salinity) and biological factors (e.g. seed bank composition, predation and competition). The influence of local factors under low-flow conditions could thus lead to divergence of biotic patterns between the disparate geomorphic regions.

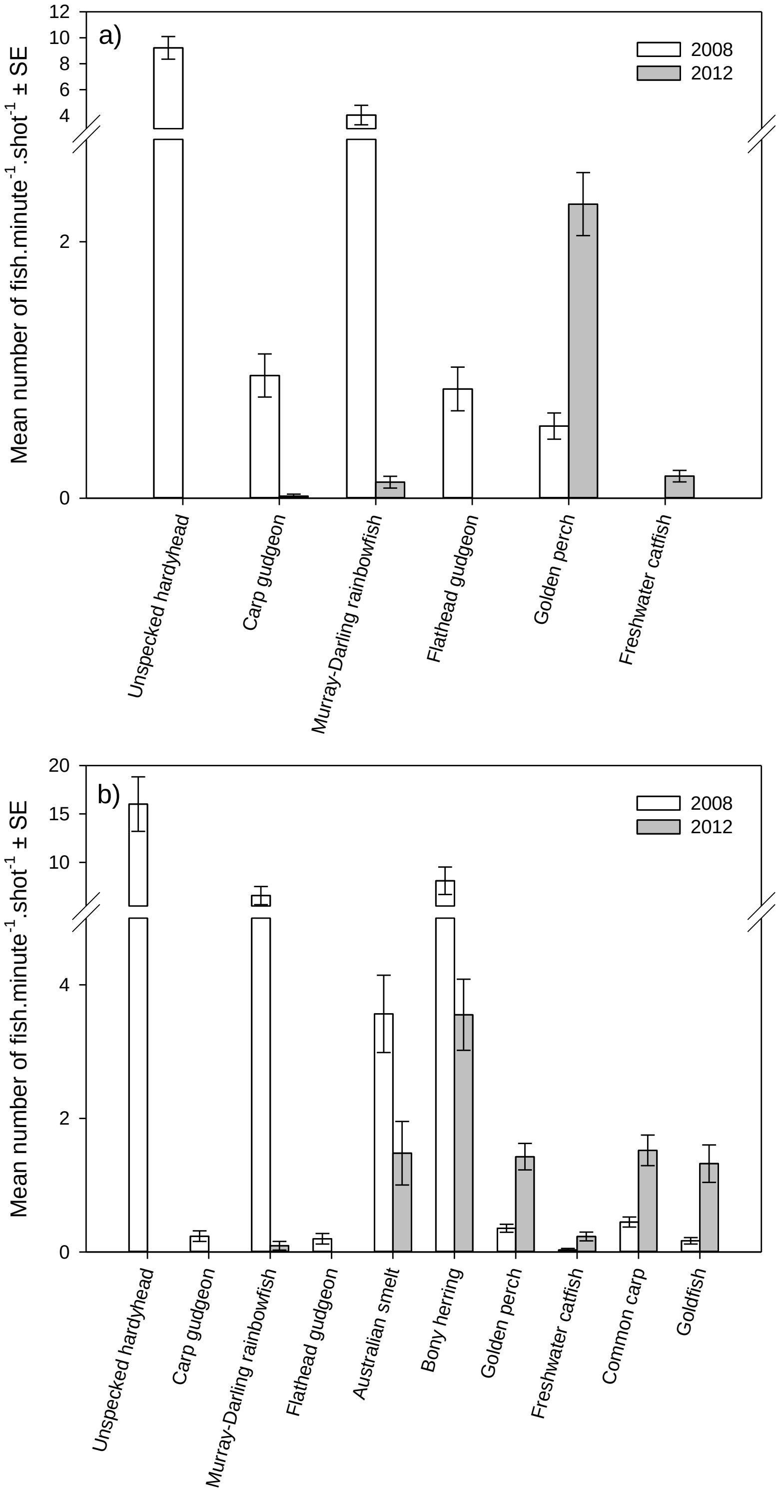

Figure 14. Relative abundance (mean number fish.minute of electrofishing^{-1}.shot^{-1} ± S.E.) of fish species determined to contribute to differences in fish assemblage structure by SIMPER or deemed significant indicators of fish assemblages in the a) gorge and b) floodplain geomorphic region of the lower River Murray in 2008 and 2012.

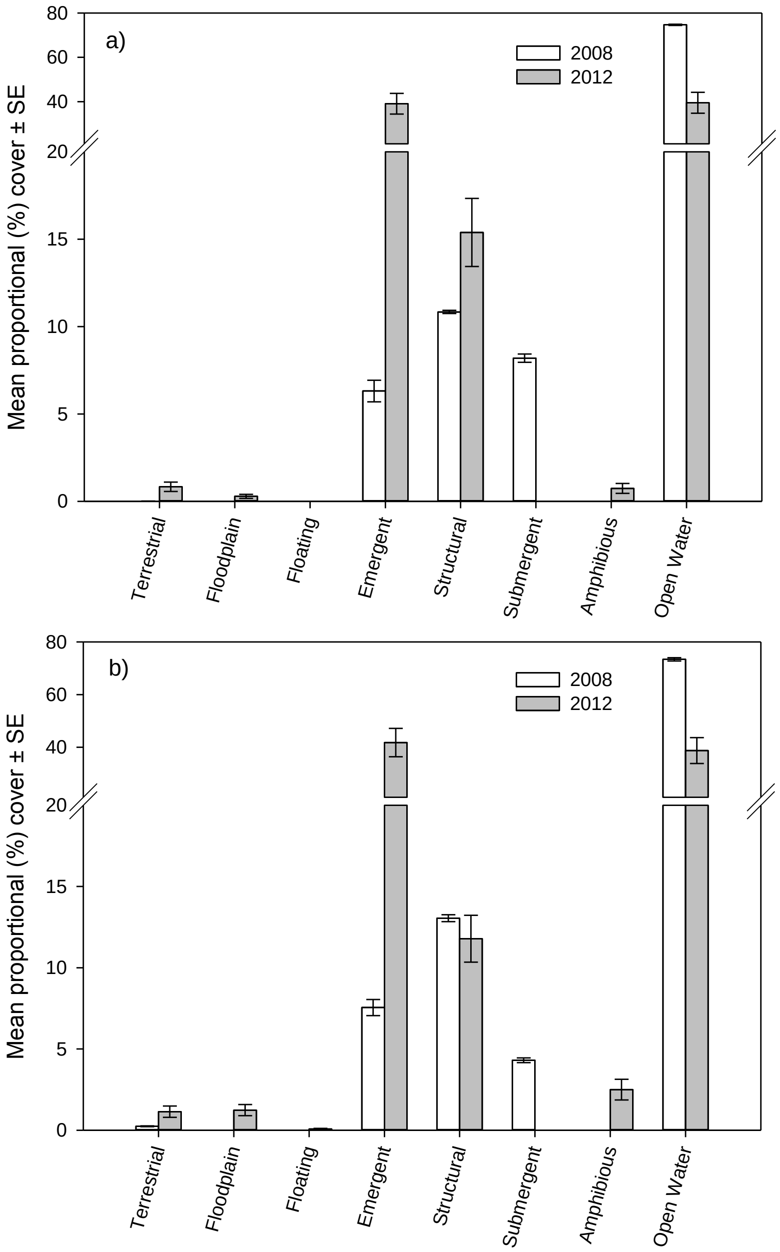

Figure 15. Mean proportional (%) cover ± S.E. of different microhabitat functional groups in a) the gorge and b) the floodplain geomorphic regions of the lower River Murray in 2008 and 2012.

Response of fish in wetlands

Wetland fish assemblages in the LRM are diverse and often include a large proportion of fish species with conservation significance (MDBA 2014). Thwaites and Fredberg (2014) compared the autumn 2012 post-flood fish assemblages at 12 selected wetlands (Floodplain=3, Gorge =5, Swamplands=3, Lower Lakes=1) in the LRM (Figure 1) with before-flood autumn data from surveys which were conducted in either 2005 or 2006 (Smith 2006). See Thwaites and Fredburg (2014) for wetland-specific information. This project aimed to build on previous and current research to determine the response patterns of various fish species from drought to flooding, focusing on the role that drying and re-wetting may have for a range of fish species (i.e. native vs. exotics, large-bodied vs. small-bodied).

A total of 17 species, including 12 native species and 5 invasive species, were captured during 2012 using a combination of gill nets, fyke nets and bait traps (Table 2). Carp gudgeon and bony herring were the most abundant native species, while common carp and eastern gambusia (*Gambusia holbrooki*) were the most abundant invasive species (Table 2).

Table 2. Catch summary of species and number of fish sampled in all wetlands during autumn (all gear types combined), before floods (2005/06) and post floods (2012). Similar sampling effort was applied before and post floods. Note that specific wetlands were sampled in either 2005 or 2006 for pre-flood data (Smith 2006). Refer to Thwaites and Fredburg (2014) for more information on sampling effort and wetlands sampled.

	Species		**Counts**	
	Common name	**Scientific name**	**2005/2006**	**2012**
Native	Australian smelt	*Retropinna semoni*	262	19
	Bluespot goby	*Pseudogobius olorum*	1	0
	Bony herring	*Nematolosa erebi*	1,028	695
	Carp gudgeon	*Hypseleotris* spp.	1,700	816
	Common galaxias	*Galaxias maculatus*	58	2
	Congolli	*Pseudaphritis urvilli*	0	10
	Dwarf flathead gudgeon	*Philypnodon macrostomus*	42	2
	Flathead gudgeon	*Philypnodon grandiceps*	910	172
	Freshwater catfish	*Tandanus tandanus*	3	2
	Golden perch	*Macquaria ambigua*	47	48
	Lagoon goby	*Tasmanogobius lasti*	159	0
	Murray hardyhead	*Craterocephalus fluviatilis*	7	0
	Murray-Darling rainbowfish	*Melanotaenia fluviatilis*	197	3
	Sandy sprat	*Hyperlophus vittatus*	1	0
	Silver perch	*Bidyanus bidyanus*	0	1
	Smallmouthed hardyhead	*Atherinosoma microstoma*	5	0
	Southern pygmy perch	*Nannoperca australis*	2	0
	Un-specked hardyhead	*Craterocephalus stercusmuscarum fulvus*	401	98
Exotic	Common carp	*Cyprinus carpio*	196	1,501
	Eastern gambusia	*Gambusia holbrooki*	1,485	1,141
	Goldfish	*Carassius auratus*	51	97
	Redfin perch	*Perca fluviatilis*	16	45
	Tench	*Tinca tinca*	0	1
	Total number of fish		**6,571**	**4,653**
	Count of species		**20**	**17**
	Overall number of fish		**11,224**	
	Overall number of species		**23**	

In comparison with 2005/06, there was a decrease in the total number of species collected and in total abundance of fish in 2012. There was also a change in the relative proportions of native and invasive species between years. Of the twelve wetlands sampled in 2005/06 and 2012, six shifted from a native-dominated fish assemblage in 2005/06 to an invasive-dominated assemblage in 2012. This overall change in the fish assemblage was driven by a decrease in the relative abundance of the native species carp gudgeon and flathead gudgeon (*Philypnodon grandiceps*) and the invasive species eastern gambusia and an increase in the relative abundance of the invasive species common carp. Bony herring showed no consistent pattern of change between 2005/06 and 2012. This species increased in abundance in some wetlands and decreased significantly in others likely reflecting high mobility, pelagic schooling behaviour and local differences in hydrology and habitat.

Bice *et al.* (2013) suggested that increased inundation of off-channel habitats (i.e. wetland, floodplains) may have resulted in lateral movement of small-bodied fish into these newly inundated habitats, however this was not recorded during the current autumn wetland surveys, where overall small-bodied fish abundances decreased. Although vegetation surveys were not conducted in conjunction with this fish study in wetlands, Nicol *et al.* (2013) (see next section) recorded an overall decline in submergent vegetation during the drought period (2008/09) and further losses in 2010 (over 1–2 months) as a result of high velocities, turbulence and decreased euphotic depth associated with flooding. It is possible that the decreased abundance of small-bodied species within wetlands may have been associated with a decrease in this preferred habitat (i.e. submergent macrophytes; see Bice *et al.* 2013).

While common carp were collected in low relative abundances during 2005/06, they displayed the greatest positive response to the flood with significant increases in relative abundance within seven of twelve wetlands sampled in 2012 following flooding. A similar response may be expected during future floodplain/wetland inundation. Nevertheless, natural flooding will promote recruitment of large-bodied native species (e.g. golden perch) (see Zampatti and Leigh 2013b) along with carp; whereas artificial floodplain inundation is unlikely to benefit recruitment of large-bodied native species (Mallen-Cooper *et al.* 2008; 2011). The response of carp to floodplain/wetland inundation will require careful management in order to minimise benefits for carp while maximising benefits for native species (e.g. carp screens vs. native fish passage).

It is important to note that the findings of the present study may have been subject to dilution effects as similar sampling methods and effort were applied during all sampling events and the relative size/volume of each individual wetland was larger during 2012. While it appears the relative abundance of native fish either did not change or decreased in 2012, this result must be viewed with caution due to the greater area of wetland habitat post flooding. In addition, for species that were found to increase significantly (i.e. common carp), it is likely that the relative abundance of these species is actually higher than reported. Further monitoring is required to evaluate the long-term response of both native and invasive species to both natural and human induced inundation of individual floodplains/wetlands. Such monitoring should consider the potential for density effects due to the contraction and expansion of wetland size and aim to determine the long-term persistence of both native and invasive species recruited associated with the 2010–12 floods/high flows (i.e. age frequency distributions, etc).

Aquatic and floodplain vegetation response to flooding

Changes in river hydrology have led to a decline in the condition of many dominant riparian trees, understory vegetation and aquatic macrophytes in floodplains and the main channel of the LRM (Bren 1992; Walker and Thoms 1993). Recent drought has exacerbated the situation with effects on plants likely to be more severe (LeBlanc *et al.* 2012). During the drought floodplains and wetlands became disconnected from the main channel during the drought and dried out, particularly in the lower reaches of the system (Nicol 2010). Flooding plays an important role in the recruitment and maintenance of floodplain vegetation condition by increasing plant water availability (Akeroyd *et al.* 1998; Overton *et al.* 2006). Summaries of the responses by aquatic plants below Lock 1 (Nicol *et al*. 2013), river red gums (Doody *et al.* 2014) and plant assemblages in floodplains of the LRM (Holland *et al.* 2013) to flooding are presented below.

Aquatic plant resilience

Temporal variation in the aquatic plant communities of the LRM (between Lock 1 and the barrages) were investigated by Nicol *et al.* (2013) to assess resilience (ability to recover after the period of low water levels) and resistance (capacity to survive through the period of low water levels), during a period of record low water levels (2004–09) and following an overbank flow (2011/12).

Vegetation surveys were undertaken in seven floodplain wetlands between Mannum and Blanchetown (gorge geomorphic region) and 11 fringing wetland in the Lower Lakes (Figure 1). All of these locations, with the exception of three Lower Lakes wetlands, were also surveyed between 2004 and 2007. In addition, surveys were conducted at sites on the shorelines of Lake Alexandrina, Lake Albert and Goolwa channel (Figure 1) in spring and autumn 2008/09, and 2011/12. Plant communities were compared between pre- and post-flood surveys to elucidate flood-related vegetation responses.

The response of the plant community to low water levels (2004–09) was generally consistent throughout the study area. This included submergent species being replaced by terrestrial species (generally agricultural weeds for lake sites) recruiting on exposed wetland beds and lakeshores. The response to reinstatement of water levels in 2011/12 (return to normal pool level) was inconsistent across sites. Emergent species persisted throughout the study area whilst water levels were low and increased in abundance when water levels were reinstated, except at the lowest elevations. Terrestrial species were extirpated when water levels were reinstated; however, for wetlands between Mannum and Blanchetown, terrestrial and floodplain species recruited at higher elevations after water levels receded, following overbank flows. Submergent species, which were abundant in wetlands, Goolwa channel and areas of Lake Alexandrina prior to water levels falling (most likely due to fact they were protected from wave action), recruited extensively in Goolwa channel. They also recruited in all but one of the surveyed Lower Lakes wetlands and two small sheltered areas of the Lake Alexandrina shoreline after water levels were reinstated, but were absent in all other areas.

Emergent plants showed resistance to disturbance because they survived (albeit in lower numbers) whilst water levels were low. The submergent plant communities in Goolwa channel, Lower Lakes wetlands and to a lesser degree Lake Alexandrina exhibited resilience because they were able to recolonise after water levels were reinstated. However, the areas that have been recolonised after 2010 were much smaller (<50%) than were occupied prior to 2007 (Gehrig *et al*. 2012b). In addition, several submergent species (e.g. *Lepilaena cylindrocarpa, L. priessii* and *Ranunculus trichophyllus*) that were common before 2007 and present in the seed bank (Holt *et al.* 2005; Nicol *et al.* 2006) have not yet been recorded (Gehrig *et al.* 2012b). Between Mannum and Blanchetown, the submergent plant community appeared to lack resilience, although water levels were above pool level for an extended period. Submergent species are expected to recover and recruit between Mannum and Blanchetown after water returns to pool level for several consecutive months.

Results provided evidence of a capacity by aquatic plant communities to establish after disturbance in the LRM, downstream of Lock 1 (especially in the Lower Lakes). Understanding the mechanisms of resilience and resistance (e.g. seed bank assessment and desiccation tolerance studies) will further improve our understanding of the vegetation dynamics of the LRM and enable managers to make evidence-based decisions regarding river operations and environmental water allocations.

River red gum response

River red gum (RRG), *Eucalyptus camaldulensis*, is one of three tree species that dominate the floodplain of the LRM. This flood-tolerant species plays a key role in recycling nutrients between rivers and floodplains, and provides habitat for a range of terrestrial and aquatic species (Briggs and Maher 1983; Baldwin 1999; Cunningham *et al*. 2007). Anthropogenic flow alteration and drought have led to a serious decline in RRG health along the River Murray, with just 30% of RRG considered to be in good health condition in VIC/NSW during 2009 (Cunningham *et al.* 2009). Whilst this species can tolerate dry periods, it is believed to require inundation once every three to five years (Wen *et al.* 2009; Roberts and Marston 2011).

Doody *et al.* (2014) investigated the relationship between flooding (that occurred in 2010/11) and lateral recharge and condition of RRG between 2007 and 2011 using Landsat (LTM5) Normalised Difference Vegetation Index (NDVI) (see Doody *et al.* (2014) for more details). Linking the river hydrograph with the River Murray Floodplain Inundation Model (RiM–FIM) allowed exploration of the relationship between inundation duration and RRG water requirements. Results indicated that lateral bank recharge is an important mechanism in the maintenance and improvement of vegetation condition along the LRM. A lateral recharge zone of influence 30 to 90 m from the main channel and feeder creeks was identified as important in maintaining RRG in better condition compared to areas beyond 120 m from the main channel (Figure 16). Higher NDVI values represent higher vegetation vigour. Lower values in the 0–30 m zone result from mixed Landsat pixels containing both water and vegetation. Water typically has NDVI values less than 0, therefore reducing NDVI in the 0–30 m river bank zone (Figure 16).

RRG trees were inundated for more than 130 days along the main channel between November 2010 and May 2011. A total of 58% of RRG (65% and 51% for forest and woodlands respectively) were inundated for more than 60 days. Forests are denser and generally line permanent channels whereas woodlands are less dense and exist at a distance from the river channel. The flow duration and magnitude of the 2010/11 flood was lower than required to meet the environmental water requirements of both RRG forest and woodlands for the Chowilla floodplain (refer to Doody *et al.* 2014 for Basin Plan target). However, errors associated with the reported methods may have reduced accuracy of results.

Higher within-channel irrigation water delivery during summer months was identified as critical to tree survival adjacent to the main channel during the drought (Figure 17). Research suggests that weir pool manipulation to create within-channel flood pulses will aid RRG maintenance. Furthermore, release of environmental flows once every three to five years to create bank-full flow or preferably overbank flows, will increase hydrological connectivity between river banks, wetlands and riparian zones, providing positive ecological benefits to RRG and other floodplain and aquatic ecological assets. Lateral bank flow, flooding and wetland connectivity are therefore essential in maintaining and improving RRG health within the LRM.

Analysis linking river flow, inundation duration and RRG condition using the River Murray Floodplain Inundation Model (RiM-FIM) and NDVI, indicated that RRG response to flooding was greatest when inundated between 7 and 60 days. Inundation durations of less than 7 days appeared to have little effect on RRG condition, whilst prolonged inundation duration (>60 days) caused a decline in condition. Preliminary assessment indicates an inundation period of 30–60 days was optimal, before NDVI declined for trees on the Chowilla floodplain.

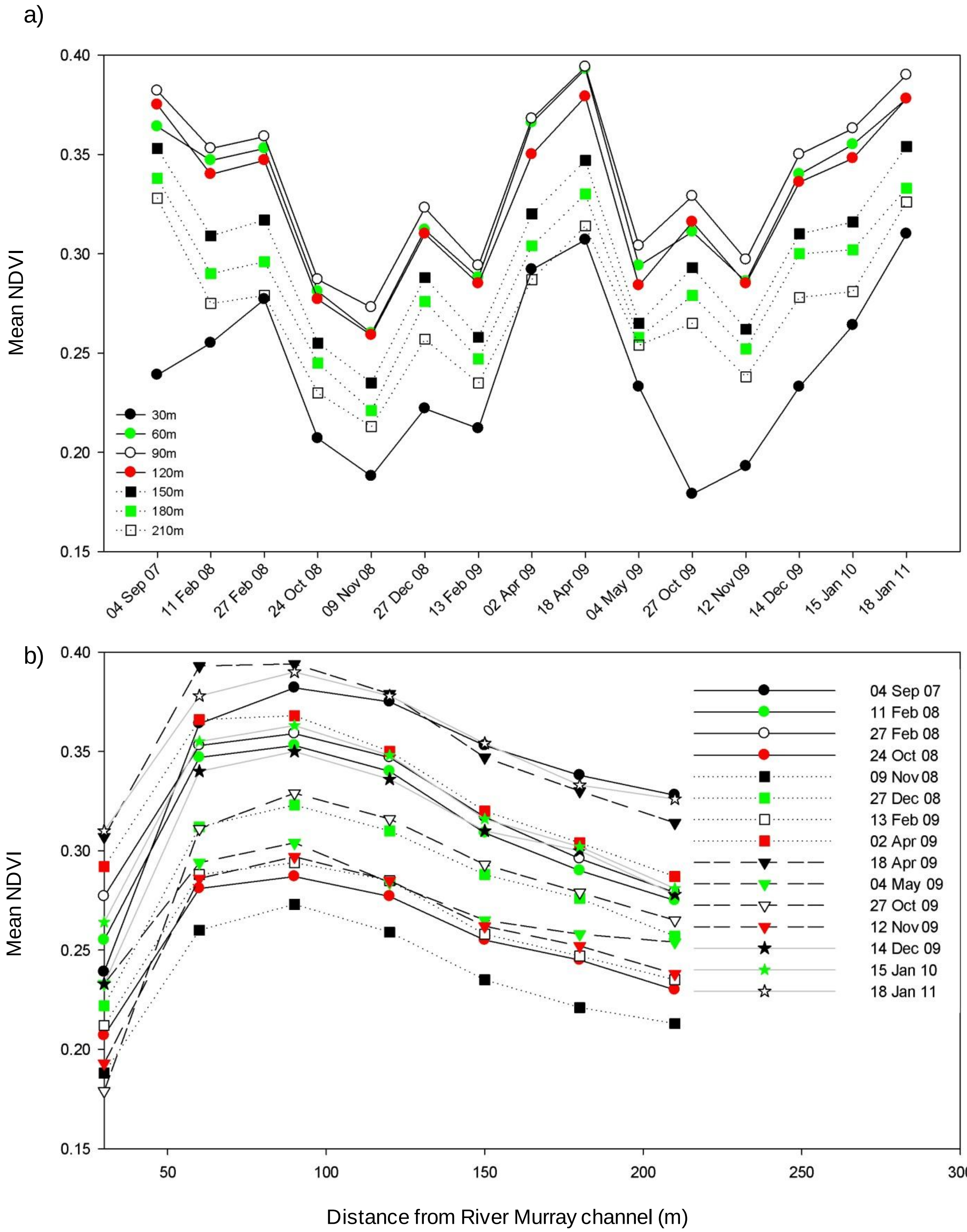

Figure 16. Change in NDVI (condition) with distance from the main channel for the period 2007–2011 for river red gum forest communities (a). Change in NDVI with distance from the main river channel river red gum forest communities, by image date (b).

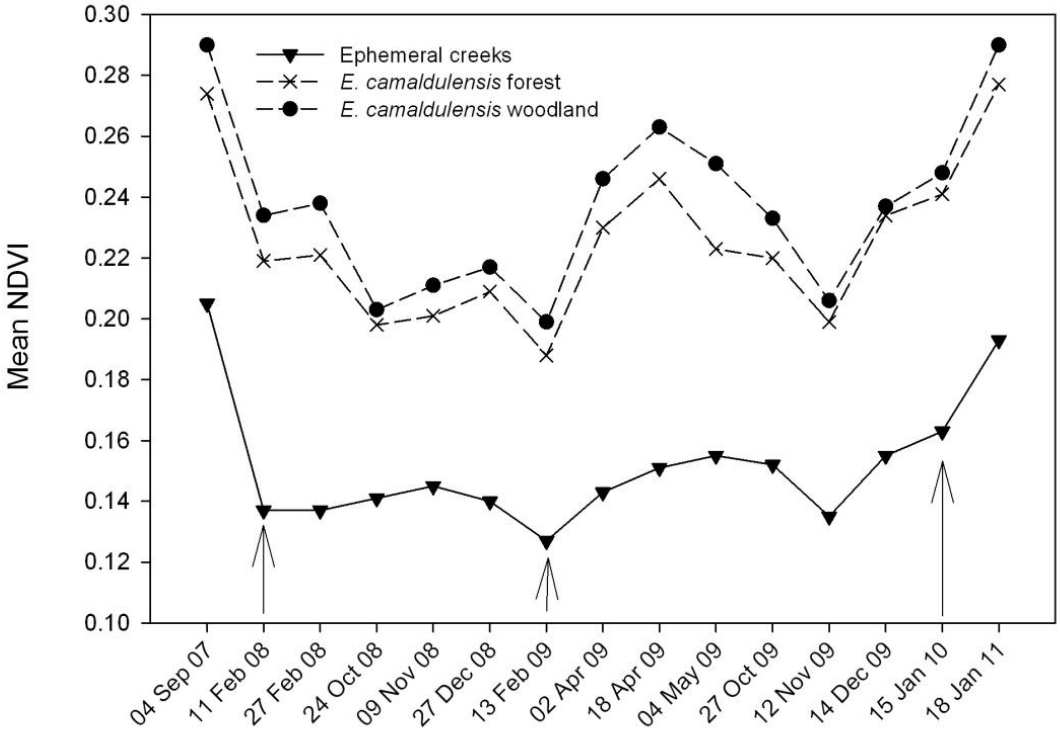

Figure 17. Change in NDVI over the period 2007–2011 for river red gum (*E. camaldulensis*) communities and ephemeral creek floodplain areas. Arrows show images taken during summer higher flow events in 2008, 2009, 2010.

Effects of natural and artificial flooding on trees and understorey plants in floodplains

Artificial watering and groundwater management were used during the drought to combat severe water stress and decline in the condition of long-lived vegetation on floodplains in the LRM. Artificial watering involved pumping water from the river into temporary floodplain wetlands, in order to improve tree condition and promote recruitment of native floodplain and amphibious understorey plants within a limited area. Groundwater management used groundwater production bores to lower the floodplain water table to draw low salinity river water into the floodplain aquifer to improve tree water availability. Holland *et al.* (2013) revisited sites that had been artificially watered after the 2010/11 flood to compare the response of the floodplain to natural and artificial floods.

Changes in soil, groundwater and tree condition at Bookpurnong (floodplain geomorphic region of the LRM, Figure 1) were investigated after artificial watering and groundwater management (2005–08) and the 2010/11 flood. Groundwater levels rose >2 m above normal pool level during the flood in response to the hydraulic gradient created by the flood river water level. Overbank flooding reduced soil and groundwater salinities in three ways: 1) bank recharge (over 200 m from the river); 2) vertical infiltration from the soil surface; and 3) movement of low salinity groundwater upwards into the unsaturated zone, which increased tree water availability at all sites. The extent and degree of soil and groundwater freshening after the flood at Bookpurnong was significantly greater than after artificial watering and groundwater management (Figure 18). The persistent high water tables caused by elevated river levels in the eight months after flooding appear to have suppressed or delayed the tree canopy response to the flood. However, increased tree water availability after the flood and the opportunistic water use strategy of the LRM floodplain trees suggests that tree health will improve.

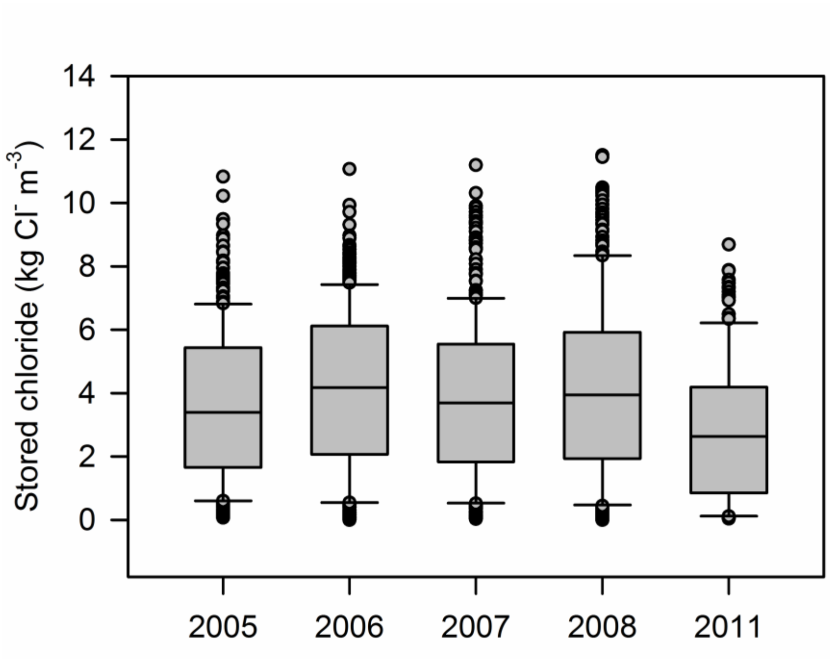

Figure 18. Bookpurnong soil salinity (stored chloride, kg Cl^- m^{-3}) between 2005 and 2011.

Changes in the understory plant community following the 2010/11 flood were compared between two locations in the floodplain geomorphic region of the LRM: the Chowilla (artificial watering between 2004 and 2010) and Pike floodplains (no artificial watering) (Figure 1). The understorey plant community responded to flooding on both floodplains; there was an increase in species richness at both sites but the response was not consistent between the Pike and Chowilla floodplains. The change in floristic composition before and after the 2010/11 flood was greater on the Pike Floodplain (24 taxa before, 68 taxa after) than the Chowilla floodplain (43 taxa before, 66 taxa after). This was due to the large number of floodplain and amphibious species that were present on the Chowilla floodplain prior to the 2010/11 flood (due to artificial watering), which were not present on the Pike floodplain until after the 2010/11 flood. The sedge, *Eleocharis acuta* was the only species that was present exclusively in areas that were artificially watered. The amphibious fern *Marsilea angustifolia* was present in greater numbers in areas that were artificially watered, but was present on both floodplains after the flood. Some species (e.g. bushy groundsel, *Senecio cunninghamii*) were only present in floodplains after natural flooding.

Results from this study showed that the floodplain understory plant community retained the capacity to respond to flooding despite an extended period (up to 14 years) without overbank flooding or artificial watering. This response of the understory plant community may have been due to recruitment from the resident seed bank and/or transportation of propagules to sites by hydrochory (dispersal by water) and highlights the importance of maintaining diverse refugia during droughts and the need to maximise connectivity during flow events. Species richness of understorey vegetation is expected to further decline in the absence of natural or artificial watering due to most species being short-lived (Cunningham *et al.* 1992). Monitoring in February 2012 confirmed a decrease in species richness, but this did not decline as much as after artificial watering during the drought (Gehrig *et al.* 2012a).

Artificial watering may be an appropriate management action to maintain the resident seed bank of understory species at selected high value sites. It also remains an important management action to maintain the condition of long-lived tree and shrub species that do not form long-lived seed banks (e.g. *Acacia stenophylla, Eucalyptus camaldulensis, Eucalyptus largiflorens and Duma florulenta*) in the absence of natural flooding. However, artificial watering is not a direct substitute for regular natural floods given the limited extent and degree of salt leaching, bank recharge and groundwater freshening in comparison to natural floods.

Conceptual river–ecosystem model

To date, no tools exist for South Australia that enable managers to predict the relative benefits of strategies to optimise the delivery of environmental water to the various channel, wetland and floodplain environments in the LRM. Such a tool would be based on an understanding of how the river system as a whole responds to flow, across the various ecological components (e.g. vegetation and fish), processes (e.g. carbon and nutrient cycling) and habitat types (e.g. channel, wetland, floodplain). To develop such a tool, Lester *et al.* (2014) collated data and hypotheses from integrated research sub-projects (Table 1) from the MFE project into a conceptual model of how the LRM as a whole responds to flow events (both high and low).

Model objective

The objective of this model was to provide a framework to capture our current understanding of the impact of high flows and floods on ecological processes that occur in the LRM. This model has the potential to be used as a basis for future development of tools to assist in the management of the LRM by providing a mechanism for quantifying and evaluating the expected impact of managed and natural flow events in the future.

Model development

Before research sub-projects had been undertaken, an initial conceptual model was designed (Figure 19). This model has restrictions in that: 1) it assumes that all biotic components will respond in the same way to each lever and environmental conditions; 2) thresholds may be needed as responses to conditions are not expected to be linear and 3) subtraction of existing links or addition of factors may be required. Project members undertook sampling activities and yielded new datasets, where the main findings were synthesised across sub-projects to develop synthesis models at multiple levels (species-specific to whole ecosystem). After a review process, the final model was created (Figure 20).

The overall model (Figure 20) draws together the relationships identified by the MFE group between high-flow events and the response of the various biotic components studied. Low flows are omitted from this overall model. In creating a synthesised model for the ecological response of the LRM as a whole, drivers, levers and impacts from the generic model have been included, based on the response of each group represented. In most cases, there was insufficient information to describe the shape and nature of the relationships among the drivers and the impacts, or the relationship was likely to vary among different functional groups. Where possible, additional information about how each driver or impact would respond under high-flow conditions has been included. Simplification of complex relationships, where understood, was needed to capture the overall response of the ecosystem to high-flow events.

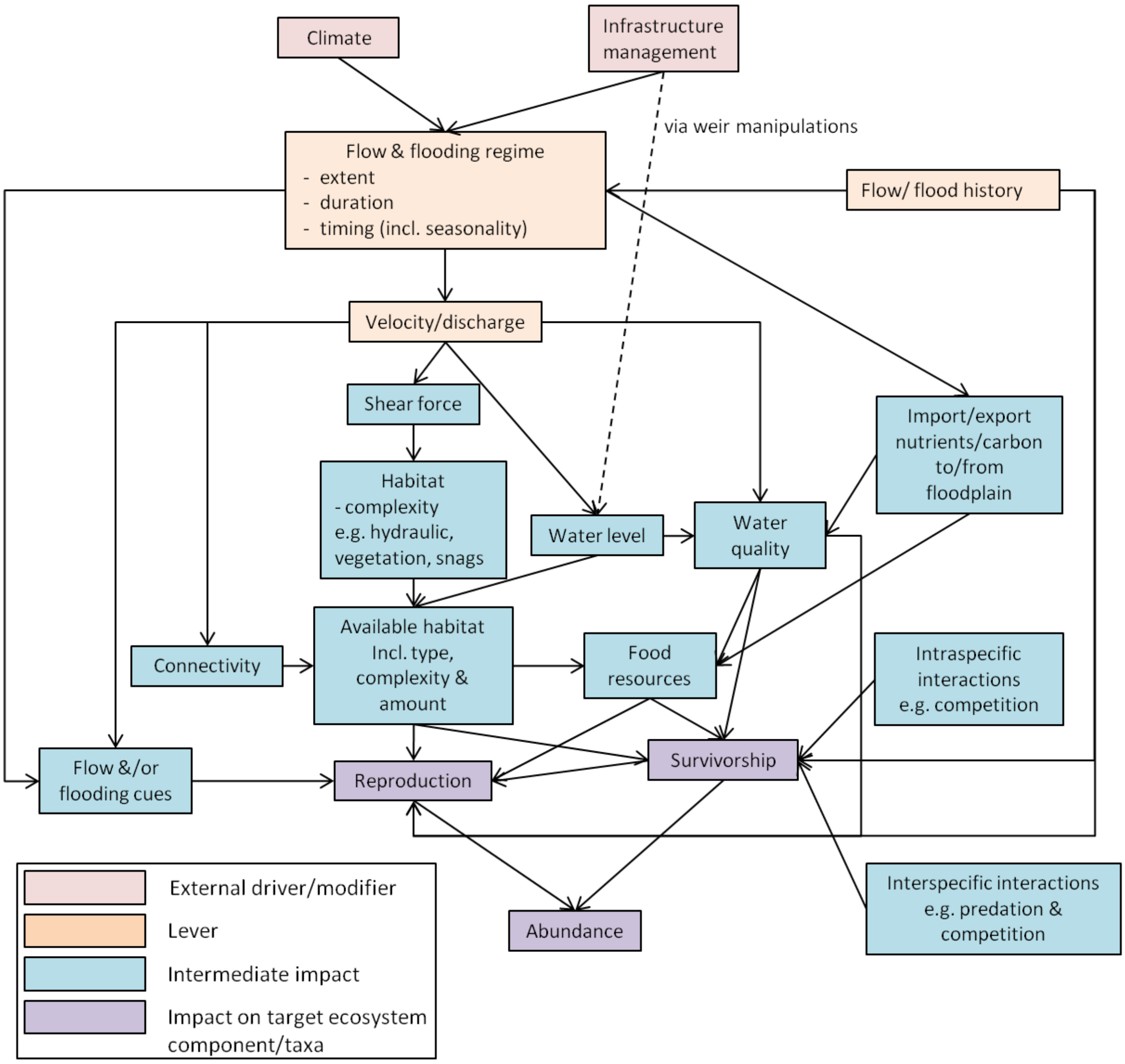

Figure 19. Initial floodplain and in-channel conceptual model (including connected wetlands). External drivers are those that operate at larger scales than the model encompasses (e.g. climate). Modifiers influence the effects of those external drivers (e.g. upstream water extraction or infrastructure management). Levers include those factors that can be changed most easily by river operators, at least in theory. The impact of manipulating those levers on the target ecological component is the endpoint of the model, while intermediate effects represent the links between the two (i.e. how the levers change the river environment that will then influence the biota).

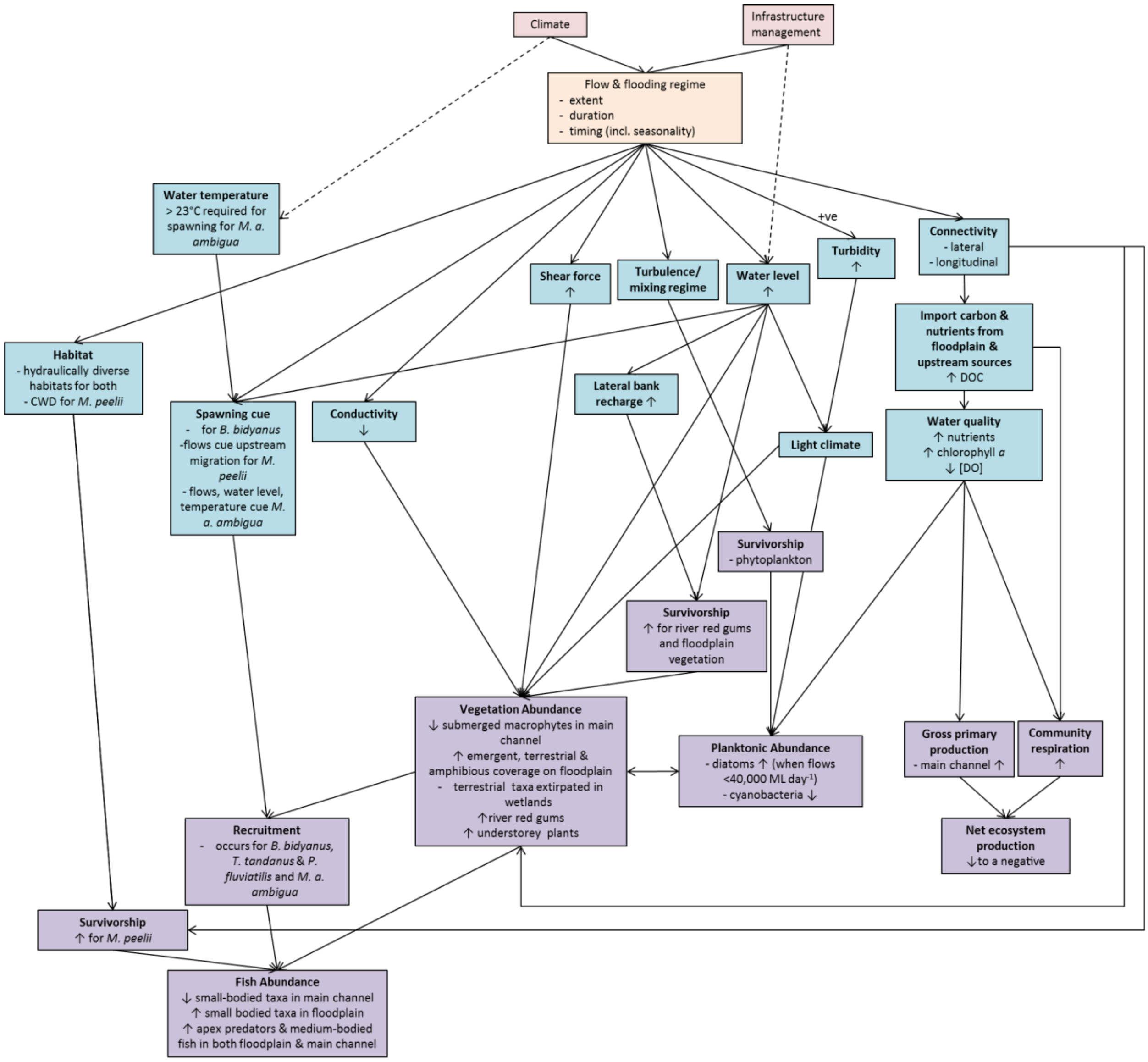

Figure 20. Overall conceptual model for ecological response to high flows in the lower River Murray. Dotted lines indicate indirect interactions. Fish species mentioned include flathead gudgeon (*Philypnodon grandiceps*), carp gudgeon complex (*Hypseleotris spp*.), bony herring (*Nematalosa erebi*), silver perch (*Bidyanus bidyanus*), freshwater catfish (*Tandanus tandanus*), Murray cod (*Maccullochella peelii*) and golden perch (*Macquaria ambigua ambigua*), and the non-native common carp (*Cyprinus carpio*), goldfish (*Carassius auratus auratus*) and redfin perch (*Perca fluviatilis*).

Final conceptual models

A hierarchical modelling approach was used to characterise ecological responses in the LRM to the 2010/11 flood (Figure 21). In addition to the overall model, models were developed for functional components of the study (fish, vegetation and phytoplankton/water quality/metabolism), species-specific models for two large-bodied fish species (Murray cod and golden perch) and sub-project-specific models (can be viewed in Lester *et al.* 2014).

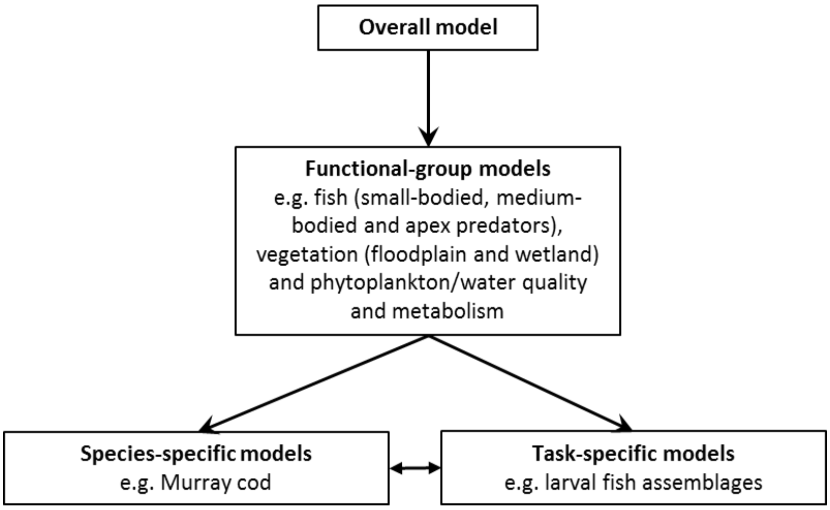

Figure 21. Hierarchical organisation of the models developed for the Murray Flood Ecology project.

For most groups, flooding was thought to have a positive impact as depicted in the overall model (Figure 20). The generic model performed well in allowing the relationships across a range of taxa to be represented at the scale of the flow events surveyed. Synergies were apparent across the various taxa, with links apparent, for example, between nutrient concentrations, primary productivity and habitat complexity. Very little information was available to describe the shape of the relationships. However, this may not be surprising given that sampling and investigation occurred only during one flood event as a part of this project, and more research will be needed to understand how each taxon and each group respond functionally to high flows/floods with different characteristics.

Application, limitations and further development

Models are intended to be applied at several spatial and temporal scales, depending on the target ecological component, but for effective application, scale must be specified in advance. It is likely that relevant scales will depend on the size of the flow event being considered, the ecological component being modelled and the likely lag time between the flow and any response.

One of the major limitations of this approach is that the relationship between flow and water level in the LRM is complex, due partly to the influences of the weirs (e.g. can have a high river water level but zero flow). So whilst flow is a relevant currency for management, water level often may be more significant within this system for some ecological components, which makes it very difficult to identify clear flow-ecology relationships in a highly regulated river such as the Murray. Another limitation is that many other possible links are likely to be important (i.e. groundwater, zooplankton and macroinvertebrates) are not currently represented in the models. Furthermore, this model has not been created for the Lower Lakes and Coorong region and should eventually be linked to those extant downstream models (e.g. Lester and Fairweather (2011) or to their replacements in time), to enable state-wide responses to be assessed simultaneously.

It would be of interest to test the model outside the bounds of the event that has been monitored as a part of the MFE project and investigate the potential implication of multiple large flow events, or the response related to a within-channel flow compared with an overbank flow. The aim of such an activity would be to generate hypotheses regarding ecological responses to such scenarios, thus providing testable hypotheses for future events, allowing the model to be refined in time. A major limitation of the current data sets available for development of these models was that only a single (natural) high-flow event had been documented in many data sets, which does not enable elucidation of the response of the ecosystem to any variety of flooding regimes. The response of the ecosystem to flooding following extended drought is likely to be very different to response to flooding in multiple years, and cumulative effects are likely. Broadening our experience across multiple flood events (and indeed, multiple droughts) will greatly improve the reliability of the conclusions drawn for the LRM. For example, additional information will enable us to describe the form of relationships among drivers, levers and impacts shown in the conceptual diagrams. Understanding those relationships is critical to the development of appropriate flow regimes and environmental watering for the LRM.

Conclusions and recommendations

The MFE project has filled key knowledge gaps regarding the ecological responses of key processes (e.g. water quality and metabolism) and components (e.g. plants and fish) to flooding in the LRM after an extensive drought. The results generally present a coherent package of positive ecological responses to natural flooding, including enhanced recruitment, condition and recovery of key communities as a result of various flow-related processes (increased productivity, lateral and longitudinal connectivity, flow cues etc.) in the LRM. Whilst the research sub-projects were undertaken across different ecological themes with different emphases, there is a high level of concurrence in findings from sub-projects.

- For instance, there are complementary findings between the fish sub-projects: flood and increased within-channel flows facilitated spawning and recruitment of golden perch, a flow-cued spawning species in the LRM; however floods also led to increased recruitment and abundance of common carp, a flood opportunistic invasive species, in the main channel and most wetlands. This implies that careful management of flow is required to minimise benefits for carp while maximising benefits for native species.

- Additionally, both larval and adult fish assemblages in the main channel showed a structure shift from drought to flood mainly due to the reduction in relative abundance of small-bodied fish and the increases of large-bodied fish during the flood. This was likely caused by the alteration of microhabitats (i.e. reduction of submerged aquatic macrophytes that small-bodied fish are associated with) and enhanced spawning, recruitment and abundance of large-bodied fish (e.g. golden perch and carp).

- Both water quality and golden perch studies suggest that maintaining flow integrity and continuity (e.g. Darling or upper-, mid-Murray to the LRM) are important to facilitate nutrient transport, larval drift and juvenile fish dispersion. This also supports the notion that environmental flow management needs to consider appropriate spatio-temporal scales (e.g. river scale).

- River metabolism and Murray cod movement studies have both highlighted the importance of maintaining connectivity between the main channel and key off-channel habitats to facilitate carbon/nutrient and biotic movements. Similarly, the vegetation studies demonstrated the importance of inundation and lateral bank recharge in the maintenance of species diversity and longevity of floodplain and wetland plant communities.

The conceptual model developed using findings from sub-projects captures our understanding of these responses. It gives a simplified view of a complex system but also indicates that there are knowledge gaps to be addressed in flow-ecology relationships. This model has the potential to be used as a basis for future development of tools to assist in the management of the River Murray by providing a mechanism for quantifying the expected responses of managed and natural flow events in the future. It recognises trade-offs between functional groups and allows managers to work from the bottom up, by looking at their expected outcomes and tracking back to the processes and levers that are leading to achieving those outcomes.

Key messages

Flooding is an integral part of the natural flow regime that is critical in maintaining the ecological integrity of floodplain rivers. In general, natural flooding will increase productivity and connectivity and enhance recruitment, abundance and condition of key native biota. Key findings/messages from the MFE research sub-projects are as follows:

- Extended low-flow periods led to increased salinity from evaporation and saline water intrusion in the lower reaches of the LRM.
- Floods led to the mobilisation of nutrients and a shift in the phytoplankton community from a Cyanophyta dominated community during the low-flow period in 2008/09 to a mixed community during the high-flow period in 2010/11 that was dominated by diatoms on the rising and falling limbs of the hydrograph and Chlorophyta during peak flow. Such community shift would have reduced risk of Cyanophyta blooms and increased nutritional benefits for the aquatic foodwebs.
- Chowilla and Barmera floodplains were identified as major sites for phytoplankton photosynthetic production and important sources of organic matter during the flood. This highlights the importance of lateral connectivity between the main channel and off-channel habitats, and the significance of specific floodplain areas.
- Larval fish assemblages differed significantly between the drought and flood years, reflecting different spawning responses to flows in different fish species/groups. The changes in larval assemblage structure suggested that golden perch and silver perch do not spawn under prolonged periods of low flows in the LRM; whereas most small- to medium-bodied species spawn annually, including during low flow periods.
- Spawning and recruitment of golden perch is facilitated during both overbank flows and increases in flow contained within the river channel.
- Connectivity between the River Murray main channel and Chowilla anabranch system is important for the movement of Murray cod. Large-scale, generally upstream, movements of Murray cod occurred just prior to the peak of the flood. Mortality of Murray cod was significant (~25%) during a hypoxic blackwater event following flooding.
- High-flow events can alter microhabitats in the main river channel, which can restructure fish assemblages. Post-flood fish assemblages in the River Murray main channel were characterised by large-bodied riverine species whose recruitment is directly linked to flow variability (e.g. golden perch). Conversely, under low-flow conditions, proliferation of submerged aquatic macrophytes results in the dominance of small-bodied fish species that are significantly associated with such habitats.
- Common carp displayed a positive response to the flood with significant increases in relative abundance within the main channel and most wetlands.
- Emergent plants persisted throughout the study period exhibiting resistance to disturbance (drought to flood). Submergent plants were extirpated from the Lower Lakes and floodplain wetlands between Mannum and Blanchetown during the drought but recruited in shallow areas of the Lower Lakes after water levels were reinstated showing resilience. Submergent plants did not recruit between Mannum and Blanchetown between spring 2010 and autumn 2011 and appear to lack resilience; however, the lack of recruitment was probably due to extended high water levels during the study period.
- Lateral bank recharge was an important mechanism in the maintenance and improvement of RRG tree condition along the LRM. Higher within-channel water level for irrigation water delivery during summer was critical to tree survival adjacent to the main channel during the drought.
- Artificial watering is a useful management action to maintain the condition of long-lived tree and shrub species on the floodplains during the drought. It may also be appropriate to maintain the resident seed bank of understory species at selected high value sites. However, artificial watering is not a direct substitute for natural floods given the limited extent and degree of salt leaching, bank recharge and groundwater freshening in comparison to natural floods.

Limitations and further research

While knowledge gaps remain regarding flow/flood related responses of various ecosystem components and associated processes, the major limitation of this research is that all the flood response data were collected during a single flood event, which followed an enduring drought. This was specifically identified from the conceptual model. Ideally, data would be collected over multiple flooding and high-flow events (including instances without prior drought) for a more comprehensive understanding of flood and flow ecology to enable reliable predictions of ecological responses. These should also incorporate a range of within-channel flows. Such knowledge will inform environmental water planning and flow management.

Water level changes that are associated with flooding may be significant for the ecological components within the system; however, they are coupled with increased discharge (including water velocity and turbulence), which makes it difficult to identify relationships between ecological responses to flow versus water level. A better understanding of the importance of water level (without the effect of flow) is needed, including the effects of the rate of rise and fall of water levels.

Some species may have a lag in response time to environmental conditions and this will vary between species. There is currently uncertainty behind the time frames in which different species responded to the flows observed during this project. Identifying the appropriate time frames in which to monitor responses of different species is required. Further monitoring on the delayed recovery of some species (e.g. RRG, black box and Murray cod) as a result of the 2010/11 flood event should be undertaken.

Knowledge gaps also remain with regard to understanding the link between flooding, food resources and processes involved in the river food web (trophic dynamics). For instance the effect of flooding on primary consumers (i.e. zooplankton and macroinvertebrates) was not investigated in the current study. Further research is required in flow related trophic ecology in the LRM.

As carp will likely benefit from floodplain/wetland inundation through natural floods or the delivery of environmental water, further targeted research will be required to inform flow management to mitigate carp impact while maximise ecological benefits to native species.

Management implications

The results of the MFE, and other research projects, will underpin future environmental water delivery and river management in a way that maximises ecological benefits from available water. Specific management considerations from MFE sub-projects are provided below in Table 3, which relate to the key findings/messages given in a previous section:

Table 3. Management considerations for Murray Flood Ecology sub-projects.

Sub-project	Management considerations
Nutrients and primary production	During extended low-flow periods adequate water needs to be supplied to the LRM if the intrusion of saline and nutrient rich water below Lock 1 is to be minimised. Reducing the interval between floods may reduce the risk of hypoxia. Provisions of water to the floodplain should be complemented with elevated river flow rates that favour a phytoplankton community dominated by diatoms (high flows), particularly during periods of warm, calm conditions to limit nuisance algal blooms. These provisions would have environmental, social and economic benefits.
Organic matter and metabolic activity	It is important to maintain the dynamic connection between the river and floodplains, especially connections to significantly flooded areas for river productivity.
Golden perch recruitment and abundance; larval fish assemblages	Environmental flow management that incorporates floodplain and in-channel processes, at spatio-temporal scales concordant with life-history processes (e.g. river scale), will result in more robust populations of flow-cued spawning fish, particularly golden perch.
Murray cod movement and mortality	The Chowilla anabranch system provides hydraulic and physical habitats for Murray cod that, due to river regulation, are now rare in the main-channel of the LRM. Maintaining connectivity between these lotic perennial off-channel and main-channel habitats is

	important.
Fish-habitat associations	Delivery of environmental flows should consider fish species-specific variability in direct (e.g. spawning/recruitment) and indirect (e.g. mediated through habitat re-structuring) responses to flow variability.
Wetland fish response	Increased carp abundances may be expected during floodplain/wetland inundation. This will require careful management to disadvantage carp, while minimising impact and maximising benefits for native species.
Aquatic plant resilience	Water levels below Lock 1 need to be maintained above +0.5 m AHD (at the barrages) to maintain submergent plant communities and ensure connectivity of fringing emergent vegetation. The submergent plant community showed a capacity to recover after water levels were reinstated and the emergent plant community persisted during the drought; but the mechanisms and longevity of resilience and resistance of aquatic plant communities need to be investigated further to improve understanding and enable managers to make evidence-based decisions.
River red gum response	Environmental flows once every three to five years to create bank-full flow or preferably overbank flows, will increase hydrological connectivity between river banks, wetlands and riparian zones, providing positive ecological benefits to RRG and other floodplain and aquatic ecological assets. Weir pool manipulations to create within-channel water level variability may aid in RRG maintenance.
Natural vs. artificial flooding for trees and understory plants	Artificial watering is a useful management action to maintain the condition of long-lived tree and shrub species in the absence of natural flooding, but is not a direct substitute. Watering has also been shown to facilitate the recruitment of floodplain understorey plants during periods of drought, providing ecosystem services for the biota that depend on these species, but it is not critical for the long-term survival of these species. However, the longevity of the seed bank of floodplain species is unknown and extended drought may deplete the seed bank. Therefore, watering may be an important management action to maintain localised areas with high density seed banks, however, this can be achieved by watering to maintain trees and shrub condition.

Whilst these management considerations were identified as being beneficial to the focus species or area of each sub-project, the high level of concurrence in findings from sub-projects reinforces that the LRM is an integrated ecosystem, and the recommended management actions are intended to be complementary to achieve ecosystem outcomes. Furthermore, when considering implementing management practises, it is important that environmental water management should consider the 'river scale' (i.e. a river scape view, sensu Fausch *et al*. 2002) and not be limited to the site or reach scale. Connectivity at the large scale (river or basin level) is important for maintaining a healthy and diverse river (MDBC 2004; Barrett and Mallen-Cooper 2006). The spatial scale at which some species of plants and animals operate is often much larger than just a section of the river or within State boundaries (e.g. Zampatti and Leigh 2013b). In order for these species to maintain and improve their populations it is imperative to maintain connectivity across the entire MDB. Flow delivery to maintain lateral connectivity is also critical between the main river channel and productive off-channel wetland and floodplain habitats.

Returning a more natural flow regime that includes a mix of flooding, low- and medium-level flows where various species and functional groups can meet their specific life-history requirements is suggested to restore and maintain aquatic ecosystems of the LRM. Currently, environmental flows are delivered to the LRM typically to create spring/summer flow pulses, aiming to increase flow variability and achieve ecological outcomes (DEWNR 2013). Within-channel flows (e.g. 15,000-50,000 ML day^{-1}) are a key management focus, which could be restored within the current constraints of system operation (Goyder Institute 2012). In contrast, using engineering to mimic natural floods is more challenging and has clear limitations as manipulated flood events are unlikely to replicate the complete ecological function of a natural flood and could create risks by disconnecting riverine processes and functions.

In order to further understand the role of flow in the ecology of the LRM, ongoing investigations during various flow scenarios are required. These can be conducted during natural flow events or through environmental water deliveries. The MFE project has improved our conceptual understanding of flow-related ecology in the LRM and this can be used to guide flow restoration and develop hypothesis driven monitoring to adaptively manage environmental flows. Integral to this are rigorous and robust long-term monitoring programs (Lindenmayer and Likens 2010).

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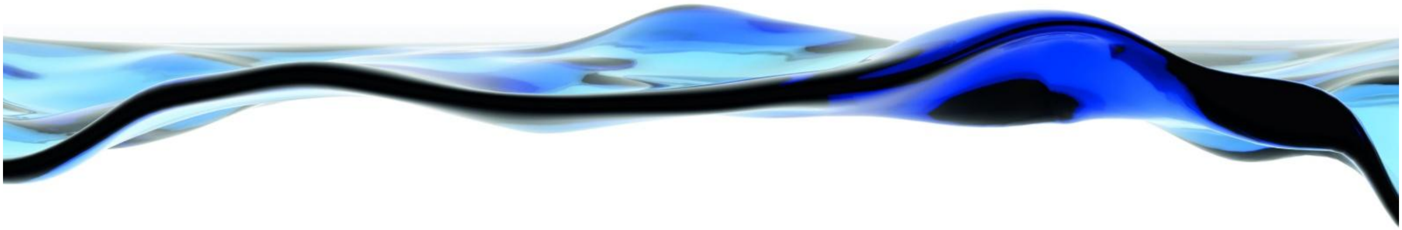

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