Flow dependent ecological responses

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A technical report from the Ecological Responses to Altered Flow Regimes Flagship Research Cluster (SubProject 3)
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The Ecological Responses to Altered Flow Regimes Collaboration Cluster acknowledgements:

The Ecological Responses to Altered Flow Regimes Cluster is a collaboration between: CSIRO Water for a Healthy Country Flagship; Griffith University; The University of New South Wales; Monash University; Charles Sturt University; La. Trobe University; Victorian Department of Environment and Primary Industry (Arthur Rylah Institute).
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  - Malcolm Hodgen (CSIRO)
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### 1 Introduction

#### Background

Freshwater ecosystems around the world are threatened by many different factors including changes to flow regimes affecting habitats, pollution, climate change, overharvesting, pest species and disease (Millennium Ecosystem Assessment 2005; Dudgeon et al. 2006). Many of the threats interact to produce confounded impacts on ecosystems, dependent biota and processes. Anthropogenic changes to flow regimes are widespread and affect all hydrological, geomorphological ecological processes. They affect flow quantity and temporal and spatial variability, directly impacting on the requirements of many flow dependent organisms and processes.

Flow regimes define the character of a river and its dependent ecosystems and their characteristic biota and driving processes. The size, frequency, timing and duration of flows and their associated floods provide the template for understanding the responses of different organisms and dependent processes at all the different spatial and temporal scales associated with a river. Periods of low flow are also important restructuring phases in the organization of freshwater ecosystems (Lake, 2000b, Lake, 2003). Freshwater ecosystems are highly dependent on the full range of flows from large structuring floods (booms) to the periods of low to no flow (bust) as well as flows in between which trigger a subset of process and responses from dependent organisms (Kingsford et al. 1999; Bunn et al. 2006).

High flows and floods can trigger the germination of aquatic plants and emergence of invertebrate biota (Brock et al. 2006; Boulton et al. 2006). These form the food web for higher order organisms such as frogs, fish species and waterbirds which can occur in large abundances, particularly in wetlands, following large flooding. Floods which move across the floodplain connect different parts of the river, allowing for the movement of invertebrates and fish which colonise highly productive aquatic habitats on the floodplain. These integrated processes are critical to the entire food web, linking the many different dependent organisms and processes operating at longitudinal and lateral dimension on the river. Humans have disrupted all of these processes, particularly through the building of dams, extraction of water and development of structures on floodplains that alter flow connectivity across floodplains (Kingsford 2000; Bunn and Arthington 2002; Arthington and Pusey 2003; Steinfeld and Kingsford 2012).

Flow regulation changes the flow regime across a range of temporal and spatial scales (Figure 1). Specifically, this relates to effects on the size, timing, frequency and duration of specific flow events. The effects of flow regulation vary among systems and may include reductions in average or event-specific discharges. River regulation may also change in the frequency, duration and timing of specific flow events such as floods, cease-to-flow periods
or in-channel flow pulses. Such changes are widespread across rivers of the Murray-Darling Basin, which has a long history of river regulation. In recent years, governments have invested in the buyback of water to provide environmental flows across the Murray-Darling Basin with the aim of restoration of ecosystems as well improving planning and management frameworks. Such restorative actions will be effected through mechanisms such as the Murray-Darling Basin Plan, its watering strategies and water sharing plans. There is increasing need to focus on effective ways of measuring the impacts of different management approaches on ecosystem responses in freshwater ecosystems.

Figure 1. Conceptual spatial framework used to focus research on the ecological responses to flow in the Murray-Darling Basin (inset) focusing on the Edward-Wakool in-channel system (EW) and three major floodplain wetlands: Macquarie Marshes (MQ), Lowbidgee wetland (LB) and the Barmah-Millewa Forest (BM). These conformed with the spatial conceptual framework for freshwater ecosystems in the Murray-Darling Basin, typical of regulated river systems with large dams in the upper catchment (D) and including river channels (C) with their in-channel benches (B) and floodplains downstream (F, stippled area) with distributary creeks and more perennial wetlands (W).

To maximize the value of this research we chose to focus our efforts on systems where there was already substantial scientific knowledge amongst the project team, which capitalised on available long-term data on existing knowledge of the organisms and processes operating at each site. This provided more explanatory power over the high variability experienced by rivers and wetlands, thereby increasing our ability to quantify
relationships among the considerable spatial and temporal variability always encountered in freshwater ecosystems. Consequently, the research focus was on four major research areas in the Murray-Darling Basin including one in-channel system, the Edward-Wakool river systems and three floodplain systems; the Macquarie Marshes, the Lowbidgee wetland and the Barmah-Millewa Forest, each respectively supplied by the Macquarie River, the Murrumbidgee River and the River Murray (Figure 1).

Conceptual framework

In order to best integrate the research being conducted in this large multi-disciplinary project, we developed a generic conceptual model that could be applied to different biota or processes within in-channel ecosystems. This model could be applied across different systems (in-channel, floodplains), organisms (e.g. flood-dependent vegetation, fish) or processes (e.g. food web productivity). There was clear understanding and agreement that flow was a major driver of ecosystem responses, but that flow’s influence may be direct or indirect through its influence on food, competition or predators for instance (Figure 2, Table 1). The team undertaking this work were highly experienced in their respective fields, and drawn from a range of disciplines. Consequently, while there was an appreciation that other factors may also influence ecological responses to flows, this model provided a sufficient framework to guide our collective research efforts.

**Figure 2.** Generic conceptual model used to define the responses of different organisms or processes (target) for measuring ecological responses to flows and inundation of floodplains and wetlands. This conceptual model was applied across different freshwater ecosystems (in-channel, floodplain and wetland) and the range of organisms and processes (Table 1).

Flow and inundation are the primary drivers which can be measured by various elements and provide the input into physical changes; inputs, production and food resource; competition; outputs, consumption and predators which influence the target organisms or processes (Table 1; Figure 2). Flow is the major driver of inundation of floodplains (Thomas et al. 2011) although local rainfall is sometimes important. Both flow and inundation have key measures which are important for ecological responses including timing, frequency,
duration and magnitude as well as other indices. These can all influence ecosystem responses in different and subtle ways. Similarly flow is a fundamental factor determining the type of physical habitat available whether these are floodplains or in-channel benches (Figure 1) but mediated by connectivity (Table 1).

Together flow and the physical habitat available provide the source for the inputs, production or food resources which drive much of the biological response of freshwater ecosystems (Table 1, Figure 2). These are not always available for target organisms but may be intercepted by competitors which can include exotic species. Ultimately remaining resources in the form of outputs are available for target organisms or processes, once predation is also considered. Finally, there are a range of aspects of an organisms biology that can be measures of ecosystem response to flow as well as various ecosystem processes (Table 1, Figure 2).

Table 1. Drivers of ecological responses and metrics that can be used to identify ecological responses within a generic conceptual framework (see Figure 2).

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<td>Flow and inundation</td>
<td>Timing; frequency; duration; magnitude (area, height); depth; rate of rise and fall; sequence (pattern of events); time since last event</td>
</tr>
<tr>
<td>Physical</td>
<td>Scale; geomorphology; habitat (type, structure, size, connectivity)</td>
</tr>
<tr>
<td>Inputs/ production/ food resources</td>
<td>Sediment; carbon; nutrients; organic matter; new growth; nectar; seeds; invertebrates (micro and macro)</td>
</tr>
<tr>
<td>Competition</td>
<td>Invasive species; nomadic species; migratory species; resident species; chemical competitors</td>
</tr>
<tr>
<td>Outputs/ consumption/ predators</td>
<td>Carbon; nutrients; organic matter; new growth; nectar; seeds; invertebrates (micro and macro); fire; human impacts</td>
</tr>
<tr>
<td>Target ecological response</td>
<td>Processes including productivity, rate of reproduction, dispersal, survival, persistence and extinction and states including biodiversity assemblage (diversity, species richness, abundances), breeding effort, breeding success</td>
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We derived specific conceptual models for each of the organisms and processes investigated in this project. While these organisms and processes are inextricably linked to one another through river flows and flooding conditions, they can be conveniently defined spatially in terms of (i) in-channel, and (2) floodplain and wetlands.
In-channel Ecosystems

Flow is a major structuring influence on river in-channel ecosystems, affecting physical habitat availability (including hydraulic environment, sediment composition and water quality), patterns of connectivity (longitudinal, lateral and vertical) or inputs to ecosystem functions (e.g. nutrient cycling, primary production and decomposition). Flow also drives in-channel interactions with other systems, including groundwater, tributaries, wetlands, floodplains, downstream reaches, the estuary and ocean. As a consequence, there is no known component of a river channel ecosystem that is not influenced by flow, although the influence may be either direct or indirect and may act over a large range of spatial and temporal scales.

Despite the importance of flow to river channels, there is still considerable uncertainty around the role of flow in determining the condition of in-channel river ecosystems. As the temporal and spatial scales decrease, the level of uncertainty grows. At the largest temporal scales of the long-term flow regime (i.e. up to 100 years), there is strong evidence of the relationship between flow regulation and declines in river condition. At a decadal time-scale, there is also enough knowledge to identify ecosystem water requirements to support identification of environmental flow requirements. For environmental flow management and restoration, there remains considerable uncertainty in understanding responses of in-channel ecosystems to individual flows or sequences of flows which can inform decisions at fine temporal scales (i.e. days, months, years).

For instream systems, the most direct influence of flow is on the availability of physical habitat in rivers, which is one of four principles identified as mechanisms by which flow affects biodiversity (Bunn and Arthington, 2002). Using fish as an example, the key physical habitat attributes include hydraulic habitat (i.e. velocity and depth), structure (e.g. instream vegetation, substrate) and water quality, including water temperature, dissolved oxygen and salinity (Mathews, 1998). Different species and life-stages display habitat preferences, reflected in high levels of spatial heterogeneity driving spatial segregation and co-existence of multiple species (Amoros and Bornette, 2002, Bunn and Arthington, 2002, Schiemer and Zalewski, 1992, Schlosser, 1991). In riverine systems, the key driver of physical habitat heterogeneity is the interaction between geomorphology and flow (Copp, 1989, Lake, 2000a, Schlosser, 1991, Ward et al., 1998).

Given the profound influence of flow on river channel ecosystems, Bunn and Arthington (2002) proposed that aquatic species have evolved life history strategies adapted to natural flow regimes and their associated patterns of habitat availability (Principle 2). While there is a wealth of evidence supporting this principle from wetland and floodplains, there is less certainty concerning the role of individual flow events on Australian river channels.
Flow and physical habitat also influence the availability of resources required to sustain processes or populations. For example, flow influences the amount of dissolved organic carbon available to microbial decomposition which can, under appropriate conditions, lead to major blackwater events (Kerr et al., 2013). Flow also influences the amount of food available to higher trophic levels. For example, rate of primary production, whether by algae (Leland, 2003, Sherman et al., 1994) macrophytes (Franklin et al., 2008, Greet et al., 2013) or trees (Cunningham et al., 2009, Sims et al., 2009) are influenced by flow and then provide food or resources for microbial or metazoan communities.

Flow also has the capacity to influence competitive interactions. Bunn and Arthington (2002) proposed that flow mediated changes may facilitate the invasion and success of exotic and introduced species (Principle 4). For example, loss of flooding creates opportunities for riparian weeds (Catford et al., 2011) while stabilization of flows can promote willows (Stokes, 2008, Stokes and Cunningham, 2006). Within the fish community, both carp and Gambusia are believed to do better when flow regimes are modified (Gehrke et al., 1999, Walker et al., 1995).

Projects within this study focussed on two broad areas: ecosystem functions (primary production and decomposition) and responses of the fish community. Primary production (Figure 3) is the formation of organic matter by plants (macrophytes and algae). Algae and macrophytes provide a source of food (Bunn et al., 2003, Hladyz et al., 2012, Zeug and Winemiller, 2008), and habitat for many high level consumers (Humphries, 1996, Warfe and Barmuta, 2006). The rate of primary production in aquatic ecosystems is spatially and temporally variable and influenced by many factors besides flow, including light, nutrients, carbon dioxide (e.g. turbulence, depth, reach residence time) (Reynolds, 1996).
Decomposition (Figure 4) is influenced by flow which transports allochthonous organic matter (as particulate or dissolved material) into the water body (for example, during floodplain inundation (Junk et al., 1989)) and the location of autochthonous and allochthonous organic matter decomposition (Webster et al., 1999). Flow also degrades organic material by abrasion (Wipfli and Merritt, 1994; Ryder et al. 2004) releases organic matter from the soil matrix (Findlay and Sinsabaugh, 1999) and controls habitat quality for macro-invertebrates (Figure 5) (Gore et al., 2001) which in turn consume or shred organic material (Graça, 2001). Photodegradation is also promoted by low, shallow flows but inhibited by highly coloured or turbid water (Amon and Benner, 1996).
The second focus area was the fish community (Figure 6). The native fish community in the MDB has undergone significant modification with dramatic declines in the abundance and distribution of a significant proportion of the Murray-Darling Basin’s species. Of the 46 naturally occurring native species, 26 are of conservation concern (Lintermans 2007). These include species that have undergone localized extinction such as, Trout cod (*Maccullochella macquariensis*), and Macquarie Perch (*Macquaria australasica*) or suffered widespread or sudden rapid declines such as Silver Perch (*Bidyanus bidyanus*), Murray Cod (*Maccullochella peeli*) and Freshwater Catfish (*Tandanus tandanus*) (Lintermans 2007). Native fish have been subjected to a number of stressors, including over-exploitation (Humphries and Winemiller 2009), habitat loss (e.g. de-snagging, Koehn et al. 2004), population fragmentation due to barriers (Barrett and Mallen-Cooper 2006) and invasive species (Koehn 2004).
In addition to these stressors, flow modification has played a significant role in decline in the condition of the native fish community (Gehrke et al. 1995, 1999; Kingsford et al. 2011; Arthington and Pusey 2003). One of the key pathways by which flow modification is believed to affect native fish is through its influence of reproduction and recruitment. For example, recruitment of some Australian native fish species is cued by flooding while others appear dependent on low flows (Humphries et al., 1999). Understanding the ways that flow has affected native fish will be important in restoring native fish diversity in the MDB.
Floodplain and wetland ecosystems

Floodplains are ecotone ecosystems that straddle aquatic and terrestrial environments. The unpredictable and changeable hydrological regime across the floodplain creates a mosaic of varying habitat conditions in terms of water perenniality, depth and chemistry, the composition of terrestrial and riparian vegetation communities and submerged structural complexity (Amoros and Bornette 2002; Boulton and Brock 1999; Ralph and Rogers 2011). Floodplains may also contain more highly diverse aquatic communities than adjacent riverine habitats (Boulton and Lloyd 1991; Hillman and Shiel 1991).

Connectivity between the in-channel ecosystem and other flow-dependent ecosystems (e.g. floodplains) underpins two major conceptualisations of river systems: the River Continuum Concept (RCC) (Vannote et al., 1980) which emphasized the transport of organic matter from upstream to downstream, and the Flood Pulse Concept (FPC) (Junk and Wantzen, 2004) which highlights the importance of lateral connectivity in facilitating the exchange of organic matter between rivers and floodplains. These processes are critical for maintaining stocks of bioavailable carbon (Baldwin et al. 2013) and for the maintenance of populations of riverine species (Principle 3; Bunn and Arthington 2002).

In this project we focussed on four main elements of floodplain and wetland ecosystems: aquatic macrophytes (Figure 7), terrestrial floodplain vegetation (Figure 8), the relationship between Black Box (*Eucalyptus largiflorens*) and woodland bird communities (Figure 9) and frogs (Figure 10).
Flow dependent ecological responses

Figure 7. Conceptual model for Floodplain macrophytes

- Physical habitat
- Nutrients?
- Light availability
- Magnitude / area
- Timing
- Duration
- Depth
- Rate of rise and fall
- Flow velocity
- Frequency
- Sequence (pattern of events)
- Time since last event

Flow

Macrophyte primary production

- Competition
- Predators

Open water wetland, red gum and black box woodlands have different historic water regimes, as a result different macrophyte community structures and periods when habitat is suitable for macrophyte germination and establishment.

Floodplain inundation is predicted to have a positive effect on net floodplain primary production by:

a) Increasing soil moisture and producing conditions which enable macrophyte germination and growth.

b) It is uncertain how inundation will affect soil nutrient status and what effect this has on macrophyte production.

c) Flow will ultimately increase competition and predation but it is uncertain if this will result in increased or decreased primary production.

The strength of the relationships will change spatio-temporally and depending on habitat type:

a) Flood duration needs to be sufficient for germination and recruitment.

b) Flood duration will change interspecies competition (particularly light) as communities move through different successional stages possibly having a negative effect of production.

c) Changes in depth will favour particular species that have different growth rates and change light availability.

d) Rate of production will be influenced by season/temperature (timing)

Habitat Types
- Woodlands:
  - Black Box, Red Gum, Coolibah
- Wetlands:
  - Open water, Woodland
- Understorey/macrophytes:
  - Lignum
  - Nitregoosefoot
  - Canegrass
  - Phragmites
  - Typha
- Groundcover:
  - Grass/herb/forblands

Invasive spp
- Lippia
- Scleroleana
- Giant rush
- Terrestrialisation

Other factors affecting Target
- Grazing
- Fire
- Clearing
- Veg patch size and connectivity
- Extinction debts

Figure 8. Conceptual model for floodplain terrestrial vegetation

- Physical habitat
- Food production
- Competition
- Predators
- Floodplain vegetation

- Organic matter
- Nutrients
- Invasive spp
- Invertebrates
- Native mammals
- Bushbirds
- Waterbirds
- Reptiles
- Domestic and feral mammals (e.g. rabbits)

(vegetation community, metapopulation, population)
- Productivity (function)
  - Growth, condition
  - Reproduction – flowering, seedset, seedfall, viability
  - Dispersal
  - Germination
  - Seedling establishment
  - Survival
  - Biodiversity (assemblage / structure)
  - Species richness
  - Structural complexity
  - Age structure
  - Distribution and extent
  - Density
Flow dependent ecological responses

Figure 9. Blackbox and woodland bird conceptual model

- Event (on-site or adjacent)
  - Magnitude / area
  - Timing
  - Duration
  - Rate of rise and fall
  - Antecedent conditions (flow history)
- Regime (flow history on-site or adjacent)
  - Time since last event
  - Prior wetting frequency
  - No. of events in past 10 years
  - Degree of alteration from natural

- Flow
- Physical → Food → Competitors → Predators → Resident woodland birds
- Woodland type:
  - Black Box
  - Coolibah
  - Red Gum
  - Upland
- Wetland type:
  - Temporary
  - Semi-permanent
  - Permanent
- Structure and composition of:
  - Overstorey
  - Understorey
  - Groundcover
- New growth
  - Nectar
  - Seed
  - Invertebrates
- Invasive spp
  - Nomadic spp
  - Migratory spp
- Predators
  - Raptors
  - Reptiles
  - Foxes
  - Cats
  - Humans
- Other factors
  - Grazing
  - Fire
  - Clearing
  - Veg patch size and connectivity
  - Extinction debts

- Local rainfall
- Allocation
- Upstream rainfall

Breeding habitat vs. feeding habitat

Figure 10. Conceptual model for frogs

- Magnitude / area
- Timing
- Duration (hydroperiod)
- Frequency
- Sequence (pattern of events)
- Time since last event

- Flow
- Physical habitat → Food production → Competition → Predators → Target
- Terrestrial and semi-aquatic Macroinvertebrates
- Size ranges and nutrient value of macroinvertebrates
- Interspecific competition
- Predators:
  - Frogs
  - Water birds
  - Snakes
  - Foxes and pigs

- Population persistence
  - Age structure
  - Movement patterns
  - Recruitment into adult population

- Other factors affecting Target
  - Climatic patterns
  - Existing community structure, abundance of adults, reproductive fitness of adults
  - Habitat patchiness (availability of refuge habitats, connectivity and dispersal pathways)
  - Land use and terrestrial habitat

Spatial habitat types:
- Floodplain (spatial arrangement of rainfed, flood fed and persistent refuge habitats)
- Flooding pathways and movement corridors
- Wetland - hydrological heterogeneity
- Aquatic vegetation complexity and structure
- Tree hollows (tree frogs)
- Burrowing sites (burrowing species)/soil type, soil moisture, ground water quality and depth
Australian floodplain wetlands are areas of extraordinary biodiversity (Kingsford 1995; Boulton and Lloyd 1991; Roberts and Ludwig 1991). Yet, despite their ecological significance they are increasingly under threat in Australia (Kingsford 2000) and throughout the world (e.g. Sparks 1995). Water resource development is the principle threat to the decline in the number and health of wetlands (Dynesius and Nilsson 1994; Kingsford 2000; Bunn and Arthington 2002). The construction of dams and weirs, and the cumulative impact of diversions have either reduced connectivity or entirely isolated many floodplains and wetlands from their main river channel.

The broad implications of river regulation are widely known (see Bunn and Arthington 2002), and in wetland systems the impacts can vary from localised loss of aquatic species adapted to unpredictable flooding regimes, to complete transition of wetlands to terrestrial ecosystems. For taxa such as waterbirds, fish and frogs that utilise wetlands for breeding and rearing of their young, reduced flooding may have significant impacts on wider, regional-scale populations (Kingsford and Johnson 1999). However, we have very limited understanding about the possible lag effects of flooding, or how the less frequent, larger floods influence longer-term populations or processes (Kingsford et al. 1999).

**Precis**

Environmental flows, which involves providing water to an ecosystem to maintain its structure and functioning, aim to alleviate some of the effects of river regulation (Arthington 2012). However, water resource managers must aim to optimise the use and allocation of environmental water so they can efficiently meet multiple ecological targets. A key part of this process is to improve our understanding of the responses of organisms and processes to environmental flows. The aim of this project was to contribute to that improved understanding through a series of targeted field campaigns, which are described in this report.

Section 2 contains the research project reports. In general, each study is presented as a stand-alone report. However, this section commences with a description of the Edward-Wakool river system (Watts et al., Section 2.1), which is the study area for several subsequent research reports contained in this volume (Sections 2.2 to 2.6). Section 2 closes with a review of the importance of antecedent conditions for determining contemporary ecological responses to changes in flow.

Section 3 summarises the management and research implications of this work in terms of broader fields of research.
References


INTRODUCTION

This section provides background information on the study area, hydrology and study design for five CSIRO Flagship Cluster studies on the Edward-Wakool system within this SP3 report: in-channel inundation modelling (Section 5.2); whole stream metabolism (Section 5.3); leaf-litter breakdown rates in response to changes in flow regime (Section 5.4); invertebrate response to in-channel unregulated flow pulses and small in-channel environmental flows (Section 5.5) and; timing of fish spawning and recruitment in lowland river channel ecosystems (Section 5.6). We outline the approach used to assess ecosystem responses to in-stream environmental flows in the Edward-Wakool system. We describe the use of ‘control’ rivers to assess the benefits of the environmental flows and inform decisions on the timing, duration and magnitude of flows. The Flagship Cluster projects were conducted concurrently with other projects in the Edward-Wakool system (see Watts et al. 2013).

THE EDWARD-WAKOOL SYSTEM

The Edward-Wakool system in south-eastern Australia is a major anabranch and floodplain of the Murray River in the Murray-Darling Basin in southern-eastern Australia. It is a complex network of interconnected streams, ephemeral creeks, flood runners and wetlands intersected by irrigation channels. The system begins upstream of Deniliquin in the Barmah-Millewa Forest, and travels northwest before discharging back into the Murray River (Figure 1).

This system is considered to be important for its high native species richness and diversity including threatened and endangered fish, frogs, mammals, and riparian plants. It is listed as an endangered ecosystem, as part of the ‘aquatic ecological community in the natural drainage system of the lower Murray River catchment’ in New South Wales (NSW Fisheries...
Management Act 1994). Fish kills reported in 2007-08 and 2010 were related to hypoxic blackwater events and resulted in the loss of many hundreds of native fish.

![Location of the Edward-Wakool system in south-eastern Australia.](image)

**Figure 1** Location of the Edward-Wakool system in south-eastern Australia.

This system has a long history of regulated flows for irrigation, stock and domestic water supply and the water regime has been significantly altered with changes to the timing and volume of flows (Green 2001). Natural flows in the river system would have been high in spring and very low in summer and autumn. Between February 2006 and September 2010 there were periods of minimal or no flow in the Edward-Wakool system (Figure 2) due to severe drought conditions. At the break of the drought several large unregulated flow events occurred in the system between September 2010 and March 2011 (Figure 2).

![Daily discharge between 01/01/08 and 28/02/13 in three rivers in the Edward-Wakool system.](image)

**Figure 2** Daily discharge between 01/01/08 and 28/02/13 in three rivers in the Edward-Wakool system. Discharge data was obtained from NSW Office of Water website for three stations: Colligen Creek regulator (409024), Wakool River offtake regulator (409019), Yallakool Creek offtake regulator (409020).
Environmental watering in the Edward-Wakool system in 2011-12

The ecological objectives for environmental watering in the Edward-Wakool system focus on supporting the on-going recovery of this system following the drought (CEWO 2013), with a particular focus on supporting the condition and reproduction of native fish. This involves the delivery of instream flows to maximise available breeding habitat, create flow conditions favourable for reproduction or contribute to the survival of native fish. When very low flow periods are experienced, the focus of environmental watering is on the delivery of base flows to provide refuge habitat for fish and contribute to managing water quality issues.

In 2011-12 environmental water was delivered to this system on three occasions (Figure 3):

![Daily discharge in four rivers in the Edward-Wakool system in 2011-12. Discharge data was obtained from NSW Office of Water for four gauging stations: Colligen Creek regulator (409024), Wakool River offtake regulator (409019), Yallakool Creek offtake regulator (409020), and Little Merran Creek at Franklings Bridge (409044). Black triangles indicate timing of monthly sampling (From Watts et al 2013a).]
1. November 2011 environmental watering in Colligen Creek. The objective of this watering was to “encourage movement of large bodied native fish such as Murray cod, silver perch and golden perch to initiate spawning and recruitment of these species” (CEWO 2012a) and also to maintain and enhance in-stream habitat.

2. February 2012 environmental watering in Colligen Creek and the Wakool River. The objectives of this watering were to “provide opportunities for small-bodied fish to access important breeding and feeding habitat and improve the condition of the river and riparian ecosystems” (CEWO 2012b). The watering in the Wakool River was suspended on 6/3/2102 due to rainfall.

3. April to May 2012 environmental watering via irrigation escapes to the Edward and Wakool Rivers. The objective of this environmental watering action was to “provide and maintain refuge habitats for remnant fish populations, particularly Murray cod, from hypoxic blackwater that can severely impact fish” (CEWO 2012c).

**ASSESSMENT OF ECOSYSTEM RESPONSES TO ENVIRONMENTAL WATERING IN THE EDUCED-WAKOOL SYSTEM IN 2011-12**

The Edward-Wakool system provided a unique opportunity to assess responses to environmental watering. There are several distributary rivers in this system with regulators that control inflows. In addition, water can be delivered to several rivers via escapes from the Mulwala canal. This facilitates a comparison between rivers in close geographic proximity that are receiving environmental water (treatment rivers) with those not receiving environmental water (serving as ‘controls’). Such opportunities are relatively rare in testing the effectiveness of environmental flows as control systems are often difficult to find (Konrad 2011).

In 2011-12 four rivers (Figure 4) with differing hydrology were selected to assess ecosystem responses to environmental watering. Yallakool Creek, Wakool River and Little Merran Creek were controls for the November 2011 and February 2012 watering events, and Little Merran Creek served as a control for the environmental watering from March to May 2011 (Figure 4).

Parameters monitored in 2011-12 include water chemistry, whole stream metabolism, phytoplankton, biofilms, leaf-litter breakdown rates, zooplankton, macroinvertebrates, frogs, and fish movement, spawning, recruitment and population structure.

Sampling was undertaken at different temporal frequencies depending on the response time of the indicator. Sampling of fish larvae, zooplankton and water chemistry was undertaken fortnightly. Other parameters were sampled monthly.
CONCLUSION

The assessment of ecosystem responses to instream environmental watering in the Edward-Wakool River system was undertaken in 2011-12 using multiple indicators in multiple rivers, with some rivers serving as controls. Results of the Flagship Cluster studies on the Edward-Wakool system are contained in this SP3 report in sections 5.2 to 5.6.

ACKNOWLEDGEMENTS

We also thank the Wakool River Association and landholders in the Edward-Wakool river system for allowing access to their properties and their interest in this project. State Water Corporation provided information on river and escapes discharge and NSW OEH provided information on watering actions. Maps were prepared by Simon McDonald and Deanna Duffy (Charles Sturt University Spatial Analysis Unit). Monitoring and evaluation results referred to in this paper were funded by the CSIRO Flagship cluster project and the Commonwealth Environmental Water Office with in-kind contributions from Charles Sturt University, Murray Catchment Management Authority, Industry and Investment NSW, Monash University, NSW Office of Environment and Heritage.
REFERENCES


2.2 Lateral connectivity and availability of slackwater habitat in the Edward-Wakool system during in-channel flows

Watts, R.J.¹, Grace, M.², McCasker, N.¹, Watkins, S.¹, Bowen, P.³, Conallin, J.³

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² Water Studies Centre, School of Chemistry and School of Biological Sciences, Monash University
³ Murray Catchment Management Authority

INTRODUCTION

Growing awareness of the impacts of river regulation has led to increased interest in the delivery of environmental water to restore the ecological function of regulated river systems (e.g. Poff 2009; Arthington et al. 2010). The two major types of environmental watering are overbank flows that inundate wetlands and floodplains, and instream flows that are contained within the channel. Internationally, there have been a few high profile examples of the monitoring and evaluation of in-stream environmental flows, such as the experimental flood downstream of the USA’s Glen Canyon Dam in the mid-1990s (e.g. Shannon et al. 2001; Valdez et al. 2001) and more recently in 2009 (Cross et al. 2011), and an experimental flood in the Spöl River in Switzerland (Robinson et al. 2004). In Australia in-stream flows have historically been used to disperse algal blooms and other contaminants (e.g. Maier et al. 2004; Mitrovic et al. 2003). Prior to 2010 there were few examples in Australia where environmental water was used to create in-stream pulsed flows (Watts et al. 2009). The ecosystem benefits of this type of environmental watering action are not well understood and they are being assessed through monitoring and evaluation programs.

Inundation of riverbanks is important for river productivity and the creation of low flow zones (or slackwaters, having low velocities and shallow depths) is important for riverbank plants and the survival of organisms such as larval fish and larval shrimp through provision of habitat and food. Modelling is a useful method for comparing estimates of the extent of inundation under different discharge scenarios because it provides results more cheaply and efficiently than ground based survey methods.

Previous studies modelling river flow and floodplain inundation have been undertaken for wetlands on the Darling River (Shaikh et al. 2001), and floodplains on the Murrumbidgee River (Frazier et al. 2003) and the River Murray (Overton 2005; Overton et al. 2006). These studies have generally focussed on estimating floodplain inundation during overbank flows. The use of digital elevation models is considered to not give the best representation of floodplain inundation, because even small impediments on a predominantly flat floodplain can affect the models. However, in systems where environmental watering is contained within the channel, the use of digital elevation models to create flow path assessments below bankfull is an appropriate approach to compare the extent of in-channel riverbank...
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inundation under different discharge scenarios. Vietz et al (2013) used two dimensional hydraulic modelling to examine the impacts of flow regulation on slackwaters in the Broken River, south-eastern Australia. They demonstrated that the area of slackwaters decreased with increasing discharge until inundation of higher-elevation bars and benches.

The aim of this project was to undertake hydrodynamic modelling for four river reaches in the Edward-Wakool system to estimate the extent of wetted benthic surface area and the area of slackwater (0-0.02 m/sec) for six discharge scenarios, ranging from low flows up to bankfull flows. The modelling will contribute to the interpretation of ecological responses to flows, to decision making regarding the magnitude of environmental watering and will assist the communication of likely outcomes of planned watering events with landholders.

METHODS

Discharge scenarios were modelled for a 2 to 4 km reach of Colligen Creek, Yallakool Creek, Wakool River and Little Merran Creek. The study area was previously described in section 6.1. Each reach was represented within the hydraulic model using a digital elevation model (DEM) supplied by the Murray Catchment Management Authority-NSW. Several significant artefacts were removed from the Little Merran Creek and Colligen Creek DEMs to ensure normal stream flow was not impeded. Artefacts were removed by identifying erroneous elevation values and integrating corrected values directly into the elevation surface using a process of data fusion. To account for vegetation in each reach the surface friction coefficient (Manning’s n) within the model was set to a value of 0.05 with the exception of the Yallakool Creek site where a value of 0.04 was deemed more appropriate.

Estimates of daily discharge ML/day) at low flow, base flow, half bank and bankfull scenarios were provided by D. Green (MDBA). Six discharge scenarios were modelled for Colligen Creek and the Wakool River ranging from low flow to estimated bankfull flows (Table 1). In Colligen Creek the estimated half bankfull discharge (800 ML/d) was approximately the same as an environmental watering action undertaken in 2012. For Yallakool Creek the six discharge scenarios plus an additional discharge of 560 ML/d was modelled (referred to as environmental watering scenario) to estimate inundation resulting from an environmental watering action in Yallakool Creek between October and December 2012. In Little Merran Creek only three scenarios could be successfully modelled because the LiDAR survey was undertaken when discharge was approximately 200 ML/day, so the low flow and base flow scenarios could not be modelled in this system.

Discharge values were converted from ML/day to m³.sec⁻¹ and supplied to the model as static flow values. Discharge scenarios were modelled using the 2D grid implementation of Eonfusion Flood (Myriax Software) with model outputs post-processed using the GIS functionality of Eonfusion (Myriax Software). Post-processing, including surface area calculations, was achieved using Eonfusion (Myriax Software), Quantum GIS and made
distributable using Google Earth. Post processing was also undertaken to quantify the spatial configuration of four velocity categories:

- Zone 1: 0 – 0.02 m.sec⁻¹ (still water/slackwater)
- Zone 2: 0.02 – 0.3 m.sec⁻¹ (slow water)
- Zone 3: >0.3 m.sec⁻¹ (fast water)
- Zone 4: >0 m.sec⁻¹ (entire flow field)

Stable state data frames captured during the modelling were used as the starting point for determining the benthic surface area exposed to the four water velocity zones. Stable state data frames were converted into multiband raster data frames containing water depth, velocity and absolute elevation attributes. Multiband rasters were then converted into vector format, triangulated and trimmed to produce discrete spatial features for each velocity zone. Calculation of benthic surface area, and the depth range within each velocity zone, was undertaken on the 3D surface to take into account the vertical relief of the river bed. Summary statistics of the depth range (minimum, maximum, mean, standard deviation) were calculated for each velocity zone under each discharge scenario. Post-processing, including surface area and depth calculations, was achieved using Eonfusion Quantum GIS and Excel and made distributable using Google Earth.

Table 1. Summary of discharge scenarios modelled for the four focus reaches; Colligen Creek, Yallakool Creek, Wakool River and Little Merran Creek.

<table>
<thead>
<tr>
<th>Scenarios</th>
<th>Discharge (ML/day)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Wakool</td>
</tr>
<tr>
<td>1 - low flow (estimated)</td>
<td>25</td>
</tr>
<tr>
<td>2 - base flow (estimated)</td>
<td>50</td>
</tr>
<tr>
<td>3 - median flow (2011-2013)</td>
<td>110</td>
</tr>
<tr>
<td>Environmental watering</td>
<td>560</td>
</tr>
<tr>
<td>4 - half bank (estimated)</td>
<td>500</td>
</tr>
<tr>
<td>5 - maximum daily discharge (2011-2013)</td>
<td>1442</td>
</tr>
<tr>
<td>6 - bankfull (estimated)</td>
<td>3000</td>
</tr>
</tbody>
</table>

RESULTS

The estimates of wetted benthic surface area (Table 2) and representation of the spatial coverage of the water surface (Figure 1) illustrate that estimated low flow scenario, estimated base flow scenario and the median flow scenario for 2011-2013 were mostly constrained within the river channel.
In Colligen Creek, an environmental flow of 800 ML/day resulted in a 14% increase in wetted benthic surface area relative to the base flow of 200 ML/day. Similarly, in Yallakool Creek an environmental flow of 560 ML/day resulted in a 22% increase in wetted benthic surface area relative to the base flow of 170 ML/day (Table 2). The estimate of wetted benthic surface area during the maximum daily discharge scenario experienced in 2011-2012 during high unregulated flows (maximum daily discharge scenario) was considerably higher than during the modelled base flow or environmental flow scenarios in these rivers. On the peak of this unregulated flow event the wetted benthic surface area relative to the base flow 200 ML/day scenario is estimated to have increased by 47.8% in Colligen Creek and 59.7% in Yallakool Creek. The models estimate there would be a considerable further increase in wetted benthic surface area during a bankfull flow, however this type of flow event has not occurred since 2010.

In contrast, in Little Merran Creek the estimated half bankful and maximum discharge 2011-13 scenarios resulted in considerable lateral connection and inundation of low lying geomorphic features (Figure 1).

<table>
<thead>
<tr>
<th>Scenarios</th>
<th>Wakool</th>
<th>Yallakool</th>
<th>Colligen</th>
<th>Merran</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 - low flow (estimated)</td>
<td>42,196</td>
<td>33,159</td>
<td>43,257</td>
<td>-</td>
</tr>
<tr>
<td>2 - base flow (estimated)</td>
<td>43,587</td>
<td>38,169</td>
<td>48,292</td>
<td>-</td>
</tr>
<tr>
<td>3 - median flow (2011-2013)</td>
<td>46,222</td>
<td>41,510</td>
<td>49,982</td>
<td>160,908</td>
</tr>
<tr>
<td>Environmental watering</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>4 - half bank (estimated)</td>
<td>58,547</td>
<td>49,924</td>
<td>55,110</td>
<td>242,902</td>
</tr>
<tr>
<td>5 - maximum daily discharge (2011-2013)</td>
<td>200,455</td>
<td>60,989</td>
<td>71,337</td>
<td>542,584</td>
</tr>
<tr>
<td>6 - bank-full (estimated)</td>
<td>264,109</td>
<td>86,404</td>
<td>84,820</td>
<td>-</td>
</tr>
</tbody>
</table>

The relationship between discharge and wetted surface area in these rivers was not linear (Figure 2). The modelling has demonstrated that if there were a similar increase in discharge in two rivers, it would not produce in the same increase in wetted benthic surface area in the two rivers. For example, an increase from 200 ML/day to 800 ML/day in Colligen Creek resulted in a modelled 14% increase in wetted benthic area, whereas a similar increase from 170 ML/day to 800 ML/day in Yallakool Creek resulted in a modelled 30% increase in wetted benthic area (Table 2). There was a very large increase in estimated wetted surface area with increasing discharge in Little Merran Creek.
Figure 1 Maps showing representation the spatial coverage of the water surface in Colligen Creek, Yallakool Creek, Wakool River and Little Merran Creek under different discharge scenarios. Environmental watering occurred only in Colligen Creek and Yallakool Creek.
The representation of the spatial coverage of the benthic surface extent for each velocity zone for Colligen Creek is illustrated in Figure 3. There was a large area of slackwater available in the low flow scenario (63 % of the total available benthic surface area, 27,391 m²), but slackwater was very low during the base flow (9.8 %, 4,712 m²), median flow (6.4%, 3,184 m²) and half bankfull scenarios (3.1 %, 1,708 m²). Slackwater was created along the margins and particularly in low lying geomorphic in-channel features during the maximum discharge scenario (7.4 %, 5,308 m²) and bankfull scenario (13.6%, 11,575 m²)(Figure 3). The results for Yallakool Creek and the Wakool River are not presented here, but were similar to those for Colligen Creek.
Figure 3 Maps showing the spatial coverage of the water surface extent for each velocity zone in Colligen Creek under different discharge scenarios.
The spatial coverage of the benthic surface area for each velocity zone in Little Merran Creek is presented in Figure 4. In contrast to the results for Colligen Creek, in Little Merran Creek there was a large percent of slackwater available for the median flow scenario (70% of the total available water surface area). Slackwater was also abundant during the half bankfull scenario (25.5%) and maximum discharge scenario (41.5%). Only a very small percent of the area was classed as fast water in each of these scenarios.

**DISCUSSION AND CONCLUSION**

The in-channel hydrodynamic modelling results demonstrate that the relationship between discharge and wetted surface area and the area of slackwater in these four rivers in the Edward-Wakool system is not linear and is most likely strongly influenced by geomorphology. Similar to the findings of Vietz et al. (2013), we found that in some river reaches (e.g. Colligen Creek) the area of slackwaters decreased with increasing discharge until inundation of higher-elevation bars and in-channel benches. However, in another river
reach (e.g. Little Merran Creek) a different pattern was observed with large area of slackwater available at a range of different discharges. As the data presented here are for only a small 2-4 km section of each river, it is important to consider that the relationships may be reach specific and that these relationships need to be examined over longer river distances in the study rivers.

These results have important implications for studies of ecology-flow relationships for in-channel flows. They suggest it may be more appropriate to examine the relationship between inundation area and ecosystem responses to in-channel flows rather than focussing on relationships with daily discharge data, as has commonly been the practise.

In-channel hydrodynamic modelling under different flow scenarios can be used to:

i) better understand the relationship between in-channel flows and ecosystem responses,

ii) predict the consequences of in-channel flows on slackwater dependent biota and ecosystem functions, and

iii) facilitate better planning and management of the future in-channel environmental flows. In particular it may assist managers examine trade-offs between ecosystem benefits and third party impacts, such as inundation of private land, prior to the delivery of environmental water. The modelling can help managers determine the optimum discharge at which there can be an increase in inundation and creation of slackwater to produce ecosystem responses to environmental flows, but with minimal third party impacts.

ACKNOWLEDGEMENTS

Thanks to the Wakool River Association and landholders in the Edward-Wakool river system for allowing access to their properties and their interest in this project. Maps were prepared by Simon McDonald and Deanna Duffy (Charles Sturt University Spatial Analysis Unit). The modelling was undertaken by Dr Hugh Pederson from Marine Solutions. The modelling presented in this paper was partly funded by CSIRO Flagship cluster project with cash contributions from Charles Sturt University, Murray Catchment Management Authority and Monash University.

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2.3 Whole stream metabolism

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This section examines the effects of stream flow on metabolism. The collected diel dissolved oxygen profiles are interrogated to explore the relationships between the key variables controlling metabolism (light, nutrients, organic carbon supply) and the metabolic parameters (primary production and ecosystem respiration). Flow effects are both direct – through scouring of biofilms and inundating previously dry bank areas – and indirect, through mediating supply of nutrients and carbon as well as altering water column light attenuation through increased turbidity.

INTRODUCTION

‘Whole Stream Metabolism’ provides estimates of rates of the key ecological processes of photosynthesis and respiration (Odum 1956) by measuring the production and consumption of dissolved oxygen gas (‘DO’). Aquatic ecosystems need photosynthesis to generate new biomass (food for higher trophic levels) and respiration to break down plant and animal detritus to recycle nutrients to enable such growth (Figure 1). Hence metabolism provides assessment of the energy base underpinning aquatic foodwebs.

Rates vary seasonally as warm temperatures and increasing direct sunlight enhance primary production; warmer temperatures and fresh organic carbon increase ecosystem respiration. Streams with naturally higher concentrations of nutrients and with open canopies have much higher natural rates of primary production than forested streams (Roberts and Mulholland 2007).

Low process rates limit the amount of food (e.g. bacteria, algae and water plants) available to consumers, constraining the populations of larger organisms including fish and amphibians. Unnaturally low rates can indicate introduced agrochemicals (e.g. Ruzycki et al. 1998). Sometimes rates of these processes are particularly high. Such elevated primary production usually indicates excessive plant growth (e.g. pondweed (Potamogeton sp. and Azolla sp.) and more problematically algal blooms (often cyanobacteria), with the well-defined range of deleterious effects including blocking of sunlight (mortality of submerged plants), possible toxin production (affecting drinking water for animals and humans) and large swings in diel DO (including predawn anoxia with potential fish kills) (Paerl et al. 2001). When an algal bloom eventually collapses, there is usually widespread anoxia, often accompanied by toxin release.
Many of the factors controlling stream metabolism are mediated by stream discharge patterns. For example, Uehlinger (2000) demonstrated that scouring caused by higher water velocities after rainfall can ‘reset’ primary production to very low rates, which are then maintained until primary producer biomass is re-established, typically over a period of several weeks. Resource limitation of metabolic rates may be overcome when materials (organic carbon, nutrients) are transported into the stream channel by higher flows. These materials may originate within the stream channel or on the floodplain. Higher discharges normally result in greater stream power and the ability to carry and resuspend larger particles (Gordon et al. 2004) which may then inhibit primary production (Oliver et al. 1997).

Vink et al. (2005) examined the effects of irrigation flow releases on the middle reaches of the Murrumbidgee River and found that these releases stimulated primary production through addition of bioavailable P and also stimulated ecosystem respiration through additional organic carbon. Consequently, in this current study, metabolic parameters have been measured under a range of discharge conditions to assess how flow changes impact on rates of primary production and ecosystem respiration and hence the energy base of these aquatic foodwebs.

**METHODS**

**Metabolism Measurements**

Rates of primary production and respiration can readily be estimated by continuously recording DO, temperature and photosynthetically active radiation (PAR) over many months, under a range of meteorological conditions and flows (Grace and Imberger 2006).

![Figure 1 Relationships between photosynthesis (algae and plants) and respiration (bacteria and fungi) with inputs of energy and organic matter, highlighting the role of sunlight, nutrients, dissolved gases and food resources.](image)
Rates were calculated for each day so that the relative influences of flow, cloud cover and season could be deconvoluted. DO changes in a sinusoidal pattern over 24 hours (Figure 2), with DO increasing once the sun comes up, reaching a peak in mid-late afternoon (due to photosynthesis throughout daylight hours) and then declining overnight, as ecosystem respiration (which consumes DO) continues 24 hours a day. Gross primary production and ecosystem respiration rates, plus reaeration (physical re-equilibration of DO to 100% saturation across the air-water interface) were calculated daily from each diel data set, using the daytime regression method (Atkinson et al. 2008). Only parameter estimates from diel curves which reasonably matched the sinusoidal shape (Figure 2), and where the inverse modelling approach produced excellent fits ($r^2 > 0.80$) to these diel curves, were included in the subsequent analysis.

![Typical Dissolved Oxygen (DO) Concentration profile over a 24 hour period. Data were from the Wakool River at Moorabee, on 18th September, 2011.](image)

Battery-powered ZebraTech data sondes, attached to star pickets in the thalweg at least 30 cm below the water surface under base flow conditions, recorded DO and water temperature every 10 minutes. Every month, data were downloaded and the sondes recalibrated. PAR data were also recorded at the same frequency in open fields near each of the stream sites to avoid shading of the sensor by individual trees (hence the PAR sensor accounts for effects of cloud cover).

Samples for bioavailable nutrient analysis (FRP, ammonia and NOx) were collected monthly from the thalweg of each stream, then filtered through a 0.2 μm membrane at the time of sampling. Samples were stored on ice then frozen before transportation to the laboratory.
Nutrient analysis was undertaken by the NATA-accredited laboratory at the Monash University Water Studies Centre.

**Study sites**

Two DO sondes were used in each of the four study streams, Wakool River and Little Merran, Colligen and Yallakool Creeks, with each sonde pair separated by 1-4 river km. The overall study design and site information are described in section 6.1.

**RESULTS AND DISCUSSION**

Rates of gross primary production rates (‘GPP’), ecosystem respiration and daily discharge varied as a function of time for the Wakool River and Yallakool Creek (Figures 3 and 4) and for Colligen and Little Merran Creeks (Figures 5 and 6).

*Figure 3. Gross Primary Production (GPP) rates and stream discharge (ML/Day) for the Wakool River and Yallakool Creek from July 2011 to April 2012. The green ovals identify GPP during and immediately after the October 2011 flow event on the Wakool River. Data from both upstream and downstream sondes at each site are included.*
Flow dependent ecological responses

Figure 4 Ecosystem Respiration (ER) rates and stream discharge (ML/Day) for the Wakool River and Yallakool Creek from July 2011 to April 2012. The brown arrows indicate the trend in ER after the flow events in the Wakool River in September and October 2011; the black arrows show contemporary trends in Yallakool Creek. Data from both upstream and downstream sondes at each site are included.

Figure 5 Gross Primary Production (GPP) rates and stream discharge (ML/Day) for the Little Merran and Colligen Creeks from July 2011 to April 2012. The green arrow indicates the trend in GPP after the flow event in Colligen Ck in Aug-Sep 2011; the black arrow shows the contemporary trend in Little Merran Creek. Data from both upstream and downstream sondes at each site are included.
Rates of primary production and respiration remained relatively constant over the entire study period. There were longer term (seasonal) trends where both primary production and respiration rates increased during summer due to increased water temperatures, and for primary production, more hours of sunshine. For days when flow was rapidly changing, during and immediately after heavy rainfall or major water releases, the model was unable to adequately estimate metabolic rates. When successful model fits were obtained during high flow events, these mostly showed a highly significant depression in rates of primary production. For example, data within the small green oval compared to the larger oval, during and after environmental watering in October-November 2011 (Figure 3). The large green oval (Figure 3) indicated a stimulation of GPP in the two weeks after the October 2011 flow in the Wakool River. The increase was above the seasonally-related upward trend detected in the Yallakool Creek (Figure 3). This could be attributed to an influx of nutrients from the flow event. Similarly, ER increased more after the flows in the Wakool River (brown arrows, Figure 4) than could be attributed to warming temperatures alone (black arrows for Yallakool Creek). The influx of fresh organic material during the flow probably caused this enhanced respiration in the Wakool River.

The stimulatory role of a flow event is also seen in the slightly greater enhancement of GPP in Colligen Creek in the months after the large unregulated flow in late August-early September 2011 (and subsequent smaller flows) when compared to the GPP increases in Little Merran Creek: the slope indicated by the green arrow for Colligen Creek is significantly higher than that for Little Merran Creek.
greater \((p = 0.003)\) than the black arrow for Little Merran Creek (Figure 5). Increases in Ecosystem Respiration in these two creeks tracked each other over this October-December period (Figure 6). In summary, the effects of these discharge events on ecosystem metabolism rates were relatively small and idiosyncratic. This lack of a large response to flow events is almost certainly due to the constraint of the additional water to the existing stream channel and the low nutrient and organic carbon concentrations in the water comprising the flow events. This finding is likely to be replicated in other catchments with low nutrients (with the proviso that the water introduced by flow events is also low in these analytes). Reasons for this behaviour are discussed below.

At no stage did any of the loggers record very low dissolved oxygen concentrations \(< 20\%\) DO saturation, even during or straight after high flow events. Elevated flows decreased %DO maxima each day by 0-20\% and also decreased minimum %DO by the same magnitude. Consequently, the environmental flows in November and February did not constitute a black water event. Although these flows filled low-lying backwater areas, they did not spread onto the floodplain. When this happens, water remains for days-weeks and then returns commonly producing ‘black water’ (high dissolved organic carbon and very low or no dissolved oxygen; Howitt et al. 2007).

There was considerable variation in GPP and ER rates within each river (Table 1). The P/R ratio measures the balance between primary production and ecosystem respiration rates; a value of \(< 1\) indicates that more organic carbon was being consumed in the study reach than was produced by primary production. The source of this organic carbon may have been from overbank flow, upstream in the catchment or from riparian vegetation. Primary production within the stream channel was also an extremely important contributor to organic carbon supply, sustaining high level consumers in the food web.

The rates (Table 1) were at the lower end of the typical range found for non-polluted, slow flowing rivers elsewhere in the world (e.g. Bernot et al. 2010; Marcarelli et al. 2011). They were also similar among these four streams with median primary production rates differing by less than a factor of two and respiration by less than a factor of three. This is unsurprising given the similarity in land forms, biogeography and stream size. Median P/R ratios indicate that for almost all the time these rivers were net heterotrophic \((P/R < 1)\) indicating that there must be an external source of organic carbon fuelling respiration.
As light (PAR) is required for photosynthesis, it might be expected that an increase in light would increase rates of GPP. However, there were only weak positive relationships (e.g. Yallakool: \( GPP = 0.158 \times \text{PAR} + 0.881, \ r^2 = 0.37, \ p < 0.001 \); Wakool: \( GPP = 0.092 \times GPP + 1.33, \ r^2 = 0.027, \ p = 0.044 \)), with an extremely large variation in GPP at any particular PAR. This variability at a fixed PAR indicates that another factor (or factors) was contributing heavily to controlling GPP. One such factor was the presence and quantity of organisms (autotrophs) capable of photosynthesis. In the water column, photosynthesis can only occur when there is sufficient light. Turbidity or ‘cloudiness’, caused by suspended fine soil and sediment particles, limits how far light can penetrate into the water column. The point below which photosynthesis is no longer biologically viable is known as the ‘euphotic depth’, \( Z_{eu} \). We used the empirical turbidity-euphotic depth relationship from the Darling River (a large, turbid, lowland river; \( Z_{eu} = 4.6 / (0.04 \times \text{Turbidity} + 0.73) \) (Oliver et al., 2000)) to estimate \( Z_{eu} \) in our study rivers. There was considerable variation in the euphotic depth for each river based on the regular measurements of turbidity (Table 2).
The euphotic depths indicate that for all river reaches deeper than $Z_{eu}$, insufficient light will reach the sediment surface to allow plants (macrophytes, benthic algae) to grow. Biofilms will be restricted to shallow regions on the stream edges. This will decrease the overall primary productivity of the rivers. Site observations throughout the study period confirmed that macrophytes were confined to shallow marginal areas within the stream channel. Benthic algae were noted in the littoral zones and also seen in drying sediment after the recession of higher flows.

Increasing water temperatures associated with seasonal change result in faster physiological rates in individual organisms and hence it was expected that higher temperatures would result in greater rates of GPP and ER. This hypothesis was confirmed. Table 3 shows that there were highly significant linear relationships between daily water temperature and GPP and respiration (Table 3). It is pertinent to note that temperature is one of several controlling variables (along with light, nutrients, organic carbon), hence a “high” $r^2$ is not necessarily expected here.
The temperature relationship with GPP and ER rates (Table 3), indicated a potential problem during hot, dry summers. High water temperatures automatically mean lower dissolved oxygen solubilities. This is rarely problematic as, even at 40°C, solubility is 6.4 mg O_2/L, well above the ANZECC trigger value of 4.0 mg O_2/L. However, as temperature increases, the net drawdown of O_2 also increases as respiration rates increase more rapidly with temperature than GPP. This net drawdown increases the likelihood of suboxic, even anoxic conditions, with fish kills being one likely consequence (Paerl et al. 2001). It is highly pertinent to note that re-aeration across the air-water interface is significantly higher from a moving water column than from a still one, especially if this current increases water turbulence (Demars and Manson 2013). Thus maintenance of even slow flow rates by periodic environmental releases is far preferable to standing water in the streams as a means of addressing potential anoxia during hot, dry periods. This is a different scenario to ‘blackwater’ events, where rapid oxygen drawdown is induced by direct contact with high levels of organic carbon on the floodplain.

Nutrients, particularly nitrogen and phosphorus, are key controllers of photosynthesis. The bioavailable nutrient concentrations in the water column of the rivers in this study were extremely low, as shown in Figure 7. In most cases, the nitrate (NO_3) concentration was below the detection limit of 1 μg/L. The ANZECC Water Quality Guidelines (ANZECC 2000) typically recommend that the risk of algal blooms (and other adverse outcomes) in lowland rivers in south-eastern Australia is minimised when bioavailable concentrations are below 20, 20 and 40 μg/L for ammonia, FRP and NOx respectively. The median concentrations in the four rivers were nearly an order of magnitude lower than these levels. Occasional high values coincided with the large flow events in mid-March 2012 which would also have decreased the overall primary productivity of the rivers.
Figure 7 Summary of monthly sampling of bioavailable nutrient concentrations in the four study streams (September 2011 to April 2012). Note that the concentration axis is on a logarithmic scale for ease of presentation. All concentrations less than the detection limit of 1 μg/L are plotted as 0.5 μg/L. The boxes represent the data range 25th to 75th percentile, with the ‘middle’ line in the box being the median. The “whiskers” indicate 10th and 90th percentiles in the data. Outliers are shown as circles.

This nutrient limitation of primary productivity means that large algal blooms are unlikely in these streams. It also indicates that at least good land management practices and nutrient uptake by benthic biofilms and macrophytes are effective in keeping nutrients from human activities (including fertilizer usage in agriculture) from entering these waterways in problematic concentrations.

REFERENCES


2.4 Leaf-litter breakdown rates in response to changes in flow regime

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2 Water Studies Centre, School of Chemistry, Monash University - Clayton, Australia
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INTRODUCTION

Primary production and leaf-litter breakdown rates are key ecosystem functions which are well recognised river health metrics in the literature but are not routinely undertaken in bioassessment monitoring programs (Gessner and Chauvet 2002; Woodward et al. 2012). Functional assessments usefully synthesise responses across entire ecosystems (Kingsford et al. 2010) and provide the information needed to understand the processes which underpin negative impacts, such as hypoxic blackwater events and fish kills (Hladyz et al. 2011b).

Leaf-litter breakdown has been proposed as a useful functional indicator of river health because it responds to natural (e.g. climate) and anthropogenic stressors (e.g. organic pollution, land use) and is relatively easy to measure with inexpensive equipment (Gessner and Chauvet 2002; Young et al. 2008; Hladyz et al. 2011a). The rate of litter break-down represents an integrated response to both biological (microbial degradation via fungi and bacteria, invertebrate feeding by shredders) and physical (i.e. abrasion, fragmentation by current) processes (Webster and Benfield 1986). This makes it useful as a bioassessment tool (Gessner and Chauvet 2002; Young et al. 2008; Hladyz et al. 2011a). Litter breakdown rates respond to various aspects of the flow regime (e.g. flow magnitude, flow velocity, timing of flows, Ferreira et al. 2006; Watkins et al., 2010; Niu and Dudgeon 2011). However, the understanding of functional responses to altered flow regimes is limited (Poff and Zimmerman 2010).

We conducted a study that examined the effects of two environmental flow pulses on leaf-litter breakdown rates in Colligen Creek, a regulated river in the Edward-Wakool river system, NSW, south eastern Australia. We hypothesised four different mechanisms whereby flow pulses could influence leaf-litter breakdown rates (see leaf-litter breakdown conceptual model in Appendix).

1. Increased flows increase abrasion, increasing breakdown rates.
2. Increased flows disturb shredder communities, reducing breakdown rates.
3. Increased flows increase organic matter supply from river margins, providing an excess of resources to shredders, decreasing breakdown rates.

4. Increased flows result in wash-out of organic matter, resulting in a shortage of resources to shredders, increasing breakdown rates.

To test these hypotheses, we compared leaf-litter breakdown rates in Colligen Creek (which received environmental flows and unregulated flows) with rivers that received only unregulated flow pulses (Wakool River, Little Merran Creek) or no flow pulses (Yallakool Creek).

METHODS

Study sites

Study design and study site information is provided in Section 2.1.

Leaf-litter breakdown rates

Leaf-litter breakdown rates assessed overall changes in flow regime among the four rivers. Two sites were chosen per river to examine the variability within each river. The field study was done during early spring 2011 (late September) and early autumn 2012 (March) and ran for six months. Placement of litter bags occurred after the large unregulated flow pulses in September therefore breakdown rates were not influenced by these flows.

Methods used were based on a standard approach (see Hladyz et al. 2010). Leaves of two common native trees, river red gum (*Eucalyptus camaldulensis*) and blackwood (*Acacia melanoxylon*), were collected. Browning pre-abscised (leaves were collected from branches that had fallen recently onto the ground from gusts of wind) river red gum leaves were collected from floodplain forest. Blackwood leaves were collected immediately after abscission. These species were chosen because they are widespread in southeast Australia and because they differ markedly in terms of resource quality, with the former having higher carbon: nutrient ratios (Glazebrook and Robertson 1999; Wedderburn and Carter 1999). All leaves were air-dried to constant mass and five grams (±0.25 g) of air-dried leaf material was added to experimental plastic-mesh bags of two mesh aperture sizes. The mesh size of 0.5mm (which excludes macroinvertebrates) was used to measure leaf-litter breakdown due to microbial breakdown and abrasion by fine sediments. A mesh size of 10mm was used to measure total breakdown caused jointly by microorganisms, invertebrates and physical processes. Metal stakes were anchored on the river banks and litter bags were attached and weighed down with lead weights within each reach. Of the 4 rivers each was sampled on 6 occasions (monthly; 2 replicates x 2 mesh sizes x 2 leaf species x 2 reaches x 4 rivers), thus giving a total of 384 litter bags (64 litter bags per monthly sampling). On each sampling occasion bags were collected with a 250 µm mesh net (to trap accompanying macroinvertebrates), placed in ziplock bags and then frozen.
laboratory after thawing, leaf material was separated from invertebrates (using a 250 µm sieve), and sorted leaf material was oven-dried at 105°C to constant mass and then weighed. Breakdown rates were expressed as proportion of mass remaining. Correction factors derived for leaching losses (determined after 24 h under running tap water in the laboratory) and moisture content were applied to the initial air-dry masses, to calculate post-leaching dry mass loss over time (after Hladyz et al. 2009). Macroinvertebrate data from bags are not presented here.

Data analyses

Exponential breakdown decay coefficients (-k) were estimated using linear regression analyses on ln(x) transformed dry mass data. This calculated decay coefficient allows comparisons with other studies and can be used to estimate the time required for 50% of the leaf litter to breakdown. Decay coefficients were classified according to the scheme of Petersen and Cummins (1974). “Fast” breakdown groups decay coefficient > 0.010, “medium” groups are between 0.005 – 0.010 and “slow” groups <0.005. An analysis of covariance (ANCOVA) was used to test for differences in breakdown rates between treatments with time as the covariate (Boulton and Boon 1991). Among rivers, leaf species and mesh-sizes were analysed separately. Within rivers, mesh-sizes were analysed together to examine varying contributions from differing agents of breakdown (i.e. microbial degradation vs. macroinvertebrate feeding and mechanical fragmentation).

RESULTS AND DISCUSSION

Breakdown rates were similar among rivers for coarse and fine-mesh bags for both litter types (Table 2, Figure 1). For river red gum, in comparison to other studies decay coefficients from coarse-mesh bags in the Edward-Wakool system were categorised with the “fast” processing category and were similar to values from a study carried out in the Murray River (Table 3). Values calculated from fine-mesh bags were categorised with the “medium” processing category and were more similar to processing rates in wetlands and a temperate rainforest stream (Table 3). Within rivers, red gum breakdown rates in Colligen Creek were approximately 1.7 times faster in coarse-mesh than fine-mesh bags (Table 4). In contrast, in the other three rivers there was more variability in breakdown rates and rates did not differ between coarse and fine-mesh bags (Table 4). These findings suggest that increases in unregulated flows and environmental flows in Colligen Creek may affect breakdown by physical fragmentation of litter and potentially increased abrasion from suspended particulate material (Bird and Kaushik 1992; Lepori et al. 2005; Paul et al. 2006) or via increased invertebrate shredding (Ferreira et al. 2006). Shredder abundances in the Edward-Wakool system were relatively low which may suggest that the differences between mesh sizes may be more attributed to physical fragmentation via increases in flow.
Figure 11 Leaf-litter breakdown rates (-$k$) of river red gum (A) and blackwood leaves (B) in four rivers in the Edward-Wakool system. Solid bars denote coarse-mesh and hatched bars denote fine-mesh. Data displayed are mean values ± 1 SE.
Table 2 Analysis of covariance (ANCOVA) of leaf-litter breakdown rates comparing among rivers. Results displayed are the time by leaf-litter interaction term (comparison of slopes)

<table>
<thead>
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<th>LITTER TREATMENT</th>
<th>DF</th>
<th>RESIDUAL DF</th>
<th>F-RATIO</th>
<th>P</th>
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Blackwood leaves in coarse and fine-mesh were in the “slow” processing rate category and were slower than values calculated from other streams in south-eastern Australia (Table 3). Within rivers, blackwood breakdown rates did not differ between coarse and fine-mesh bags (Table 4). Blackwood leaf-litter breakdown rates in Colligen Creek were similar between mesh sizes, though these leaves were less refractory than river red gum (slower to breakdown) and therefore may be more resistant to physical fragmentation via flow. Blackwood leaf-litter breakdown rates between mesh-sizes were also similar in the other three rivers suggesting microbial degradation of leaf-litter was the primary agent in controlling breakdown rates in the Edward-Wakool system (Table 4).

Table 3 Decay coefficients (\(-k\)) and half-lives (\(T_{50}\) in days) of River Red Gum (RRG) and Blackwood (B) leaves compared with published data. Category refers to the processing categories of Petersen and Cummins (1974) “Fast” breakdown groups decay coefficient > 0.010, “medium” groups, 0.005 – 0.010 and “slow” groups < 0.005. "Double exponential models used to calculate decay coefficients

<table>
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<th>LEAF</th>
<th>(-k(D^{-1}))</th>
<th>(T_{50}) (D)</th>
<th>CATEGORY</th>
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<td>RRG</td>
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<td>58 / 100</td>
<td>F / M</td>
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<td></td>
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<td>RRG</td>
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<td>F / M</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td>98.51, 0.004*</td>
<td>134 spring</td>
<td>M</td>
<td></td>
</tr>
<tr>
<td>Wetland</td>
<td>10</td>
<td>RRG</td>
<td>10.281, 0.007*</td>
<td>70</td>
<td>M</td>
<td>Janssen and Walker (1999)</td>
</tr>
<tr>
<td>Stream</td>
<td>Leaf pack</td>
<td>B</td>
<td>0.005</td>
<td>141</td>
<td>M</td>
<td>Campbell et al. (1992)</td>
</tr>
<tr>
<td>Stream</td>
<td></td>
<td>B</td>
<td>0.007</td>
<td></td>
<td>M</td>
<td>O’Keefe and Lake (1987)</td>
</tr>
</tbody>
</table>
Leaf-litter breakdown rates did not show any marked differences among rivers and were highly variable and therefore may not be a good indicator for changes in flows. There was some evidence that differences in rates between the coarse and fine mesh bags were higher in Colligen Creek which received environmental flows, suggesting that physical abrasion may be an important underlying mechanism driving processing rates. In general however, there was no clear evidence that the delivery of environmental water alters rates of leaf-litter processing in these rivers. This may suggest that leaf-litter breakdown rates are not sensitive to changes in hydrological regimes or to the delivery of environmental flows in the Edward-Wakool system, or that the positive and negative impacts on breakdown are acting to cancel one another out (see hypotheses).

The lack of a response in the coarse mesh bags (measuring macroinvertebrate-mediated breakdown) may be due to the low densities of shredders (leaf-eating invertebrates) in the Edward-Wakool system (Hieber and Gessner 2002). Other studies have also found no effect on breakdown rates from restoration of natural flow regimes or reduced flow variation (Muehlbauer et al. 2009; Casas et al. 2000) and have suggested that other factors such as heavy sedimentation of leaf bags and high magnitude flows can override any differences between controls and restored or impacted sites. Studies which have found differences in breakdown have found contrasting responses to reduced flow variation, including faster litter breakdown rates (Short and Ward 1980) and slower breakdown rates (Nelson and Roline 2000; Mendoza-Lera et al. 2012). No consistent patterns with provision of flows have emerged to date from published studies, or the current study, and it is likely that understandings of underlying mechanisms that drive differences in processes are needed.
ACKNOWLEDGEMENTS

We extend our thanks to the Wakool River Association and landholders in the Edward-Wakool river system for allowing access to their properties and for their keen interest in this project. Field surveys and community liaison were supported by staff at the Murray Catchment Management Authority, with particular thanks to Josh Campbell and Patricia Bowen. Vincent Kelly at the State Water Corporation provided information on river and escapes discharge. We thank Josh Campbell, Anthony Conallin, Philip De Zylva, Chris McCormack, Kelsey Tucker and Katrina Wilson for assisting with field and/or laboratory work. This project was funded by the Cluster Collaboration Fund and the Ecological Responses to Altered Flow Regimes Research Cluster which represents a collaboration between the CSIRO Water for a Healthy Country Flagship, Griffith University, the University of New South Wales, Monash University, Charles Sturt University, La Trobe University and the Arthur Rylah Institute of the Victorian Department of Sustainability and Environment. The project also was supported by in-kind contributions from Commonwealth Environmental Water, Charles Sturt University, Murray Catchment Management Authority, and Monash University.

REFERENCES


2.5 Invertebrate response to in-channel unregulated flow pulses and small in-channel environmental flows

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INTRODUCTION

Balancing human demands for water and the ecological integrity of regulated rivers is a complex issue. There is general acceptance in society that the river is a legitimate user of water to sustain aquatic biodiversity and ecological functions (Naiman et al. 2002). In support of this, there is increasing investment in the restoration of natural flow regimes through managed water releases from reservoirs, or through the return of flow to rivers and wetlands via a reduction in abstraction (Feld et al. 2011; Pittock and Finlayson 2011). Returning water to regulated rivers as ‘environmental flows’ can improve ecosystem condition by mimicking a more natural flow regime and potentially restoring natural ecological processes and patterns (Arthington et al. 2010). The financial costs of delivery of environmental flows are large (e.g. in terms of opportunity cost for irrigation water) and a means of demonstrating the ecological benefits from these flows is greatly needed by water managers.

Few studies have explicitly tested if delivery of environmental flows to regulated rivers can improve biodiversity. Invertebrates are a major component of the biodiversity of flowing water systems and are a critical resource to high trophic levels such as fish (Balcombe et al. 2005; Strayer 2006). Invertebrate communities have been widely used as biological indicators, as they are abundant, diverse, occupy a range of ecological niches and can respond relatively quickly to changes in environmental management, due to their relatively rapid life-histories (Norris and Thoms 1999; Chessman 2003). Altered flow regimes in regulated rivers can influence invertebrate communities through changes in food and physical habitat availability (Bunn and Arthington 2002; see invertebrate conceptual model in Appendix). In the few studies that have looked at environmental flows in relation to invertebrate biodiversity, effects on invertebrate communities are variable. Environmental flows can increase (Mackie et al. 2003; Chester and Norris 2006) or decrease invertebrate richness (White et al. 2012), and either alter (Lind et al. 2007) or not alter community composition (Brook et al. 2011).

We conducted a study that examined the effects of two environmental flows on invertebrate biodiversity (abundance, biomass, taxon richness, composition) in Colligen...
Creek, a regulated river in the Edward-Wakool river system, NSW, south eastern Australia. We predicted that environmental flows would increase invertebrate biodiversity and alter community composition through the provision of additional habitat and food resources. To determine this, we contrasted Colligen Creek with rivers that received only unregulated flow pulses (Wakool River, Little Merran Creek) or no flow pulses (Yallakool Creek).

**METHODS**

**Study sites**

Study design and study site information is provided in Section 2.1.

**Invertebrate abundance, biomass, taxon richness and composition**

Sampling methods were consistent across all rivers. Macroinvertebrate communities were sampled each month for seven months, from September 2011 until March 2012. A small snag bag sampler (70 cm length, 250 µm mesh) was used to estimate ambient invertebrate abundance and characterise community structure on small natural snags (small woody debris, approx 50 cm length, surface area: 450 cm$^2$) (after Growns et al., 1999). These snags were collected by approaching from downstream and placed quickly into the snag bag with as little disturbance to the invertebrates on the snag as possible. All surfaces were scrubbed vigorously to dislodge invertebrates into the collecting jar at the bottom of the snag bag sampler. The surface area of each snag was calculated by measurement of snag length and diameter after all animals were removed. The invertebrate sample was then frozen until further processing. Three replicate snag samples were taken per river.

In the laboratory, snag samples were defrosted and sorted under a dissecting microscope at 4-10x magnification. Invertebrates were enumerated and body length measured for all taxa to the nearest 0.1 mm (except Chironomidae where the first 30 individuals encountered per sub-family were measured). Animals were identified to genus level in most cases and assigned to Functional Feeding Groups (FFG) using The Murray-Darling Freshwater Research Centre online bugguide (Hawking et al. 2009) except for nematodes which were not identified further, Chironomidae which were identified to sub-family, and mites which were identified to either the order Oribatidia or other. Some samples included zooplankton taxa (e.g. copepods, cladocerans) which were identified to family level. These are not typically considered as macroinvertebrates, but for the purposes of consistency and due to their periodic high abundance in these samples, we included these taxa. Abundances of invertebrates were expressed as individuals per 100 cm$^2$ of snag. Biomasses of invertebrates were calculated using published body length-to-mass relationships to calculate the total biomass in each sample (after Feller and Warwick 1988; Towers et al. 1994; Benke et al. 1999; Tod and Schmid-Araya 2009; Baumgärtner and Rothhaupt 2003) per 100 cm$^2$ of snag.
Where length–mass regressions were not available for a particular family or genus, the closest relative was used.

Data analyses

We used a BACI (Before-After-Control-Impact) design to assess differences in flow treatments. We analysed the differences in invertebrate biodiversity (abundance, biomass, taxon richness) in the months before and after the delivery of environmental flows in Colligen Creek and compared these changes in the same time period with rivers that received unregulated flow pulses (Wakool River and Little Merran Creek = UR) and no flow pulses (Yallakool Creek). We compared between time periods, ‘before’ and ‘after’ for each river and then among rivers to examine treatment effects. The statistical model used was:

\[ y_{irm} \sim N(\mu_{rm}, \sigma^2); \mu_{rm} = \beta_r + \delta_r I_{after} + \epsilon_m + \epsilon_{rm} \text{ (model 1).} \]

Where; \( \beta_r \) was the mean value of the response \( y \) (abundance, biomass etc.) in river \( r \) during the before period, \( \delta_r \) is the mean difference in \( y \) between before and after periods (\( I_{after} = 1 \) if month \( m \) is in the after period, 0 otherwise), and \( \epsilon_m \) and \( \epsilon_{rm} \) are month and month-by-river random effects, respectively.

The model was fitted as a Bayesian hierarchical model. We calculated the posterior probabilities that response variables increased after environmental flow delivery, \( Pr(>0) \), and that changes in Colligen Creek exceeded any concurrent changes in Yallakool Creek, \( Pr(>) \), and in the rivers which received unregulated flow pulses, the Wakool River and Little Merran Creek (UR), \( Pr(>) \), \( (\bar{\delta}_{UR} = \text{mean of } \delta_{Wakool}, \delta_{Merran}) \). We also compared changes in Yallakool Creek with changes in the Wakool River and Little Merran Creek (UR), \( Pr(\bar{\delta}_{UR} > \delta_{Yallakool}) \). Posterior probabilities exceeding 0.9 indicate strong evidence of a positive difference, while values <0.1 are evidence of a negative difference (these values correspond to ca. 10-fold change from prior to posterior odds of an effect in each direction).

We assigned uninformative, independent, normal prior distributions to main effects: \( \beta_r \sim N(0,1000), \delta_r \sim N(0,1000) \). The monthly errors were modelled with a first order autocorrelation structure, \( \epsilon_m | \epsilon_{m-1} \sim N(0.5(\epsilon_{m-1} + \epsilon_{m+1}),0.5\sigma_m^2) \), and the month-by-river errors were assigned exchangeable normal prior distributions, \( \epsilon_{rm} \sim N(0, \sigma_{rm}^2) \). Error variances, \( \sigma^2, \sigma_{rm}^2, \sigma_m^2 \), were assigned uniform prior distributions on the corresponding standard deviation, e.g. \( \sigma_{rm}^2 \sim U(0,100) \). All models were fitted via Markov chain Monte Carlo (MCMC), using WinBUGS software (version 1.4, Lunn et al., 2000), with 3 independent chains of 50000 iterations each, including 5000 iteration burn-in periods. Inspection of chain histories and Gelman-Rubin-Brooks diagnostics (Brooks and Gelman, 1998) verified adequate MCMC mixing and convergence.

Analyses were run separately on zooplankton and macroinvertebrate abundance and biomass data due to differences in size class which may mask potential differences in responses. Variables were transformed (e.g. 4th root transformed, log10 transformed) prior
to statistical analyses when necessarily to normalise data and stabilise variances. Model residuals were also checked for normality. If model residuals were not normally distributed the model was re-run using a Poisson distribution for the response variable:

\[ y_{irm} \sim \text{Poisson}(\lambda_{rm}); \log(\lambda_{rm}) = \beta_r + \delta_{r,\text{after}} + \epsilon_m + \epsilon_{rm} \text{ (model 2)}. \]

Rarefaction was used to compare the taxon richness of sampling sites with varying numbers of individuals as sample size can affect the number of taxa recorded in a sample (Gotelli and Colwell, 2001). Taxon richness was estimated using 10 individuals which was the lowest amount of individuals in one sample. Taxon richness was estimated using Primer 6 (v 6.1.13) (PRIMER-E Ltd., Plymouth, UK).

Multivariate analyses of invertebrate community composition in the rivers were carried out using PRIMER 6 (v 6.1.13) and PERMANOVA (v.1.0.3) (PRIMER-E Ltd., Plymouth, UK). Multivariate analyses were performed on square-root transformed relative abundance and raw biomass using Bray-Curtis dissimilarity. To examine community differences in relation to flow treatments a PERMANOVA was performed using a BACI design. The model incorporated three flow treatments (Colligen Creek, environmental flow treatment; rivers that received unregulated flow pulses only, Wakool River, Little Merran Creek; no flow pulses, Yallakool Creek), two time periods (‘before’ and ‘after’) and sampling months nested within time periods. An impact is indicated by a significant interaction between flow treatment x time period. The taxon contributing to Bray-Curtis dissimilarities among flow treatments were investigated using SIMPER in PRIMER 6 (v 6.1.13). To visualise patterns evident from PERMANOVA, metric multi-dimensional scaling, principal coordinate analysis (PCO) was performed.

RESULTS AND DISCUSSION

**Invertebrate abundance, biomass and taxon richness**

There was some evidence that macroinvertebrate abundance increased in Colligen Creek \( Pr(\alpha_{\text{Colligen}}>0) = 0.88 \) and the Wakool River \( Pr(\alpha_{\text{Wakool}})>0) = 0.87 \) between time periods. However, there were no differences among flow treatments. These findings suggest that overall abundances of invertebrates were not affected by changes in flow and therefore may be a poor indicator for changes in flow. This may be a result of differing responses to changes in flows between taxa and is consistent with a recent quantitative meta-analysis that found no consistent effect of flow magnitude on macroinvertebrate abundances (Poff and Zimmerman, 2010).

There was strong evidence that the total biomass of macroinvertebrates increased after delivery of environmental flows in Colligen Creek \( Pr(\alpha_{\text{Colligen}}>0) = 0.94 \) (Figure 1a). This increase in biomass was greater than the changes observed in the rivers that received unregulated flow pulses, the Wakool River and Little Merran Creek and no flow pulses,
Yallakool Creek ($Pr(\alpha_{Colligen} > \alpha_{UR}) = 0.89; Pr(\alpha_{Colligen} > \alpha_{Yallakool}) = 0.93$) (Fig. 1a). This biomass increase in Colligen Creek was largely due to sampling large sized taxa that were not present before the delivery of environmental flows (e.g. the caseless caddis larvae *Ecnomus* spp.) and due to an increase in size of taxa that were present before the environmental flow delivery (e.g. mayfly larvae *Atalophlebia* spp., dipteran larvae Chironominae). Chironominae 50% and *Ecnomus* spp. 26% made up over 75% of the biomass increase.

This increase in biomass may be due to environmental flows providing additional wetted habitat and increasing food availability (see section 5.2). Changes in flow regime can alter the quantity, quality and size fractions of organic matter (Poff et al. 1997; Small et al. 2008). The Functional Feeding Groups (FFG) of macroinvertebrates will therefore reflect these changes in supply of organic matter (Merritt and Cummins 1984). Increases in river flow should increase pelagic food sources favouring filterers, and reduction in flows should cause organic matter to settle on the benthos, favouring collector-gatherers, scrapers or shredders. In this study the increase in biomass of Chironominae (collector-gatherers) may suggest that environmental flows are transporting organic matter into depositional zones on the benthos, or inundating areas of benthic organic matter along margins. The caseless caddis larvae *Ecnomus* spp. (predators) may be benefiting from the increased biomass of the chironominae larvae. The increase in *Ecnomus* spp. may also benefit higher order predators such as fish.
Between time periods there was some evidence to suggest macroinvertebrate taxon richness declined in Colligen Creek (Pr(α\text{Colligen} > 0) = 0.18) and Little Merran Creek (Pr(α\text{Merran} > 0) = 0.16) and strong evidence that richness declined in the Wakool River (Pr(α\text{Wakool} > 0) = 0.09) and Yallakool Creek (Pr(α\text{Yallakool} > 0) = 0.09). However, the magnitude of these declines did not differ among flow treatments. These declines in taxon richness over time are most likely reflecting seasonal shifts in communities.

There was strong evidence of a reduction in zooplankton abundance and biomass between time periods in Colligen Creek (abundance; Pr(α\text{Colligen} > 0) = 0.03, i.e. probability negative change = 0.97; biomass; Pr(α\text{Colligen} > 0) = 0.02) and the Wakool River and Little Merran Creek (abundance; Pr(α\text{UR} > 0) = 0.02; biomass; Pr(α\text{UR} > 0) = 0.07). Among flow treatments, the abundance changes in the Wakool River and Little Merran Creek were substantially different to changes in Yallakool Creek (Pr(α\text{UR} > α\text{Yallakool}) = 0.05), but the changes in Colligen Creek were not (Pr(α\text{Colligen} > α\text{Yallakool}) = 0.62). This may be due to the large variation in zooplankton numbers in Colligen Creek before the delivery of environmental flows, and the lower sample size for the environmental flow treatment (n = 1 river).

Zooplankton biomass changes in Colligen Creek (Pr(α\text{Colligen} > α\text{Yallakool}) = 0.02) and the Wakool River and Little Merran Creek (Pr(α\text{UR} > α\text{Yallakool}) = 0.06) were greater than changes in Yallakool Creek (Figure 1b). The zooplankton cladocerans Chydoridae and Ilyocryptidae were the main taxa that decreased in abundance and biomass in the Wakool River and Little Merran Creek and Colligen Creek after the unregulated flow pulses.

Zooplankton abundance and biomass were higher in the Wakool River and Little Merran Creek and Colligen Creek immediately after the period of unregulated flow pulses. When rivers were exposed to no flow pulses (Wakool River and Little Merran Creek) or small magnitude environmental flows (in Colligen Creek), in the ‘after’ time period, zooplankton abundance and biomass were low. It is possible that unregulated flow pulses increased zooplankton abundance and biomass through transport of animals in from tributaries or slackwaters, as zooplankton transport increases with flooding (Ning et al. 2013). It is also possible that unregulated flow pulses increased wetted habitat (see section 6.2) and subsequently zooplankton emergence from sediments (Boulton and Lloyd 1992), but that small in-channel environmental flow pulses (in Colligen Creek river) were insufficient to generate this response.

There was only weak evidence that zooplankton diversity changed between time periods within rivers. There were marginal declines in zooplankton diversity in Colligen Creek (Pr(α\text{Colligen} > α\text{Yallakool}) = 0.10) and Wakool River and Little Merran Creek (Pr(α\text{UR} > α\text{Yallakool}) = 0.06) and a marginal increase in diversity in Yallakool Creek. The declines in taxon richness in Colligen Creek and the Wakool River and Little Merran Creek appear to track declines in abundance and biomass of zooplankton taxa.
**Invertebrate assemblage composition**

Invertebrate assemblages (expressed as patterns of abundance across all taxa, and separately, patterns of biomass across all taxa) varied between time periods (‘before’ and ‘after’), flow treatments and months within time periods (Tables 2 and 3). A flow treatment by month interaction was evident in the analyses and in order to examine whether assemblages differed between the ‘before’ and ‘after’ period for each flow treatment, separate PERMANOVA analyses were run.

Table 2 Permutation MANOVA (PERMANOVA) of invertebrate species’ relative abundance on small woody debris, based on Bray–Curtis dissimilarity measure (B-A denotes before vs. after environmental flow, Mo denotes month of sampling)

<table>
<thead>
<tr>
<th>SOURCE</th>
<th>DF</th>
<th>MS</th>
<th>PSEUDO-F</th>
<th>P (PERM)</th>
</tr>
</thead>
<tbody>
<tr>
<td>B-A</td>
<td>1</td>
<td>19868</td>
<td>7.3</td>
<td>0.001</td>
</tr>
<tr>
<td>Flow treatment</td>
<td>2</td>
<td>5212.8</td>
<td>2.7</td>
<td>0.022</td>
</tr>
<tr>
<td>Mo (B-A)</td>
<td>5</td>
<td>2725.9</td>
<td>3.3</td>
<td>0.001</td>
</tr>
<tr>
<td>B-A x Flow</td>
<td>2</td>
<td>2110.1</td>
<td>1.1</td>
<td>0.349</td>
</tr>
<tr>
<td>Mo (B-A) x Flow</td>
<td>10</td>
<td>1938.3</td>
<td>2.4</td>
<td>0.001</td>
</tr>
<tr>
<td>Residual</td>
<td>63</td>
<td>818.3</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>83</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 3 Permutation MANOVA (PERMANOVA) of invertebrate species’ biomass variables on small woody debris, based on Bray–Curtis dissimilarity measure (B-A denotes before vs. after environmental flow, Mo denotes month of sampling)

<table>
<thead>
<tr>
<th>SOURCE</th>
<th>DF</th>
<th>MS</th>
<th>PSEUDO-F</th>
<th>P (PERM)</th>
</tr>
</thead>
<tbody>
<tr>
<td>B-A</td>
<td>1</td>
<td>12090</td>
<td>2.9</td>
<td>0.02</td>
</tr>
<tr>
<td>Flow treatment</td>
<td>2</td>
<td>7410.1</td>
<td>3.1</td>
<td>0.004</td>
</tr>
<tr>
<td>Mo (B-A)</td>
<td>5</td>
<td>4206.2</td>
<td>2.7</td>
<td>0.001</td>
</tr>
<tr>
<td>B-A x Flow</td>
<td>2</td>
<td>3120.1</td>
<td>1.3</td>
<td>0.211</td>
</tr>
<tr>
<td>Mo (B-A) x Flow</td>
<td>10</td>
<td>2388.5</td>
<td>1.5</td>
<td>0.005</td>
</tr>
<tr>
<td>Residual</td>
<td>63</td>
<td>1563.8</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>83</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

For invertebrate relative abundances, Colligen Creek (Pseudo-F = 4.13, P = 0.013), Wakool River and Little Merran Creek (Pseudo-F = 5.43, P = 0.001) assemblages differed between before and after time flow periods, whereas Yallakool Creek (Pseudo-F = 1.95, P = 0.126) assemblages did not differ significantly (Figure 2a). For biomass, Colligen Creek invertebrate assemblages differed before and after delivery of environmental flows (Pseudo-F = 2.82, P = 0.034) whereas the Wakool River, Little Merran Creek and Yallakool Creek assemblages did
not (Figure 2b). SIMPER analyses revealed 17-18 taxa contributed approximately 90% to the dissimilarity between the before and after periods in Colligen Creek, the Wakool River, and Little Merran Creek for abundance, and Colligen Creek for biomass. Chironominae and the mayflies Caenidae and *Atalophlebia* spp. increased in abundance in Colligen Creek after delivery of environmental flows and the Wakool River, and Little Merran Creek after unregulated flow pulses. The unregulated flow pulses may be driving these changes in taxa abundances, since similar changes occurred in the Wakool River and Little Merran Creek as Colligen Creek. In Colligen Creek taxa that increased in biomass after delivery of environmental flow pulses were Chironominae, *Ecnomus* spp., Caenidae, and *Atalophlebia* spp. Many zooplankton taxa decreased in abundance in Colligen Creek, Wakool River and Little Merran Creek between the before and after flow periods, including cladocerans (Chydoridae, Ilyocryptidae) and the ostracod Candonidae. In Colligen Creek there was a decrease in biomass of ostracods (Candonidae, Ilyocyprididae), cladocerans (Chydoridae, Ilyocryptidae) and the copepod Cyclopoida. Most taxa that responded positively to unregulated flow pulses and delivery of environmental flow pulses were collector-gatherers and may be benefiting from the delivery of organic matter to the river channel. The predatory caseless caddis *Ecnomus* spp. also increased in biomass, potentially due to the increases in prey abundance and biomass (e.g. chironominae).

This suggests that environmental flow pulses and unregulated flow pulses generate similar changes in invertebrate assemblages, and that environmental flows effectively mimic natural flow regimes. However, environmental flows are generally of a smaller magnitude than natural flows, and there is some evidence that some effects of flow pulses are dependent on the size of the flow, likely because of the increased amount of habitat inundated and potential connections with flood runners and anabranches that are not achieved by small flow pulses. Environmental flows when delivered after unregulated flow pulses can increase invertebrate biomass and therefore, may provide additional food and habitat availability for taxa than unregulated flow pulses in isolation or low flows.
Figure 2 Two factor PCO plot of the invertebrate assemblages on small woody debris based on a) abundances and b) biomass on the basis of the Bray–Curtis dissimilarity measure, showing the factors of flow treatment (△ denote Colligen Creek, ● denotes Wakool River, ■ denotes Little Merran Creek and ◆ denotes Yallakool Creek, respectively) and time period (open symbols denote before period and closed symbols denote after period).
ACKNOWLEDGEMENTS

We extend our thanks to the Wakool River Association and landholders in the Edward-Wakool river system for allowing access to their properties and for their keen interest in this project. Field surveys and community liaison were supported by staff at the Murray Catchment Management Authority, with particular thanks to Josh Campbell and Patricia Bowen. Vincent Kelly at the State Water Corporation provided information on river and escapes discharge. We thank Josh Campbell, Anthony Conallin, Philip De Zylva, Chris McCormack, Kelsey Tucker and Katrina Wilson for assisting with field and/or laboratory work. This project was funded by the Cluster Collaboration Fund and the Ecological Responses to Altered Flow Regimes Research Cluster which represents a collaboration between the CSIRO Water for a Healthy Country Flagship, Griffith University, the University of New South Wales, Monash University, Charles Sturt University, La Trobe University and the Arthur Rylah Institute of the Victorian Department of Sustainability and Environment. The project also was supported by in-kind contributions from Commonwealth Environmental Water, Charles Sturt University, Murray Catchment Management Authority, and Monash University.

REFERENCES


2.6 Timing of fish spawning and recruitment in lowland river channel ecosystems

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INTRODUCTION

The timing of reproduction in organisms that live in flowing water environments is tightly coupled with historical patterns of the natural flow regime associated with flooding, drought and more regular seasonal cycles. Given the relatively high fecundity of fishes, small changes to the survival rates of larvae (King et al. 2013) can result in cascading effects on populations, communities the ecosystems they inhabit. Therefore, improvements in managing regulated river flow regimes have great potential to benefit native fish communities. There is, however, little information concerning the environmental flow requirements for early life history stages of Murray-Darling Basin fishes.

Information from around the world suggests that productivity and habitat derived from overbank floods is critical to adult spawning and subsequent survival of young fish across a wide variety of species (Junk et al. 1989; King et al. 2003; Baumgartner et al. 2013), although many fishes, particularly those in variable climate regions such as the of the Murray-Darling Basin, may thrive under low-flow conditions (Humphries et al. 1999). The flow requirements needed to initiate spawning and support survival of early life history stages in most species of fish in Australia remains unknown or is contested. Given the emphasis on the importance of floodplains for fish reproduction (King et al. 2003), comparatively less is known about the spawning and recruitment dynamics of fishes within river channel environments.

The aim of this study was to investigate the impact of in-channel environmental flow pulses on spawning and recruitment dynamic of fish in lowland rivers.

METHODS

Experimental design and fish sampling

This study utilised a repeated before-after-control-impact (BACI; Underwood 1991) field experimental design to examine the effects of in-channel environmental flows on the seasonal timing and magnitude of fish spawning (larval fish) and recruitment (juveniles) in four lowland rivers of the Edward-Wakool system. Methodological information concerning
the study area can be found in the previous section outlining the Edwards-Wakool project (section 2.1.1).

Larval and juvenile fish up to 31 mm standard length were sampled fortnightly using quatrefoil perspex light traps in four rivers in the Edward-Wakool system between 19/9/11 and 5/4/12. Light traps contained green bioluminescent light sticks and were covered with 5 mm diameter exclusion mesh to prevent predation of larvae by larger fish. Each river was sampled fortnightly using eight light traps distributed across two sites in 2011/12. Light traps were set at dusk, which varied among months, and retrieved the following morning. Larvae and juveniles were preserved in 70% ethanol or frozen for species and developmental stage identification and measurement of standard length (SL) in the laboratory. A sub-sample of sagittal otoliths was extracted, mounted on microscope slides and polished for daily age estimation to approximate hatch dates. Developmental stage was assigned according to Serafini and Humphries (2004) including: protolarvae (with and without yolksac), flexion, postflexion, metalarvae and juveniles. Relative abundance of larvae and juveniles was reported as the total number sampled (n) divided by effort (number of light traps) and were reported as median values at the river-scale.

Statistics

A before-after, control and impact, ‘repeated BACI’ (Underwood, 1991), statistical design with multiple controls was used to test the effect of the November and February environmental watering events on fish spawning (larvae) and recruitment (juveniles). The null hypothesis tested was that mean abundance of larvae within control rivers was not significantly different to impacted rivers before, during or after environmental watering. Statistical analyses were carried out in SigmaStat (3.5). Impacted reaches received environmental water, while controls were represented by all reaches that did not receive environmental water. Data were square root transformed to achieve equal variance and normal distribution structure prior to analysis. Differences in square root transformed values between control/impact reaches and before, during or after environmental watering events were evaluated statistically using a Two-way ANOVA with data nested fortnightly sampling periods. Post-hoc comparisons were conducted using the Holm-Sidak method.

For both environmental watering events, we compared abundance of larvae two fortnightly periods before with two fortnightly periods after the event among control and impacted reaches. For the November 2011 environmental flow, Little Merran Creek, Wakool River, and Yallakool Creek represented the controls while Colligen Creek represented the impacted river. For the February 2012 event, Colligen Creek and the Wakool Downstream represented the two impacted reaches and controls were represented by Yallakool Creek, Little Merran Creek. For both environmental flow events, a single fortnightly sampling period occurred during the flow peak and this was evaluated separately to before and after data.
RESULTS AND DISCUSSION

Eight species and 6717 larval and juvenile fish were sampled on fifteen fortnightly trips between 19/09/11 and 6/04/12. Carp gudgeon and Australian smelt were the dominant species sampled in all four rivers and they comprised of over 85% of all larvae and juveniles. Australian smelt larvae were sampled between September and early December while breeding of carp gudgeon occurred later in the season between November and April (Figure 1).

There was no evidence of elevated spawning activity or recruitment of Murray cod, Australian smelt or common carp in response to in-channel environmental flows. These species, therefore, may not be useful indicators of in-channel environmental flows. Peak abundance of Murray cod larvae occurred in light traps between 1/11/11 and 15/11/11, which coincided with daytime water temperatures ranging from 19.9°C to 25.36° prior to both environmental flows. This observation is consistent with previous studies (King et al. 2009) suggesting that Murray cod do not require high spring flow pulses to spawn but that survival of larvae or juveniles may depend on productivity derived from these events. Floodplain and flow dependent specialist fishes including golden perch, silver perch and southern pygmy perch (Baumgartner et al. 2013) occur in the Edward-Wakool system but larvae or early stage juveniles of these species were not sampled. Introduced species sampled as larvae or juveniles included common carp (n=14), redfin (n=18), mosquitofish (n=7), and oriental weatherloach (n=1), although these species were not sampled in adequate numbers to test for significant changes in spawning or recruitment.

When compared to control rivers (Figure 2), abundance of carp gudgeon larvae and juveniles increased significantly (Figure 2) in Colligen Creek during (Holm-Sidak; t = 3.96; P < 0.05) and after (Holm-Sidak; t = 2.64; P < 0.05) the November 2011 environmental watering (Figure 2) but did not change following the second event later in February. Spawning activity of carp gudgeon peaked during spring or early summer in all rivers, regardless of environmental flows. Therefore, environmental flows released in February, after the peak spring-summer spawning period of carp gudgeon and other species that spawn at this time, may be of little benefit. Based on a modal size of 8.2 mm, unvalidated otolith age estimates suggest that the majority of larvae hatched either several days before or after the November 2011 environmental flow in Colligen Creek. Given the length of time required for females to develop eggs and several days for eggs to hatch, these data suggest that survival of larvae may have been enhanced rather than these events increasing breeding activity of carp gudgeon. However, the significance of this particular event relative to the overall spawning and recruitment success of this species sampled in this study throughout the year has yet to be quantified.
Figure 1 Median abundance of the three most dominant larvae and juveniles sampled in the Edward-Wakool system during 2011/12. (From Watts et al. 2013)
Carp gudgeon are one of the most wide-spread and abundant native fish species in the Murray-Darling Basin (Lintermans 2007). We suggest that the success of this group of fishes may be in part attributed to its ability to take advantage of sporadic spawning and recruitment opportunities provided within regulated river channel environments. This opportunistic strategy of spawning appears to allow this species complex to thrive both in low-flow conditions (Humphries et al. 1999) but also take advantage of conditions provided during in-channel environmental flows or other changes that may influence riverine productivity.

Figure 2  Results from a two-way ANOVA comparing larval carp gudgeon abundance (mean number per light trap ± SD) before, during and after an environmental flow in Colligen Creek against control rivers that did not receive an environmental flow. (From Watts et al. 2013)

<table>
<thead>
<tr>
<th>Source of Variation</th>
<th>DF</th>
<th>SS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Before/During/After</td>
<td>2</td>
<td>48.20</td>
<td>9.20</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Control/Impact</td>
<td>1</td>
<td>49.55</td>
<td>18.91</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>B/D/A x C/I</td>
<td>2</td>
<td>23.40</td>
<td>4.47</td>
<td>0.019</td>
</tr>
</tbody>
</table>

The protracted spawning season of carp gudgeon in addition to other common small-bodied fishes in the Murray-Darling Basin (see Humphries et al. 2013) may be the key to their success. Depending on river channel geomorphology, in-channel rises in river discharge can increase the availability of slow-flowing slackwater habitat generally used to describe the
low-flow conditions (Humphries et al. 1999) which support carp gudgeon breeding and reproduction. Modelling presented in Section 5.2 suggested that environmental flows in the Edward-Wakool system inundated a relatively small amount of habitat-area and therefore, it appears that carp gudgeon may be one of few native species able to take advantage of small in-channel rises.

CONCLUSION

We suggest that the ability of carp gudgeon to take advantage of spawning and recruitment opportunities within a wide range of flow conditions contributes to the success of this species as one of the most wide-spread and abundant small-bodied fishes in the MDB. This study demonstrates that spawning and recruitment of carp gudgeon is not exclusive to low-flow conditions. Other fishes, such as Murray cod and Australian smelt, are also able to spawn and recruit successfully within the river channel regardless of flow conditions but further work is required to determine how, or if, overbank environmental or natural flows augment the magnitude of recruitment.

ACKNOWLEDGEMENTS

We extend our thanks to the Wakool River Association and landholders in the Edward-Wakool river system for allowing access to their properties and for their keen interest in this project. Field surveys and community liaison were supported by staff at the Murray Catchment Management Authority. State Water Corporation provided information on river and escapes discharge. We thank CSU and Murray CMA staff for assisting with field and/ or laboratory work. This project was funded by the Cluster Collaboration Fund and the Ecological Responses to Altered Flow Regimes Research Cluster which represents a collaboration between the CSIRO Water for a Healthy Country Flagship, Griffith University, the University of New South Wales, Monash University, Charles Sturt University, La Trobe University and the Arthur Rylah Institute of the Victorian Department of Sustainability and Environment. The project also was supported by contributions from Commonwealth Environmental Water, Charles Sturt University, Murray Catchment Management Authority, and Monash University.

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The importance of flow on spawning of riverine native fish in the Barmah-Millewa region, Murray River

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Further information about this project can be found in King et al. (in prep).

INTRODUCTION

Enhancing native fish populations is a commonly stated objective of many environmental flow programs. The flow regime can influence key factors in the life history of freshwater fish, including pre-spawning condition and maturation, cues for both movement and spawning, and improving larval and juvenile survival by promoting suitable food and habitat (e.g. Junk et al. 1989; Humphries et al. 1999; Marchetti and Moyle, 2001; King et al., 2003). The importance of flow characteristics for native fish of the Murray-Darling Basin has been debated over many years (e.g. Harris and Gehrke 1994; Humphries et al. 1999; King et al. 2003). For example, spawning and/or recruitment of golden perch has been variously reported as being linked to flooding, flow rises within the main channel or no flow increase (Mallan-Cooper and Stuart 2003; Balcombe et al. 2006; Roberts et al. 2008; King et al. 2009; Kerezsy et al. 2011; Cockayne et al. 2013; Zampatti and Leigh 2013). For other species such as Murray cod, flow and particularly flooding, may play little role in spawning (Humphries 2005), but may be important in determining strength of recruitment (Harris and Gehrke 1994). However, previous studies have limitations in that they have: (i) used a statistically weak correlative approach to explore the importance of flow for spawning and recruitment; (ii) failed to consider the importance of other environmental covariates; (iii) generally considered only the importance of flow discharge (particularly floods versus within channel flows) and not other flow attributes; and/ or (iv) have been conducted over limited hydrological conditions, making extrapolation to other conditions difficult.

This study explored the importance of flow as a determinant of spawning occurrence and strength for four iconic and/or recreational valuable species of freshwater fish in the Murray River, Australia. It used standardised catches of eggs or newly hatched larvae collected at fortnightly intervals over the spawning season from five hydrologically distinct years; and tested the importance of major flow attributes (such as discharge, rate of change and number of flood days), relative to other key environmental and sampling correlates. We
hypothesised that characteristics of the flow regime, both immediate and recent antecedent flow conditions, would be a major influence on the spawning occurrence and strength of all species, but that other environmental factors such as water temperature would also be important. We also hypothesised that the importance of flow would vary among species, depending upon the life history strategy employed.

METHODS

Study area
The Barmah-Millewa Forest (BMF) is a large (70,000 ha), river red gum floodplain forest on the Murray River, in south-eastern Australia. The Forest is a highly complex wetland containing a diverse range of aquatic habitats. The Murray River has a highly altered flow regime, and this is a major threat to the environmental values of the BMF (Ward, 2005) and the Murray River (Walker and Thoms, 1993). In an attempt to mitigate some of these effects, the BMF’s water regime is highly managed using a series of offstream regulators and structures, and the application of an environmental water allocation (EWA) (see King et al. 2010 for discussion).

Fish sampling occurred over five years (2003-2008) of variable hydrology. Water level during the sampling period (September to February) for the first two years (2003/04 and 2004/05) was maintained at bank-full height, with a few short duration flood events. Extensive flooding of BMF occurred in 2005/06 sampling season, when 513 GL of environmental water was used to extend the duration of a spring flood event (See King et al. 2009, 2010 for more details). The last two sampling seasons were dominated by extreme drought conditions in the Murray River catchment, resulting in unprecedented low flows in the main channel particularly during 2007/08, and large areas of the BMF drying.

Target species and sampling methods
This study was part of a broad investigation into the effects of water management on spawning and recruitment of the entire fish community at BMF (see King et al. 2009, 2010). This component focused on the spawning dynamics of four native fish species: golden perch, silver perch, Murray cod and trout cod. All four species predominantly reside in the main channel of the Murray River in the BMF region, are large-bodied and have important recreational, conservation and cultural significance. Golden perch and silver perch produce 100,000’s of small, semi-buoyant pelagic eggs (described as Mode 2 by Humphries et al. 1999); and have been postulated to require flooding for spawning, although evidence is conflicting (Lake 1967; Mackay 1973; Harris and Gehrke 1994; Mallen-Cooper and Stuart 2003; King et al. 2009; Zampatti and Leigh 2013). Murray cod and trout cod produce up to 10,000 demersal eggs and exhibit parental care of eggs and early larvae (described as Mode 1 by Humphries et al. 1999). Spawning tends to occur predictably each year and is thought
to be linked to both temperature and photoperiod, but not flow (Humphries 2005; Koehn and Harrington 2006).

The presence and density of eggs and/or larvae (back calculated to likely spawning date) was used as an indication of spawning occurrence and intensity on a particular date. Eggs and/or larvae of the four species were collected from three sites in the Murray River: upstream, mid region and downstream of the BMF (see King et al. 2009 for more details). Sampling commenced each year in mid-September and continued fortnightly thereafter until the end of February (~11 trips per breeding season), and was undertaken for five years (total of 57 sampling trips). Sampling was conducted using two passive drift nets set overnight at each site, as the eggs and/or larvae of these species are known to exhibit a drifting dispersal phase (Humphries and King 2004).

**Statistical analysis**

We hypothesised that temporal predictors of spawning occurrence (indicated by the presence of eggs/larvae in samples) or intensity (indicated by the relative density of eggs/larvae), would be influenced primarily by variation in water temperature (temp), moon phase (moon), daily discharge (flow), flooding history (Flood 90d) and the volume of water filtered through the sampling net (VolFilt). Daylength (or photoperiod) was also hypothesised to be an important predictor; however, it was highly correlated with water temperature ($r^2 = 0.745$) and was removed from the analysis.

We modelled the reproductive output of fish within a Bayesian hierarchical multispecies framework with both an occupancy and detection model portions (Royle and Dorazio 2008). Data were pooled among drift nets on each sampling occasion; and data from each site on each sampling occasion were treated as replicates. Occurrence was defined as a binary variable, indicating the presence or absence of spawning. Because the true occupancy state cannot be observed without error, we also modelled the probability of detection of spawning in the river. We assumed that the probability of detection of spawning would increase if the density of eggs/larvae was higher and if we sampled with a greater intensity (Royle and Nichols 2003). Therefore, the volume of water filtered by each drift net (VolFilt) and environmental factors that have been hypothesised to increase spawning intensity, i.e. discharge (flow) and number of flood days in the last three months (Flood 90day); were included in the detection portion of the model. We assumed that the occurrence and detection of spawning in the river for each species would therefore be affected by environmental variables and survey characteristics. We incorporated these effects as covariates in the model using a logit link function (McCullagh and Nelder 1989).

Model uncertainty was accounted for by averaging estimated parameters and derived values across all possible models weighted by model probabilities using a mixture modelling approach (Royle and Dorazio 2008). The posterior probabilities of the inclusion parameters...
correspond to the probability that the given variable was included in the “best” model. Posterior probability distributions of the model parameters were estimated using a Monte Carlo-Markov chain algorithm. All prior distributions were specified as flat normal distributions with mean equal to zero and standard deviation equal to one hundred and were specified for the parameters on the logit scale such that they would have no influence on the posterior probability distributions. Inference was drawn from 30,000 posterior samples taken from 3 chains of 100,000 samples thinned to every 10. We allowed a burn in of 30,000 samples to remove the effects of initial values. Convergence was diagnosed for the full model for each fish species by visual inspection of the MCMC chains for adequate mixing and stationarity and by using the Gelman-Rubin statistic (with values < 1.1 indicating convergence; Kery 2010; Gelman et al. 2004). Further details of the modelling and statistical methods can be found in King et al. (In prep).

RESULTS AND DISCUSSION

Posterior model probabilities for the top three models for each species were all very low, and indicated that none of the top three models were probable (see King et al. in prep). However, posterior probabilities of individual parameter inclusion in both the occupancy and detection portion in any of the models, showed that a number of parameters were important in predicting both the occurrence and intensity of spawning of the four species (Table 1).

Temperature (temp2) was the dominant parameter for all four species in the occupancy portion of the model, indicating that temperature predicted with a high certainty if spawning occurred (Table 1). Temperature has often been regarded as the dominant spawning cue for fishes living in temperate regions in freshwaters, where water temperature shows marked seasonal change (King et al. 2013). However, there is limited understanding of the relative role of temperature, compared with other factors in determining spawning occurrence. Golden perch, trout cod and Murray cod were all predicted to utilise an optimum temperature window (or range) predicting when spawning would occur (Figure 1). A threshold response was evident for silver perch. Modelling suggests that spawning was predicted to occur with a 60% probability for Murray cod between 18–23°C, trout cod 17-24°C, golden perch 15-22°C and silver perch at temperatures >19°C. The optimum spawning temperatures predicted for Murray cod and trout cod agree with previous observational and correlative studies on spawning occurrence, where spawning occurred at temperatures >15°C; however no studies have suggested an upper spawning temperature threshold for these species (Humphries 2005; Koehn and Harrington 2006). Our estimate of golden perch spawning temperature was well below previous studies that have more commonly suggested temperatures of > 20°C (e.g. Lake 1967; Roberts et al. 2008; Zampatti and Leigh 2013).
Two other parameters, chwtemp and flood90d were also important for predicting the spawning occurrence for trout cod (chwtemp: higher spawning probability with increasing weekly temperature); and silver perch and Murray cod (flood90d: decrease in spawning probability with more flood days) (Table 1; Figure 1).

We assumed that the probability of detection of spawning would increase if the density of eggs/larvae was higher and if we sampled with a greater intensity. The probability of detecting spawning was found not to be related to the volume of water filtered through the drift nets (VolFilt), however, discharge (flow) affected the probability of detection for three species (Table 1). Hence for golden perch, silver perch and trout cod, this suggests that an increase in discharge increased the density of eggs/larvae or spawning intensity.

Table 1 Posterior probabilities of parameter inclusion for the occupancy and detection portion of the models. Values in bold indicate values were model parameter estimates and their 95% credible intervals do not overlap zero. Coding for Moon is for 3 categories of moon phase.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Golden perch</th>
<th>Silver perch</th>
<th>Trout cod</th>
<th>Murray cod</th>
</tr>
</thead>
<tbody>
<tr>
<td>Occurrence model</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Temp</td>
<td>0.96</td>
<td>1.00</td>
<td>0.76</td>
<td>0.46</td>
</tr>
<tr>
<td>Temp²</td>
<td>0.97</td>
<td>0.75</td>
<td>1.00</td>
<td>0.97</td>
</tr>
<tr>
<td>Moon1</td>
<td>0.29</td>
<td>0.29</td>
<td>0.24</td>
<td>0.52</td>
</tr>
<tr>
<td>Moon2</td>
<td>0.31</td>
<td>0.29</td>
<td>0.26</td>
<td>0.50</td>
</tr>
<tr>
<td>Chwtemp</td>
<td>0.33</td>
<td>0.21</td>
<td>0.63</td>
<td>0.26</td>
</tr>
<tr>
<td>Chwflow</td>
<td>0.28</td>
<td>0.36</td>
<td>0.28</td>
<td>0.46</td>
</tr>
<tr>
<td>Flood 90d</td>
<td>0.20</td>
<td>0.58</td>
<td>0.15</td>
<td>0.77</td>
</tr>
<tr>
<td>Flow</td>
<td>0.36</td>
<td>0.28</td>
<td>0.20</td>
<td>0.32</td>
</tr>
<tr>
<td>Detection model</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Flow</td>
<td>0.73</td>
<td>0.62</td>
<td>0.86</td>
<td>0.15</td>
</tr>
<tr>
<td>VolFilt</td>
<td>0.40</td>
<td>0.40</td>
<td>0.40</td>
<td>0.40</td>
</tr>
<tr>
<td>Flood 90d</td>
<td>0.26</td>
<td>0.14</td>
<td>0.17</td>
<td>0.35</td>
</tr>
</tbody>
</table>

The probability of detecting spawning or increased spawning intensity was predicted to occur with a 60% probability at flows > 15,000ML/d for golden perch, and >10,000ML/d for silver perch and trout cod. Discharge greater than 10,000ML/d started to connect major anabranches, creeks and side channels throughout BMF, and discharge >15,000ML/d inundated significant areas of floodplain within BMF. This was the first study that suggested high flows may influence spawning intensity or occurrence of trout cod. However, flooding or high flow events within the main channel has been proposed as influencing the spawning
of golden perch and silver perch (e.g. Mallen-Cooper and Stuart 2003; King et al. 2009, Cockayne et al. 2013; Zampatti and Leigh 2013). These studies have all been correlative in nature, only weakly ascribing the influence of flow or flooding on spawning of these species. Our results suggested that discharge did not influence the probability of when spawning occurred, but did increase spawning intensity for trout cod, silver perch and golden perch. Managing flows to maximise spawning intensity should result in a greater probability of a stronger year class in recruitment. While this study covered a broad range of hydrological conditions, it did not include a major flood; therefore, further investigation is required to determine whether spawning intensity does increase linearly with increasing discharge or whether a flow threshold exists.

Figure 1 Predicted probability of (a) occurrence and (b) detection of spawning for four species in the Murray River for four key variables, temperature, number of flood days in previous 90 days (Flood days), change in weekly temperature (Chwtemp) and discharge (flow). The light grey is the 90% probability region and the dark grey is the 60% probability region.
This study clearly demonstrated that temperature was the dominant and overriding environmental parameter influencing spawning occurrence in all four species, although attributes of flow were also important and in particular affects the spawning intensity of three species. This study demonstrates the importance of considering the significance of considering the timing of water application in the design and management of environmental flows and could be used to create a stronger conceptual or analytical framework for flow management for improved conditions for native fish spawning.

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2.8 Antecedent flow: predicting the condition of young-of-year fish in a temperate lowland river system?

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INTRODUCTION

The nutrients and energy produced by inundating floodplains sustains fish production in many lowland river systems, particularly in tropical, neo-tropical and arid climates (Junk et al. 1989; Balcombe and Arthington 2009; Jardine et al. 2011, 2012). However, the applicability of models such as the Flood Pulse Concept in temperate systems has been questioned (see King et al. 2003) and less is known about the extent to which floods in temperate river systems benefit fish. This is because high flows are uncoupled from maximum water temperatures in many temperate systems, and may not increase food production or availability (Humphries et al. 1999). High flows may also reduce the availability of food for fish by spreading prey items, making foraging harder (Humphries et al. 1999; King et al. 2003; Zeug and Winemiller 2003).

The effect of floods on riverine energy production may also be progressive. Firstly, primary productivity may decline initially as the system is disturbed (Gawne et al. 2007), but increase later as populations recover and capitalise on additional available nutrients. Secondly, there may be a time lag between the pulse of energy associated with flooding and its incorporation into the high level food chains (e.g., fish) (Kitchell and Carpenter 1996). And finally, productivity in floodplain habitats may not benefit the main river channel until secondary, or follow-up, floods wash nutrient-laden water back into the channel.

Currently, we know relatively little about the extent to which flow improves the body condition (as one measure of productivity) of fish in temperate systems. However, there is some evidence to suggest that flows and floods in particular, influence the body condition of small fish (Tonkin et al. 2011; Beesley et al. 2012). This study retrospectively analysed six years of fish data with differing flows to assess if antecedent flow was associated with the juvenile body condition of two small-bodied native species in the mid-Murray River. The examination of juveniles, with limited capacity to store energy and which do not use it for reproduction, allows us to infer that their condition reflects current system energetics. This provides insight into the longevity of flow-related energy pulses, rather than the capacity of
organisms to store energy from previous energy pulses (see Balcombe et al.’s 2012 study of adult golden perch). We also investigated the interaction between antecedent flow and habitat for one species, Australian smelt.

METHODS:

Study Area, Sampling Design and Antecedent flow

Barmah-Millewa Forest (BMF) is a large, river red gum floodplain forest on the Murray River, in south-eastern Australia. The forest is a highly complex wetland containing a diverse range of aquatic habitats. Fish were collected over a five year period (2003/04 to 2007/08) as part of a larger study examining spawning and recruitment in BMF. Hydrological conditions varied significantly from bank full in-channel flows, long duration floods, to severe drought conditions where most floodplain habitats dried (Figure 1). Additional fish were collected during November 2010 during a large flood event, but before blackwater conditions started (see King et al. 2012). A detailed description of the data and sampling was provided in King et al. (2007, 2010). Briefly, early life stage fish were sampled at 14 sites in three habitats; river, creek, and wetland. Sites were sampled monthly from September to February each year using light traps and sweep-net electrofishing. All fish collected were euthanased and stored in 100% ethanol. A sub-set of the fish collected was assessed for body condition.

Figure 1 Average daily discharge (ML/day) between 2002 and 2011 in the Murray River at Barmah-Millewa Forest (Yarrawonga gauge, 30km upstream). Triangles represented sampling occasions for Australian smelt and unspecked hardyhead. The dashed line showed the discharge where water started flowing down creek lines into the Forest. Overbank flooding occurred at ~ 28,000 ML/day.
Flow metrics were developed to describe short, medium and long-term antecedent conditions and are described below and visually represented in Figure 2.

- Short-term flow: the summation of average daily discharge from the estimated spawning date of juvenile fish, until the date of fish collection. This described the flow conditions that juvenile fish were directly exposed to.

- Medium-term flow: the summation of average daily discharge from July 1 (designated as the start of each spawning year) until the approximate date of spawning. This described flow conditions leading up to spawning. Medium-term flows were highly positively correlated ($r=0.80$) with short-term flows and were excluded from the analysis.

- Long-term flow: the summation of daily average discharge from July 1 for the preceding year. This described flow conditions over the previous year.

The importance of flow metrics was used to assess the level of support for four different hypotheses about flow-related energy production in the river, see Figure 2.

![Figure 2](image_url)

**Figure 2** A conceptual relationship between river flow (discharge) and system energetics (energy) through time, and its effect on juvenile native fish condition caught at time $x$ (triangle) and spawned at time $*$, for four scenarios. Scenario (A) system energetics and fish condition are unrelated to flow; (B) system energetics is affected by flow, but with a short-lag effect, so fish condition is related to short-term flow; (C) system energetics is affected by flow, but with a medium lag effect, so that fish condition is related to short-term and long-term flow; (D) system energetics is affected by flow, but with a long lag effect, so that fish condition is related more to long-term flow than short-term flow.
Fish Condition

Fish condition was assessed for two abundant small-bodied species; Australian smelt and unspecked hardyhead. These species mature within a year, (Milton and Arthington 1985) and their larvae and juveniles feed predominantly off zooplankton (King 2005), providing a relatively direct link to ecosystem production. Juvenile Australian smelt (n=122) were collected in mid-December, with an average standard length (SLLs) of 22.70 mm. Juvenile unspecked hardyhead (n=149) were collected in mid-January, with an average length of 18.25 mm SL. A minimum of 20 individuals of each species were assessed for condition each year (sites within habitat types were pooled). Due to limited numbers of hardyhead in wetlands, analyses were restricted to the river for this species. In the laboratory, fish were measured to ± 0.01 mm standard length (SL) using vernier calipers and weighed to four significant figures. Condition was described using relative weight (Wr), and index with the formula \( Wr = \frac{W}{W_s} \times 100 \), where \( W_s \) was a length-specific standard weight predicted from length-weight relationships of all fish caught (Wege and Anderson 1978; Pope and Kruse 2007). Values between 95 and 100 indicate fish in average condition, above 100 indicated good condition and below 95 poor condition (Pope and Kruse 2007).

Statistical Analysis

We evaluated the influence of short-term (dst) and long-term discharge (dlt) on relative weight (Wr) for both species (independently) using linear regression. The influence of habitat (hab) was only evaluated for smelt as hardyhead only appeared in samples collected in riverine habitats. Models were specified with main effects and all two-way interactions. Higher order interactions were not evaluated because of data limitations. The models were specified as:

\[
wr = \beta_1 + \beta_2 \text{dst} + \beta_3 \text{dlt} + \beta_4 \text{hab} + \beta_5 \text{hab} \times \text{dst} + \beta_6 \text{hab} \times \text{dlt} + \beta_7 \text{dst} \times \text{dlt} + \varepsilon
\]

We considered all possible combinations of covariates to be candidate models representing competing hypotheses. Support for competing hypotheses was determined using the Bayesian mixture modelling approach (Royle and Dorazio 2008) where each covariate parameter in the model is multiplied by an ‘inclusion parameter’ (wc, for c covariates). Model probabilities of competing models were derived from the posterior samples of the inclusion parameters by calculating the proportion of instances of different combinations of parameters of wc in the posterior sample. Posterior probability distributions of the model parameters were estimate using a Monte Carlo-Markov chain algorithm implemented in JAGS (Plummer 2003) from within program R (R Development Core Team 2010). All prior distributions were standard uninformative distributions specified to have no influence on the posterior probability distributions. Priors for parameters were set as flat normal distributions with mean equal to zero and standard deviation equal to one hundred. Convergence was diagnosed for the full model by visual inspection of the MCMC chains for
adequate mixing and stationarity and by using the Gelman-Rubin statistic (with values < 1.1 indicating convergence; Gelman et al. 2004; Kery 2010). All continuous data were normalised prior to analysis.

RESULTS AND DISCUSSION:

The relationship between antecedent flow and juvenile fish body condition differed markedly between the two species studied. For Australian smelt, body condition was positively related to short-term flow and negatively related to long-term flow (Table 1; Figure 3a, b). For unspecked hardyhead, body condition was unrelated to short-term flow, and negatively (but mildly) related to long-term flow (Table 1; Figure 3c, d). The different responses among species with similar life histories and habitat preferences, suggests it is unwise to make generalisations about how the body condition of different species will respond to flow.

Table 1 Parameter inclusion probabilities for the general linear model of juvenile fish condition for two species (Australian smelt and unspecked hardyhead) relative to antecedent flow

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Parameter inclusion probabilities</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Australian smelt</td>
</tr>
<tr>
<td>Habitat</td>
<td>0.612</td>
</tr>
<tr>
<td>Short-term discharge</td>
<td>0.930</td>
</tr>
<tr>
<td>Long-term discharge</td>
<td>1.000</td>
</tr>
<tr>
<td>Habitat*Short-term discharge</td>
<td>0.827</td>
</tr>
<tr>
<td>Habitat*Long-term discharge</td>
<td>0.224</td>
</tr>
<tr>
<td>Short-term discharge*Long-term discharge</td>
<td>0.998</td>
</tr>
</tbody>
</table>

The importance of flows a year before fish were spawned, suggests that antecedent conditions may affect the energetics of the system in excess of a year later. While conceptually, an energy lag could follow a flood pulse, as nutrients move off the floodplain, or up the food chain (see Figure 2), the negative relationships found here did not support such a conceptual understanding. An alternative explanation is that antecedent low flows allowed nutrient mineralisation and leaf litter to build up on the floodplain, which fuelled energetics during proximal flood conditions.

The importance of short-term flow, for Australian smelt, conflicts with previous assertions that high flows are disadvantageous for larval and small-bodied fish because they dilute the density of suitable prey items (i.e., microcrustaceans) (Humphries et al. 1999). Recent research by Ning et al. (2013) has revealed that although increasing flows decrease the density of microcrustaceans, that the increased volume of water travelling down the river leads to an increase in the total number of zooplankton being transported (i.e. food...
available). One would expect that the extent to which juvenile fish are able to benefit from high flows will depend on how increased food availability trades off against increased energy use in fast flowing waters. The relationship between smelt body condition and flow is likely to be complicated, see Tonkin et al. (2011).

![Figure 3 General linear model predictions of fish condition (relative weight) versus short (several months since spawning) and long-term (year preceding spawning) antecedent flow for Australian Smelt and unspecked hardyhead in the Barmah-Millewa Forest. Solid lines indicate the mean and shaded areas indicate the 95% confidence of the mean](image)

Short-term flow was also positively related to the condition of smelt in wetland habitats; however, the relationship was considerably weaker than for smelt occupying the river (Table 1, Figure 3 c, d). The weaker relationship was probably because main-channel flow gauges were not an ideal descriptor of wetland changes in food production and habitat. This
highlights the reduced ecological sensitivity when extrapolating among habitat types, using broad hydrodynamic modelling.

In summary, this retrospective analysis provided preliminary evidence that antecedent flow conditions may alter system energetics and fish condition. We recommend additional investigation in this area, and caution against extrapolation of these findings because this study is based on only six years of flow data. The relatively low number of years limits our capacity to detect relationships, and particularly to understand how different components of flow interact.

REFERENCES


2.9 Hypoxic blackwater survival thresholds of four Australian lowland river fishes

Small, K.1, Kopf, R.K.1, Watts, R.J.1 & Howitt, J.1
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This report is based on results published in Small et al. (2014), Hypoxic blackwater survival thresholds of four Australian lowland river fishes. PLoS ONE 9(4) e94524.

INTRODUCTION

Hypoxia has been influential in shaping the evolution of freshwater fish and the environments in which they live. Hypoxic blackwater events in can be a natural and relatively common phenomenon associated with floodplain inundation and the subsequent decomposition of organic material in lowland rivers (Hladyz et al. 2011). Fish employ a variety of mechanisms ranging from air-breathing to behavioural avoidance, although severe, widespread, or prolonged hypoxia can lead to sub-lethal stress and mortalities (Gehrke et al. 1993; McMaster and Bond 2008; La and Cooke 2012).

Given the regular occurrence of drought, flooding and subsequent blackwater events in lowland rivers of the Murray-Darling Basin (MDB) in south-eastern Australia (Howitt et al. 2007; Whitworth et al. 2012), it is reasonable to assume that native fish in this ecosystem are well adapted to acute hypoxia and high levels of DOC. However, after 10 years of drought, the MDB river system experienced multiple large-scale flooding events followed by blackwater events and fish kills (Whitworth et al. 2012). Hypoxic blackwater mortalities of keystone species, such as Murray cod (Mitchell), have been the focus national and international attention (Koehn 2004; La and Cooke, 2010; Whitworth et al. 2012) and bring into question the hypoxia tolerances of these species.

This study aimed to quantify hypoxia tolerances of juvenile stages of four lowland river fishes native to the MDB. The species examined included Murray cod, golden perch, silver perch and eel tailed catfish.

METHODS

Two-hundred to two-hundred and fifty juveniles of each species were sourced from local hatcheries in south-eastern Australia and were transported the same day to a controlled temperature room. The juvenile stage of development was selected as a starting point for minimum oxygen thresholds because critical oxygen concentrations were assumed to be independent of body size among juvenile and adult fish species (Nilsson and Ostlund-Nilsson 2008).
Hypoxia tolerance of each species was determined using median lethal dissolved oxygen concentration (LC50) experiments in freshwater (no dissolved organic carbon/leaf litter) and in simulated blackwater treatments containing four different leaf litter concentrations and a control (no leaf litter). All leaf litter treatments were repeated with atmospheric air bubbled in tanks (aeration) and without aeration on each of the four species. Prior to experimentation each species was acclimated to a constant temperature of 25° C for 9 to 15 days. All experiments were undertaken in glass experimental tanks, 23 cm (L) x 23 cm (W) x 45 cm (H), custom built to achieve minimal surface area and limit oxygen diffusion with the atmosphere. A static flow during all experiments was utilised to reduce variation in DO concentration. Prior to each experiment DO sensors were calibrated against temperature-specific oxygen saturated distilled water.

Experiments started by netting 10 fish and transferring them from 750 l holding tanks to a pre-determined experimental DO treatment tank. Water from holding tanks was used in all experimental and control tanks to avoid stress during transfer. Dissolved oxygen, temperature and pH were measured in each experimental and control tank at intervals of 0 h, 1 h, 4 h, 8 h, 16 h, 24 h, 32 h, 40 h, 48 h and DO concentrations were regulated with bubbled N2 gas or atmospheric air as necessary.

**Lethal dissolved oxygen concentration**

Median lethal dissolved oxygen concentration (LC50) experiments were conducted in accordance with international guidelines for acute toxicity testing (Anon. 1992). Dissolved oxygen (DO) was regulated using nitrogen, N2, or atmospheric air. Atmospheric air and N2 were separately regulated via air stones in experimental tanks filled with 17·5 l of holding tank water. Seven oxygen treatments, each containing 10 fish per experimental tank, were maintained during LC50 experiments on each species. Treatments consisted of DO concentrations of 0·1 mg l⁻¹, 0·7 mg l⁻¹, 1·3 mg l⁻¹, 1·9 mg l⁻¹, 2·5 mg l⁻¹ and 3·1 mg l⁻¹, and a control (8 mg l⁻¹) that were maintained at 25° C for 48 h.

**Blackwater simulation**

Four simulated blackwater treatments were developed using naturally abscised dried river red gum Eucalyptus camaldulensis leaf litter collected from a fallen branch near the Murray River in Albury, NSW. Leaf litter and twigs, < 5 mm diameter, were dried in oven at 60° C for 24 to 48 hrs and four geometrically increasing masses of dried leaf litter containing 3 g, 9 g, 27 g, and 81 g were placed in separate nylon stockings weighted with 250 g of cobble. These masses resulted in effective leaf litter concentrations ranging from 0.17 g l⁻¹ to 4.59 g l⁻¹ within experimental tanks and were designed to simulate dissolved organic carbon and oxygen conditions ranging from oxygen saturated to hypoxic blackwater.
Natural blackwater event

Water quality conditions of experimental treatments were compared to a naturally occurring hypoxic blackwater event sampled in the MDB from the Edward River (Natural 1) and Wakool River (Natural 2) in December, 2010. John and Anthony Conallin from the Murray CMA and Luke Pearce from the NSW Department of Primary Industries confirmed the presence or absence of fish species mortalities in each river following the event. Water quality measurements were recorded during the hypoxic black water conditions, while fish mortalities in the field were verified during and after events. Water quality measurements of DO, pH and temperature were collected in flowing water within the main river channel during both events.

Data analysis and statistics

Lethal DO concentrations (LC50’s) and aquatic surface respiration (ASR50’s) values were estimated by fitting log transformed 48 h cumulative percent responses to a logistic regression (Anon., 2006):

$$y = a + \frac{b - a}{1 + \left(\frac{x}{ASR_{50} or LC_{50}}\right)^{Hillslope}}$$

where the fitted parameter a is the minimum y-axis value, b is the asymptote, LC50 or ASR50 represent the median response and hillslope is the slope at its midpoint and mortality responses were over the 48 h experimental period of lethal oxygen.

Species-specific LC50’s, ASR50’s were compared independently using One Way Analysis of Variance’s (ANOVA’s). A Three Way ANOVA was used to examine variation in cumulative percent mortality among species, leaf litter treatments and the presence/absence of aeration. All post hoc comparisons were undertaken using Tukey Tests (Zar, 1999).

RESULTS/DISCUSSION

The juveniles of four large-bodied fishes examined here were unexceptional in their ability to tolerate low dissolved oxygen in freshwater and simulated blackwater. Logistic models (Figure 1) predicted that hypoxia related mortalities may start at oxygen concentrations as high as 3.54 mg l^-1 and sub-lethal stress, as indicated by the onset of aquatic surface respiration (ASR), may occur above 5.00 mg l^-1 at 25°- 26° C. These results were somewhat unexpected given the variable water quality conditions and purported regular occurrence of hypoxic blackwater events in lowland rivers of the MDB (Howitt et al. 2007; Hladyz et al. 2011). There is increasing evidence suggesting that anthropogenic factors including river
flow regulation, hypolimnetic weir discharge and climate change (Whitworth et al. 2012) may be escalating the severity of hypoxic events in lowland river systems.

![Figure 1 Logistic regressions](image)

**Figure 1** Logistic regressions fitted to (a) cumulative percent mortality showing lethal dissolved oxygen concentrations (LC50’s) and (b) cumulative percent performing aquatic surface respiration (ASR50’s) at different oxygen concentrations for juvenile (black circles; solid thin line) Murray cod ($r^2 = 0.99$, $F_3;4 = 1331.7$, $P < 0.001$; $r^2 = 0.92$, $F_3;4 = 25.0$, $P < 0.05$); (white circles; solid thick line) golden perch ($r^2 = 0.99$, $F_3;4 = 603.2$, $P < 0.001$; $r^2 = 0.99$, $F_3;4 = 439.4$, $P < 0.001$); (black triangles; dashed line) eel-tailed catfish ($r^2 = 0.98$, $F_3;4 = 11960.5$, $P < 0.001$; $r^2 = 0.97$, $F_3;4 = 83.8$, $P < 0.05$); and (white triangles; dotted line) silver perch ($r^2 = 0.99$, $F_3;4 = 3393.8$, $P < 0.001$; $r^2 = 0.99$, $F_3;4 = 1331.7$, $P < 0.001$).
Our results suggest that low oxygen levels of less than 2.0 mg l$^{-1}$, in addition to the high DOC (> 10 mg l$^{-1}$) and low pH (4.2-6.3), which occurred in the Edward-Wakool system (Table 1) and across much of the southern basin for several weeks or months during these events (Whitworth et al. 2012), approached or exceeded lethal threshold limits for all species except for eel-tailed catfish. Confirmed field mortalities of the remaining three fish species in the Edward-Wakool system indeed corroborate this assumption (Table 1). It is important to consider, however, that fish in the wild may be able to avoid hypoxic blackwater by seeking refuge habitat, while fish in our study were confined within experimental treatment tanks that may have exaggerated estimates of mortality.

Table 1. Mortality (%) of four Murray-Darling Basin fishes exposed to simulated blackwater experiments and confirmed mortalities associated with natural hypoxic blackwater events in the Edward-Wakool river system in 2010/11. Water quality and dissolved organic carbon (DOC) measurements of simulated blackwater treatments (mass of leaf litter g l$^{-1}$) were aggregated across species for comparison with two natural blackwater events. Mean ± SE

<table>
<thead>
<tr>
<th>Blackwater sample</th>
<th>DO (mg l$^{-1}$)</th>
<th>pH</th>
<th>Temp. (°C)</th>
<th>DOC (mg l$^{-1}$)</th>
<th>Mortality (%)</th>
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<tr>
<td></td>
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<td>Murray cod</td>
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<tr>
<td>Natural 1</td>
<td>1.07 (0.08)</td>
<td>4.18 (0.04)</td>
<td>19.4 (0.02)</td>
<td>17.7 (0.08)</td>
<td>Confirmed</td>
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<td>Golden perch</td>
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<td>Eel-tailed catfish&lt;sup&gt;a&lt;/sup&gt;</td>
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<td></td>
<td>Silver perch</td>
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<tr>
<td>Natural 2</td>
<td>1.98 (0.11)</td>
<td>6.25 (0.09)</td>
<td>18.7 (0.05)</td>
<td>16.1 (0.07)</td>
<td>Confirmed</td>
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<td>Confirmed</td>
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<tr>
<td>Control (0 g l$^{-1}$)</td>
<td>8.4 (0.4)</td>
<td>7.41 (0.05)</td>
<td>25.62 (0.03)</td>
<td>2.7 (0.05)</td>
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<tr>
<td>Simulated blackwater (0.17 g l$^{-1}$)</td>
<td>4.83 (0.38)</td>
<td>7.22 (0.04)</td>
<td>26.26 (0.08)</td>
<td>3.58 (0.38)</td>
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<tr>
<td>Simulated blackwater (0.51 g l$^{-1}$)</td>
<td>4.0 (0.3)</td>
<td>7.05 (0.01)</td>
<td>26.09 (0.06)</td>
<td>4.93 (0.13)</td>
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<tr>
<td>Simulated blackwater (1.53 g l$^{-1}$)</td>
<td>1.8 (0.44)</td>
<td>6.76 (0.03)</td>
<td>25.93 (0.06)</td>
<td>9.45 (0.55)</td>
<td>90</td>
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<td>45</td>
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<tr>
<td>Simulated blackwater (4.59 g l$^{-1}$)</td>
<td>0.46 (0.28)</td>
<td>6.05 (0.01)</td>
<td>26.41 (0.05)</td>
<td>30.0 (0.7)</td>
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<td>&gt; 99</td>
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<td>&gt; 99</td>
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</tbody>
</table>

<sup>a</sup> Historically present in the Edward-Wakool system but not sampled in recent unpublished fisheries surveys.

The range of hypoxia tolerances (Table 2) reported here may be considered intermediate on a global-scale comparison with other freshwater fishes. For example, the crucian carp Carassius carassius (L.) and several non-air breathing fishes of the Amazon can withstand complete anoxia for several months (Kramer et al. 1978; Nilsson and Renshaw 2004), while some salmonids are vulnerable to mortality when oxygen concentrations fall below 4 mg l$^{-1}$ (Davis 1975). The hypoxia tolerances observed here ranged from 0.70 mg l$^{-1}$ to 1.29 mg l$^{-1}$ at 25°C-26°C and are comparable to other temperate stream fishes. The mean LC50 of 35
species in the mid-western United States ranged from 0.49 mg l\(^{-1}\) to 1.59 mg l\(^{-1}\) (Smale and Rabeni 1995), while other prairie stream fishes have LC50’s ranging from 0.95 mg l\(^{-1}\) to 2.66 mg l\(^{-1}\) at 25°C (Ostrand and Wilde 2001). The LC50’s of four native New Zealand fishes and rainbow trout, Onchorhynchus mykiss (Walbaum) ranged from 0.54 mg l\(^{-1}\) to 2.65 mg l\(^{-1}\) at 15°C (Landman et al. 2005).

All four species performed ASR in response to low DO and this behaviour has not previously been documented in peer-reviewed literature for any of these species. Aquatic surface respiration was initiated in all fishes before lethal oxygen levels were reached and this is a common trend in other species in which this behaviour has been documented (Chapman and McKenzie, 2009). The ASR50’s (Table 2) reported here fell within the range 0.48 to 1.98 mg l\(^{-1}\) reported by McNeil and Closs (2007) at 25°C for other Australian native fishes including Australian smelt Retropinna semoni (Weber), flat-headed galaxias Galaxias rostratus (Klunzinger), carp gudgeon compex Hypseleotris spp. and southern pygmy perch Nannoperca australis (Gunther).

One outstanding question remaining from the present study is whether or not the hypoxia tolerances of the juveniles examined here are representative of adults that are more commonly reported in fish kills in the MDB. A review on this subject across multiple species of marine fish concluded that body size itself plays little or no direct role in determining hypoxia tolerance and that the tolerance of a given species is usually size-independent after the larval stage (Nilsson and Ostlund-Nilsson 2008).

### Table 1

<table>
<thead>
<tr>
<th>Species</th>
<th>n</th>
<th>Mass (g)</th>
<th>Temperature (°C)</th>
<th>pH</th>
<th>DO (mg l(^{-1})) range</th>
<th>DO (mg l(^{-1})) LC(_{50})</th>
<th>DO (mg l(^{-1})) ASR(_{50})</th>
</tr>
</thead>
<tbody>
<tr>
<td>Murray cod</td>
<td>80</td>
<td>1.02 ± 0.02</td>
<td>25.63 ± 0.15</td>
<td>7.92 ± 0.11</td>
<td>0.16 - 8.24</td>
<td>1.29 ± 0.03</td>
<td>1.39 ± 0.02</td>
</tr>
<tr>
<td>Golden perch</td>
<td>80</td>
<td>0.48 ± 0.02</td>
<td>25.41 ± 0.09</td>
<td>7.75 ± 0.08</td>
<td>0.07 - 8.14</td>
<td>0.96 ± 0.03</td>
<td>1.40 ± 0.04</td>
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<tr>
<td>Eel tailed catfish</td>
<td>80</td>
<td>3.61 ± 0.10</td>
<td>26.35 ± 0.22</td>
<td>7.52 ± 0.18</td>
<td>0.09 - 8.68</td>
<td>0.70 ± 0.02</td>
<td>0.79 ± 0.09</td>
</tr>
<tr>
<td>Silver perch</td>
<td>70</td>
<td>0.43 ± 0.02</td>
<td>26.19 ± 0.13</td>
<td>7.52 ± 0.11</td>
<td>0.09 - 8.67</td>
<td>1.18 ± 0.01</td>
<td>1.51 ± 0.07</td>
</tr>
</tbody>
</table>

In contrast to popular anecdote, it appears that hypoxia sensitivity of Murray cod may not be entirely related to its large maximum attainable body mass (> 100,000 g). The Murray cod examined here were juveniles (< 1.2 g) and not the largest species, yet they were still the most sensitive examined. The comparatively low hypoxia tolerance of Murray cod appears to be species-specific or, at least, not entirely size-specific. We suggest that Australia’s largest freshwater fish species is sensitive to hypoxia, not because it a large-bodied apex predator per se, but because it has evolved a life-history strategy that primarily utilizes lotic river channel environments and habitats, which are less prone to severe
hypoxic blackwater conditions than floodplains, wetlands or backwater areas commonly occupied by other species.

This study simulated a relatively narrow range of blackwater types (Figure 2) compared to the potential array of conditions that fish may experience (see Howitt et al. 2007; Hladyz et al. 2011). However, the un-aerated leaf litter concentration of 1.53 mg l⁻¹ resembled the early stages of a severely hypoxic natural blackwater event which occurred in the southern MDB in 2010/11 (see Whitworth et al. 2012). The mortality rate of large-bodied fish in this simulation was 37.5% and this result was corroborated by observed fish kills of Murray cod during the natural event. However, blackwater simulations in the present study were different to the natural blackwater event in that fish were confined within hypoxic conditions and experiments were undertaken at higher water temperatures and higher pH’s.

Figure 2 Experimental leaf litter treatments showing (a) cumulative percent mortality of juvenile Murray cod, golden perch, eel-tailed catfish, and silver perch; (b) dissolved oxygen concentration; (c) dissolved organic carbon (DOC) concentration; and (d) pH. Black circles represent non-aerated treatments and white circles represent aerated treatments. Non-overlapping 95% confidence intervals represent significant differences between aerated and non-aerated treatments and asterisks indicate significant differences from respective controls (no leaf litter).
The spatial extent of the natural blackwater event extended across much of the southern basin, including the main channel of the Murray River (Whitworth et al. 2012), which probably eliminated the possibility for behavioural avoidance of hypoxia in most areas. Water quality measurements from the natural blackwater event also showed that the pH was more acidic than blackwater simulations which would have further reduced the oxygen affinity of the gills.

Mortality increased significantly with leaf litter concentration in non-aerated treatments (Three way ANOVA, $F_{4,12} = 18.8$, $P < 0.001$; Figure 2a) but no significant differences were detected among species. Mean mortality rates in non-aerated were significantly different (Tukey; $q < 8.98$; $P < 0.05$) to controls starting at leaf litter concentrations of 1.53 g l$^{-1}$ and a mean dissolved oxygen concentration of 1.83 ± 0.3 S.E. mg l$^{-1}$. There was a relatively high degree of variability in oxygen levels within non-aerated treatments but DO sharply declined with increasing leaf litter concentration (Figure 2b). Aeration elevated DO concentrations to saturation and simultaneously neutralised pH levels across all treatments (Figure 2d).

CONCLUSION

Hypoxia is a natural phenomenon in aquatic ecosystems but conservation and management intervention may be required if the frequency, severity or spatial extent of these events has changed due to anthropogenic causes such as river regulation. Despite the natural occurrence of hypoxia and blackwater in lowland rivers of the MDB, large-bodied predatory fish in this ecosystem are vulnerable to acute mortality induced by low oxygen concentration and associated water chemistry changes.

Given the extent of natural flow regime alteration and climate change predictions of rising temperatures and more severe droughts and flooding, acute episodes of hypoxia and blackwater may represent a formidable risk to aquatic biodiversity and ecosystem functioning in lowland rivers. Hypoxic blackwater fish kills in combination with the ‘modest’ survival thresholds presented here suggest that large-bodied native fishes of the MDB are not particularly well adapted to acute hypoxia when behavioural avoidance is restricted.

The thresholds reported here provide a starting point to begin developing hypoxia mitigation strategies but must be carefully interpreted in light of potential sub-lethal effects, ambient and antecedent environmental conditions. It is essential to consider that hypoxia thresholds will change according to temperature, pH and concentration of toxic polyphenols. Consequently, a better understanding how these variables interact will be essential in further developing hypoxia management plans to prevent fish kills and the loss of aquatic biodiversity. One of the proposed management approaches to avoid anthropogenic hypoxic events is to restore natural ecosystem functions and natural river flow regimes. In cases where this is not possible, other management measures such as aeration, environmental water dilution flows (Hladyz et al. 2011), or other regulatory flow diversion measures (Howitt et al. 2007) may mitigate the effects of hypoxia.
ACKNOWLEDGEMENTS

We thank Charles Sturt University for a Faculty of Science Honours scholarship and the Faculty of Science laboratory staff for assistance in maintaining fish and the controlled temperature room. This research was funded in part by the Ecological Responses to Altered Flow Regimes Research Cluster which represent a collaboration between the CSIRO Water for a Healthy Country Flagship, Griffith University, the University of New South Wales, Monash University, Charles Sturt University, La Trobe University and the Arthur Rylah Institute of the Victorian Department of Sustainability and Environment. This work was carried out with permission from the CSU Animal Care and Ethics committee protocol number 11/018.

REFERENCES


2.10  Flow changes to the Lowbidgee floodplain from the Murrumbidgee river

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INTRODUCTION

Many of the world’s rivers are fragmented by regulatory structures (Nilsson et al. 2005), affecting flows and impacting on freshwater biodiversity (Vörösmarty et al. 2010). Analysis of changes to river flows, supplying major wetlands, is critical to understanding responses of organisms, particularly long-lived biota, to changes in flows and subsequently management of environmental flows. These challenges are particularly relevant to Australian rivers which have relatively low and variable flows, reflecting Australia’s aridity (Puckridge et al. 1998). It is in the Murray–Darling Basin in the southeastern Australia where there is a strong focus on these two challenges. The Murray-Darling Basin is the most highly regulated river basin in Australia with more than 30,000 ML of storage capacity (Kingsford 2000; Kingsford et al. 2011; Leblanca et al. 2012), supplying large irrigated areas. The Australian Government has invested more than A$ 12 billion in purchasing water from the irrigation industry and improving efficiencies of irrigation systems which return river flows to the environment, including major wetland ecosystems (DEWHA 2010). Such wetlands usually lie in the lower regions of the major catchments.

One of the large river systems targeted for rehabilitation is the Murrumbidgee and its ecologically important Lowbidgee wetland, subject to considerable alteration from water resource development (Kingsford 2003; Kingsford and Thomas 2004). The Lower Murrumbidgee floodplain has exhibited symptoms of ecological decline, as a result of water resource development on the 1,690 km long Murrumbidgee River that supplies the wetland (Kingsford and Thomas, 2004; Keith et al. 2013). Understanding the level of hydrological impact to many rivers, including the Murrumbidgee River, is primarily measured by governments using the Integrated Quantity and Quality Model (IQQM) in southeastern Australia (Simons et al.. 1996; Hameed and O’Neill 2005; Brown et al.. 2007). Independent hydrological analysis of monthly river flow data is possible using time series, but the residuals are large, limiting predictive power, even though results may be generally consistent with the integrated quantity and quality model (IQQM) (Wen 2009).

METHODS

To explore long-term changes to flow in Murrumbidgee River, daily observed flow data (NSW Natural Resources Pinneena Version 9 and NSW Water Information Website
http://waterinfo.nsw.gov.au) were used at seven flow gauges, at increasing distances upstream of the Lowbidgee wetland, the major wetland in the Murrumbidgee River catchment (Kingsford and Thomas, 2002; Kingsford and Thomas, 2004; Figure 1): Gundagai (1887-2010); Wagga Wagga (1892-2010); Narrandera (1893-2010); Darlington Point (1915-2010); Hay (1914-2010); Maude (1937-2010) and Redbank (1937-2010). Maude and Redbank were gauges within the Lowbidgee wetland. Also, we assembled annual rainfall data for five locations, mainly in the upper catchment (Queanbeyan, Cooma, Yass, Tumut and Cootamundra), where most of the flows (Kingsford and Thomas 2004) to the Lowbidgee were generated (Figure 1). Daily rainfall data (Bureau of Meteorology Australian Daily Rainfall CD 2010) were transformed to monthly and then annual data from November to October to coincide with usual annual spring flooding in the Lowbidgee wetland, retaining an annual time frame. There were some missing data, so monthly rainfall data were interpolated, based on the relationship among the rainfall data at the corresponding station and nearby stations, to provide an annual rainfall record from 1880 to 2010. Annual rainfall for nine stations in the upper, middle (Wagga Wagga, Narrandera) and lower catchment (Hay, Maude) were calculated for the 131 year available record.

Figure 1: The Murrumbidgee River (thick central black line) and its tributaries and distributaries (thin black lines) flow west to the Lowbidgee floodplain wetland (shaded green) in southeastern Australia, where Burrinjuck and Blowering Dams (part of the Snowy Mountains Scheme) are the major regulatory structures; long-term models were developed using rainfall stations (filled circles) and flow gauges (open circles).

The Lowbidgee wetland, at the lowest part of the Murrumbidgee catchment, has had its flow regime affected by upstream river flows after Burrinjuck, Snowy Mountains Scheme dams and other upper catchment dams were built, followed by water resource development (Kingsford 2003; Kingsford and Thomas, 2004; CSIRO, 2008a and 2008b; Wen et al., 2011a and 2011b). We developed annual low regulated flow models, before the river
became highly regulated, at seven flow gauges (Gundagai, Wagga Wagga, Narrandera, Darlington Point, Hay, Maude and Redbank), using annual rainfall at the catchment rainfall locations as the independent variables (Figure 1). We used structural change tests to identify the two different periods of flow change in the river (Zeileis et al. 2002; 2003 and 2010). This calculated the empirical fluctuation of monthly flow at the Redbank gauge, with cumulative sums of recursive residuals providing the point beyond which there was a declining trend. This clear break point of annual structural change was in 1957, after which the most significant dam building occurred on the river (Kingsford 2003). This separated the flow record into a period of low river regulation, when total storage capacity was 1044.5GL (1927-1957) and when the river was highly regulated and storage capacity increased (3028.4GL, 1958-1971) (Kingsford 1995; Kingsford 2003). There were no significant differences (p>0.05) in annual rainfall between the two periods: 1880-1957 and 1958-2010 for the eight stations in the catchment, except Yass rainfall station (p=0.025) using K-S test. River regulation was the catalyst for diversion of water to the Murrumbidgee Irrigation Area and the Colleambally Irrigation Area (Kingsford 2003). The latter was developed when water was diverted from the easterly flowing Snow River, with the development of the Snowy Mountains Hydroelectricity Scheme, increasing flows in the river above natural levels for this part of the river (Kingsford 2003).

We used LOESS to build the relationship between annual observed flow and upstream flow / rainfall data (Ren et al, 2010), modeled in R language (R Development Core Team, 2013). LOESS fits local polynomial regressions progressively to points (Cleveland 1979; Cleveland and Devlin 1988) and has the advantage over other modelling approaches because it does not rely on the specification of a function to fit the model to all of the sample data. LOESS (Cleveland et al. 1992) does not produce a regression function, so we calculated quantile confidence intervals, based on the leave-one-out samples which successively drops the i-th observation from the original sample (Ren et al.. 2010). We used upstream annual flow data and local rainfall data for the models downstream of the Gundagai gauge, corresponding to the locations of Wagga Wagga, Narrandera, Darlington Point, Hay, Maude and Redbank gauges (Figure 1). We progressively developed a series of flow models down the river, using sequential flow gauges. We developed annual flow models at the Gundagai gauge using catchment rainfall. For subsequent gauges downstream, we used flow models from the upstream gauge. At Maude, flow models also included local rainfall at Hay station as well as flows from the Hay models. Following this process, we independently developed models for annual low regulated flow at the seven gauges - Gundagai (1887-1957), Wagga Wagga (1892-1957), Narrandera (1893-1957), Darlington Point (1915-1957), Hay (1914-1957), Maude (1937-1957) and Redbank (1937-1957); and then correspondingly highly regulated models at the seven flow gauges for the period 1958-2010. We derived annual low and highly regulated flow models for Maude and Redbank gauges, within the Lowbidgee (see Figure 1). Following development of these flow models, which coincided with the time that
flow data were available, we then extended our modelling to the full record (1880-2010), using the available rainfall data and the predicted flow data from upstream flow models to estimate long-term changes in low and highly regulated flow. We developed annual low and highly regulated flow models at the flow gauges of Maude and Redbank with overall results.

RESULTS AND DISCUSSION

The low regulated flow modelling at the Maude gauge was built with annual observed flow data at Maude, low regulated flow and rainfall data at Hay from 1937 to 1957 using LOESS and leave-one-out samples. It showed high agreement between observed data and fitted data because Nash-Sutcliffe coefficient of efficiency as the goodness-of-fit indicator is 99% (Nash and Sutcliffe, 1970), and there was no significant difference between the observed and fitted distributions of flow at Maude using Kolmogorov-Smirnov test (p>0.9999). The highly regulated flow modelling at Maude was developed using the relationship between annual flow data at Maude and highly regulated flow data at Hay after 1958. Observed and fitted flows at Maude from 1958 to 2010 were similarly close (goodness-of-fit is 98.7%) with no significant difference (p>0.9999). With our low and highly regulated flow models at the Maude gauge, we extended the predictions of these models using annual low and highly regulated flow and rainfall data at Hay (1880-2010) (Figure 2a).

The low regulated flow modelling at Redbank was built based on the relationship between annual flow data at the Redbank gauge and low regulated flow data at the Maude gauge from 1937 to 1957. The highly regulated flow modelling were developed using the relationship between annual flow data at the Redbank gauge and highly regulated flow data at the Maude gauge after 1958. Similar results were found in a comparison between the respective fitted data from the low and high regulated modelling developed for the Redbank gauge and observed data (goodness-of-fit: 91.5% and 95.1%; Kolmogorov-Smirnov test: p>0.9999; p>0.9999). And then we extended the low and highly regulated flow modelling to predict annual flow at the Redbank gauge to the Lowbidgee wetland (1880-2010) (Figure 2b).

We developed two models (low and highly regulated) for annual flows in the Murrumbidgee River, at different locations, based on annual rainfall data, extending for 131 years from 1880 to 2010. Even though climate change may reduce rainfall and related flow, rainfall remains the most independent variable available for tracking long term changes to river systems (Herron et al. 2002), without the confounding effects of river regulation (Kingsford 2000). Therefore such modelling can extend current understanding of the effects of river regulation to large wetlands and consequently for understanding biotic responses.

We found there was a significant difference (p<0.0001) between low and highly regulated flows from 1880 to 2010 of the Murrumbidgee at Maude with median highly regulated flow was 52.8% of the median low regulated flow. Similarly, these effects also occurred at the
downstream Redbank gauge where median annual highly regulated flows were 47.4% of the low regulated flows (p<0.0001).

Figure 2: Annual predictions of low and high regulated flow at Maude and Redbank gauges

Such statistical approaches to flow modelling may be useful for rivers around the world and may be linked to inundation modelling and ecosystem responses. Since April 2007, we have created and been developing new integrated flow and flood modelling (IFFM) including daily flow modelling in the Macquarie and Murrumbidgee Rivers, monthly sub-regional inundated area size modelling in the Macquarie Marshes and Lowbidgee, monthly spatial sub-regional flood modelling in the Macquarie Marshes and Lowbidgee, long-term annual unregulated and regulated flow modelling in the Macquarie River (Ren et al, 2010; Ren and Kingsford, 2011), long-term annual inundated area size modelling and long-term annual spatial flood
modelling in the Macquarie Marshes. The series of statistical modelling down the river, from the upstream gauge, extending progressively downstream, can provide another independent modelling approach to changes to flow regimes to large wetland systems. Such modelling can extend to the full record available for a river, allowing assessment of the frequency and magnitude of floods of large wetlands. Combined with understanding of requirements of biota in wetlands, this can provide critical information on whether sufficient flows are provided to sustain extent and character of floodplain wetlands.

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Inundation modelling in the Macquarie Marshes

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INTRODUCTION

There is an increasing need to understand relationships between river flows and inundation responses (Thomas et al. 2011). Such understanding of the frequency and extent of inundation provides requisite information for interpreting how much wetlands may have declined with river regulation but also serves as a background for providing information for the management of environmental flows. The growing availability of multi-temporal satellite data has increased opportunities for monitoring large rivers from space (Smith 1997). A variety of passive and active sensors operating in the visible and microwave range can estimate inundation area and delineate flood boundaries. High-resolution visible/infrared sensors provide good delineation of inundated areas, where trees and floating vegetation do not obscure the water surface (Smith 1997). These data can be used to develop relationships between flow and flooding, critical to understanding dependencies and sufficiency of environmental flow for maintaining organisms on floodplain wetlands (e.g. floodplain eucalypts). We aimed to develop such modelling for the Macquarie Marshes, a complex floodplain wetland dependent on flows from the Macquarie River. Since April 2007, we have created and been developing new integrated flow and flood modelling (IFFM) including daily flow modelling in the Macquarie and Murrumbidgee Rivers, monthly subregional inundated area size modelling in the Macquarie Marshes and Lowbidgee, monthly spatial subregional flood modelling in the Macquarie Marshes and Lowbidgee, long-term annual unregulated and regulated flow modelling in the Macquarie River (Ren et al. 2010; Ren and Kingsford 2011), long-term annual low and highly regulated flow modelling in the Murrumbidgee River, long-term annual inundated area size modelling and long-term annual spatial flood modelling in the Macquarie Marshes. These statistical modelling and approaches are useful for the inundation modelling in the Macquarie Marshes.

METHODS

The Macquarie Marshes, which flows north, is a large wetland (Kingsford and Thomas 1995; Ren et al., 2010; Ren and Kingsford, 2011) on the floodplain of the Macquarie River. They cover 379,330 ha, comprising four regions in the Macquarie Marshes (Figure 1). These regions accord with different areas interpreted for the management of environmental flows...
used by the New South Wales environmental flow management agency (Thomas et al. 2011). We used 95 observed inundated maps (2550 x 6343 pixels, where each pixel is 25m x 25m) from Landsat 5 Thematic Mapper (TM) and Landsat 7 Enhanced Thematic Mapper (ETM+) images in the Macquarie Marshes for different dates between 9 February 1989 and 21 January 2011 (Thomas et al. 2012). Each image was divided into the four regions, comprising different regions: east, north, south and west (Table 1). For each image, inundated area was classified using remote sensing analyses to provide an observed estimate of area flooded (Thomas et al. 2011).

Table 1: Descriptive statistics of areas inundated in four regions within the Macquarie Marshes on 95 dates from 09/02/1989 to 21/01/2011

<table>
<thead>
<tr>
<th>Region</th>
<th>Area (ha)</th>
<th>Min</th>
<th>Max</th>
</tr>
</thead>
<tbody>
<tr>
<td>East</td>
<td>140,186</td>
<td>46</td>
<td>100,616</td>
</tr>
<tr>
<td>North</td>
<td>68,382</td>
<td>190</td>
<td>53,016</td>
</tr>
<tr>
<td>South</td>
<td>63,757</td>
<td>316</td>
<td>44,712</td>
</tr>
<tr>
<td>West</td>
<td>107,005</td>
<td>127</td>
<td>47,811</td>
</tr>
</tbody>
</table>

Figure 1: The Macquarie Marshes and its stream network and the main flow gauges (left), and the corresponding four water management regions (East, North, South and West) used to manage environmental flows in the Macquarie Marshes

To model inundated areas in the four regions, we used daily observed flow data (NSW Natural Resources Pinneena Version 9 and NSW Water Information Website http://waterinfo.nsw.gov.au) at five flow gauges: Dubbo (January 1, 1913 - December 31, 2011); Warren (January 1, 1913 - December 31, 2011); Marebone Break (August 1, 1975 -
December 31, 2011); Marebone Weir Downstream (April 1, 1986 - December 31, 2011) and Oxley (January 1, 1943 - December 31, 2011). Marebone Break, Marebone Weir Downstream and Oxley were gauges within the Macquarie Marshes (Figure 1). The described statistics of total flow (ML) at Dubbo, Warren, Marebone Break, Marebone Weir Downstream and Oxley flow gauges were calculated for the previous 30 days before each image date (May 1, 1986 to December 31, 2011; Table 2). Some missing data of daily flow data were based on our own daily flow modelling (Ren and Kingsford, in prep.) using the daily data from the upstream flow and rainfall. Our IFFM daily flow modelling (The corresponding Nash–Sutcliffe efficiency are 99.99% at Oxley between 01/01/1943 and 31 November 2011 and 99.99% at Carinda between 1 January 1939 and 31 October 2011, Figure 2) in the Macquarie River should be better than the integrated quantity and quality model (IQQM: The corresponding Nash–Sutcliffe efficiency are 95% at Oxley and 76% at Carinda between 7 January 1991 and 30 June 2009; Wen et al., 2013).

![Observed flow vs Modelled flow](image)

**Figure 2: Comparison of the observed and fitted data from IFFM daily flow modelling at Oxley – 1 Jan 1943 to 31 October 2011**

We also calculated the total rainfall at Quambone and mean air temperature within the Macquarie Marshes (Australian Government Bureau of Meteorology http://www.bom.gov.au) for the previous 30 days of each date (May 1, 1986 - December 31, 2011) as this can also influence inundation extent. Monthly sub-regional inundated area sizes in the east, north, south and west regions of the Macquarie Marshes were then
modelled using the corresponding upstream total flow and rainfall, and mean air temperature data.

We developed a series of models linking inundation in the four regions to total flow at the Warren, Marebone Break and Marebone Weir Downstream flow gauges, total rainfall at Quambone (Figure 1) and mean air temperature in the Macquarie Marshes for the previous 30 days for each date of the 95 images and then compared these to the observed inundated area sizes. We used Voronoi-based lifting wavelets (Jansen et al., 2009), LOESS (Cleveland 1979; Cleveland and Devlin 1988) and leave-one-out samples without overfitting (Ren et al. 2010) to build the monthly subregional inundated area size modelling.

A series of subregional inundated area size modelling in the Eastern Macquarie Marshes linked the total flow at the Warren, Marebone Break and Marebone Weir Downstream flow gauges, total rainfall at Quambone and mean air temperature in the Macquarie Marshes for the previous 30 days of these 95 dates to the 95 observed eastern inundated area sizes. We also built a series of sub-regional inundated area size modelling in the Northern Macquarie Marshes to describe the relationship of the total flow at the Marebone Break, Marebone Weir Downstream and Oxley flow gauges, total rainfall and mean air temperature in the Macquarie Marshes for the previous 30 days of these 95 dates, and the 95 observed northern inundated area sizes. A series of sub-regional inundated area size modelling in the Southern Macquarie Marshes was developed to the relationship of the total flow at the Warren, Marebone Break and Marebone Weir Downstream flow gauges, total rainfall and mean air temperature in the Macquarie Marshes for the previous 30 days of these 95 dates and the 95 observed southern inundated area sizes. Similarly, a series of sub-regional inundated area size modelling in the Western Macquarie Marshes was based on the relationship of the total flow at the Dubbo and Warren flow gauges, total rainfall and mean air temperature in the Macquarie Marshes for the previous 30 days of these 95 dates, and the 95 observed western inundated area sizes.

Table 2: Descriptive statistics of total flows at five flow gauges within the Macquarie Marshes for the previous 30 days of the 95 image dates from 09/02/1989 and 21/01/2011

<table>
<thead>
<tr>
<th>Gauge</th>
<th>median (GL)</th>
<th>2.5% quantile</th>
<th>97.5% quantile</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dubbo</td>
<td>63.636</td>
<td>6.792</td>
<td>1116.519</td>
</tr>
<tr>
<td>Warren</td>
<td>33.678</td>
<td>3.342</td>
<td>371.601</td>
</tr>
<tr>
<td>Marebone Weir Downstream</td>
<td>19.173</td>
<td>1.116</td>
<td>115.047</td>
</tr>
<tr>
<td>Oxley</td>
<td>14.298</td>
<td>0.591</td>
<td>80.235</td>
</tr>
<tr>
<td>Marebone Break</td>
<td>7.56</td>
<td>0.843</td>
<td>83.652</td>
</tr>
</tbody>
</table>
RESULTS AND DISCUSSION

We compared between modelled and observed inundated area sizes for the 95 dates using Kolmogorov-Smirnov test (Weiss 1978; Gille 2004). There was no significant difference between the observed and predicted distributions of inundated area sizes for the eastern (p=0.5498), northern (p=0.5498), southern (p=0.3374) and western (p=0.5498) regions, respectively. Reflecting this, there was good agreement between observed and modelled data using the Nash-Sutcliffe coefficient of efficiency as the goodness-of-fit indicator, based on the squares of the differences between modelled and observed data (Nash and Sutcliffe 1970) for each of the four regions (Table 3): east (98.3%, Figure 3a), north (98% Figure 3b), south (97.8%, Figure 3c) and west (96.5%, Figure 3d).

Table 3: Comparison of observed and fitted area sizes (ha) for 95 images of the Macquarie Marshes

<table>
<thead>
<tr>
<th>Region</th>
<th>Median observed</th>
<th>Median fitted</th>
<th>95% CI (Q_{2.5}, Q_{97.5}) observed</th>
<th>95% CI (Q_{2.5}, Q_{97.5}) fitted</th>
<th>K-S test* p value</th>
<th>GOF (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>East</td>
<td>1,579</td>
<td>1,601</td>
<td>(73, 77,697)</td>
<td>(135, 77,698)</td>
<td>0.5498</td>
<td>98.3</td>
</tr>
<tr>
<td>North</td>
<td>5,282</td>
<td>5,430</td>
<td>(300, 46,088)</td>
<td>(1,194, 45,809)</td>
<td>0.5498</td>
<td>98.0</td>
</tr>
<tr>
<td>South</td>
<td>4,341</td>
<td>4,377</td>
<td>(628, 35,773)</td>
<td>(1,207, 35,530)</td>
<td>0.3374</td>
<td>97.8</td>
</tr>
<tr>
<td>West</td>
<td>2,653</td>
<td>2,351</td>
<td>(311, 36,391)</td>
<td>(833, 36,389)</td>
<td>0.5498</td>
<td>96.5</td>
</tr>
</tbody>
</table>

* Kolmogorov-Smirnov goodness-of-fit test

No significant differences between observed and modelled inundated area sizes allowed us to develop a series of monthly estimates of inundated area sizes (May 1986- December 2011) for each of the regions of the Macquarie Marshes, based on flow, rainfall and temperature (30 days previously) for each of the regions (Figure 3). We found that there were uncertainties in this modelling in relation to confidence limits, based on comparisons with observed data. This probably reflected variability in soil moisture, drying patterns, local water management as well as uncertainties in the mapping of the wetlands (Thomas et al. 2011). The monthly inundated area sizes are dependent on the predicted inundated area sizes on the dates of the corresponding month. If the predicted inundated area sizes on all the dates of a month in each of the regions tend to be significantly increasing or decreasing using Mann-Kendall trend test (Mann 1945), we then derived an estimate of area inundated in each of the regions in this month based on the 75% quantile of all the predicted area sizes; otherwise, the inundated area size in each of the regions in this month is the median of these predicted area sizes (Figure 4). There were three large flood peaks flood events in August 1990 (226,775 ha), December 2010 (195,772 ha), and December 2000 (166,119 ha) in Figure 4.
The monthly sub-regional inundated area size modelling performed well, but if there are more flood maps on regular dates such as 16 day periods, then these modelling need to be rebuilt and developed based on their autocorrelation information. These modelling are critical for us to build and develop the monthly spatial sub-regional flood modelling in the Macquarie Marshes that related to hydrological and ecological impacts on the large wetland systems. IFFM monthly spatial subregional flood modelling in the Macquarie Marshes (over accuracy is 99.6% on 16/12/2000, Figure 5; Ren et al. in prep.) should be better than MIKE FLOOD (about 75% of the satellite data on 16/12/2000; Wen et al. 2013).
Figure 4: Estimated monthly inundated areas for the four regions in the Macquarie Marshes (May 1986 – December 2011)

Fine temporal scale inundation data (monthly) provides opportunity to test responses of different organisms to the flooding regime (frequency, timing, magnitude). These data can be used to interpret condition of floodplain eucalypts for example to determine whether there is sufficient inundation to maintain their populations. Also, these data may be used to investigate duration of inundation over time which is critical for the breeding of organisms such as colonial waterbird. Further, these modelling can be used to predict inundation patterns for environmental flows and build a series of scenarios for potential inundation of different floodplain communities. Finally, such inundation models may save considerable time in the classification of remote sensing imagery and also provide information to fill missing data where satellite images cannot be used (e.g. cloud obscured).
Observed and modelled maps on 16/12/2000

![Observed map (OEH)](image1) ![IFFM modelled map](image2)

Figure 5: Comparison of the observed and IFFM modelled maps on 16/12/2000

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2.12 Wetland and floodplain understory vegetation

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INTRODUCTION

Riparian vegetation (encompassing wetlands and floodplains) affect floodplain and ecosystem processes in many ways, including the provision of habitat, altering biogeochemical cycles, primary production and fixing carbon (Carpenter and Lodge 1986; Bragg et al. 2005). The community can be grouped into two components: the canopy comprised of trees and the understory comprised of shrubs, macrophytes, herbs and grasses. The understory makes a significant contribution to ecosystem primary production (Gawne et al. 2007; Baldwin et al. 2013).

Flow events and their characteristics (e.g. magnitude, frequency, duration, depth, fluctuation, timing/seasonality) affect the germination, distribution, diversity and growth of riparian vegetation (Casanova and Brock 2000; Deegan et al. 2007; Franklin et al. 2008; Casanova and Brock 2000; Greet et al. 2011; Webb et al. 2012). Flow regime becomes increasingly important as the climate becomes more arid, as there is insufficient rainfall to maintain vegetation communities (Baldwin et al. 2013). Understanding floodplain production in response to environmental flows and inundation is critical to understanding energy flow and storage across the floodplain ecosystem.

A conceptualisation of the influence of flow on floodplain production identified a range of flow characteristics expected to influence production directly through impacts on physical habitat and indirectly through effects on competitors and herbivores (the model Appendix 1). Of the influences identified, current knowledge suggests that the influence on physical habitat is the major driver and so, in terms of developing predictive capacity, this causal relationship was our focus.

The aim of this project was to investigate how primary production of riparian or floodplain vegetation responds to flow and determine if understory riparian vegetation can predict ecological response models of floodplain/wetland condition. Remote sensing techniques can successfully predict changes in wetland and woodland condition in response to inundation and could be used to calculate primary production (Cunningham et al. 2007; Sims and Colloff 2012). However it is more difficult to determine the contribution of the understory because overstory canopy tends to obscure understory vegetation growth. As a result we aimed to model riparian production response using variables known to drive their production (season/timing, depth and duration of inundation) as well as determining if this was consistent across broad geographical floodplain habitat types.
Riparian understory production at the landscape scale was predicted to be dependent on the floodplain habitat type, reflecting historically different flow regimes (depth and duration) affecting community composition. In this study we have considered three habitat types, temporary open water wetlands, red gum (*Eucalyptus camaldulensis*) woodlands and black box (*Eucalyptus largiflorens*) woodlands. Water residence time within each habitat for a given flow will vary, given water remains longer in open water wetlands than red gum woodlands and black box woodlands. As a result, understory production was predicted to be greater in wetlands than in red gum woodlands, followed by black box woodlands.

Both above and below ground biomass, in the form of roots, are important (Baldwin et al. 2013). Below ground carbon is often overlooked in production estimates due to methodological difficulties. The proportional allocation of above to below ground carbon of individual species of macrophyte is affected by flood depth and water level fluctuations (Rea and Ganf 1994; Smith and Brock 2007) however few studies have investigated the whole of community responses.

**METHODS**

Two mesocosm experiments were conducted to examine the effects of the timing, depth and duration of inundation on floodplain plants from three different communities: red gum (*Eucalyptus camaldulensis*), black box (*Eucalyptus largiflorens*) and temporary open water wetlands. Soil and sediment containing seeds of plants were collected (see detailed methods in Casanova and Brock 2000 and Nielsen et al. 2007), from the three habitat types in Yanga National Park and adjoining farmlands on the Lower Murrumbidgee River floodplain, NSW in November 2011 and June 2012. Surface soil/sediment (2 – 5cm depth) was collected from within 0.01m quadrats, between 32 and 41 quadrats were collected from each habitat type and the soil pooled. Soil from each habitat type was lightly crushed, air dried, mixed thoroughly and sieved to remove vegetation, prior to subsampling.

The experiment was run using a mesocosm at Wonga Wetlands Environmental Centre, Albury, NSW (Nielsen et al. 2007), over two seasons (summer and winter). The experimental design (Table 1) had five replicate pots of each habitat by depth combination, sacrificially sampled one each sampling occasion. Emerging plant seedlings were identified, taxon richness, number of individuals of each taxon and dry weight of above and below ground biomass of each taxon recorded for each pot. Identification of vegetation species was based on Cunningham et al. (2006), Sainty and Jacobs (1981, 2003) and The Royal Botanic Gardens and Domain Trust online plant guide (PlantNET).
Table 1 Experimental design showing dates experiment 1 and experiment 2 were conducted and the levels of each of the four factors (Season, Duration, Habitat Types and Depths).

<table>
<thead>
<tr>
<th>FACTORS/TRATMENTS</th>
<th>EXPERIMENT 1</th>
<th>EXPERIMENT 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Experiment Dates</td>
<td>14&lt;sup&gt;th&lt;/sup&gt; November 2011 to 6&lt;sup&gt;th&lt;/sup&gt; April 2012</td>
<td>23&lt;sup&gt;rd&lt;/sup&gt; July 2012 to 8&lt;sup&gt;th&lt;/sup&gt; October</td>
</tr>
<tr>
<td>Season</td>
<td>Summer/autumn</td>
<td>Winter/spring</td>
</tr>
<tr>
<td>Duration/sampling occasion (weeks)</td>
<td>4, 8, 12, 16, 20</td>
<td>4, 8, 12</td>
</tr>
<tr>
<td>Habitat Types</td>
<td>wetland, red gum, black box</td>
<td>wetland, red gum, black box</td>
</tr>
<tr>
<td>Flood Depth (cm)</td>
<td>0.1 (saturated), 5, 15, 30</td>
<td>0.1 (saturated), 5, 30</td>
</tr>
</tbody>
</table>

**Data Analysis**

Species richness, abundance (count), above ground biomass and belowground biomass data were analysed within each season with a three-factor analysis of variance (ANOVA) and Holm-Sidak post hoc test in SigmaPlot v11 after assumption testing. Differences between seasons were determined by t-test across all treatments (where treatments did not exist in winter – 15 cm, weeks 16 and 20 – they were removed from the t-test analysis). Below ground biomass as a percentage of total biomass data was analysed with a three factor PERMANOVA (Primer + PERMANOVA v.6) (Anderson et al. 2008) due to not meeting the assumptions of equal variance to enable analysis by ANOVA. Multivariate community structure data analysis was undertaken within each season, using a three-factor PERMANOVA of square root transformed above ground biomass. Where significant main effects were detected, pairwise comparisons were undertaken to determine which treatment groups differed. Differences between seasons were determined by one way analysis of similarity (ANOSIM) on square root transformed data, using a Bray Curtis similarity matrix (Clarke and Warwick 2001). Data were presented in a non-metric multidimensional scaling (n-MDS) ordination using Bray Curtis similarity.

**RESULTS AND DISCUSSION**

**Seasonal variation**

Biomass, both above and below ground, species richness and abundance were all significantly lower in winter than in summer, averaged across all depth duration and habitat treatments (p<0.001). The greatest effect was on biomass accumulation where there was less above and below ground biomass in winter, after 12 weeks growth than recorded after four weeks growth in summer (Figure 1). There was also lower species richness and seedling abundance, however this was less pronounced. The community structure was also significantly different between seasons, with clear separation in the n-MDS ordination of averaged replicated data (Figure 3a). One way ANOSIM between season of all samples (not replicate means) showed a significant seasonal effect R=0.812, p<0.001.
Flow seasonality affects processes that generate and sustain riparian vegetation (Greet et al. 2011) but not on the composition of germinating community (Greet et al. 2013). Significantly less biomass was produced after autumn compared to summer flooding (Warwick and Brock 2003). Few studies have compared summer to winter, with most focusing on spring to summer with an emphasis on germination and community composition rather than biomass and growth (Greet et al. 2011). Seasonal differences in germination from seed banks have generally been attributed to temperature as a cue for germination, day length and light quality (Britton and Brock 1994; Warwick and Brock 2003). Greet et al. (2013) attributed the lack of seasonal effect to the relatively constant temperatures recorded during the growing period of the glass house between seasons. Our study was conducted outside and temperature difference, day length and light quality between seasons may account for differences in germination rate, species composition and growth. Further experimentation into temperature, day length and light quality is required to incorporate seasonal variability of growth into predictive models.

(a) Wetland
(b) Red Gum
(c) Black Box

Figure 1 Mean (±95% confidence intervals, n=5) above ground biomass in a) wetland, b) red gum and c) black box habitat types in summer (filled) and winter (open) at five different depths over time. Error bars allowed comparison of significance between depths, habitat type and duration within each season

Depth, Duration and Habitat within seasons

The main effects of depth, duration and habitat (wetland, red gum and black box) were significant (p<0.01) for all variables in each season. There were many significant interactions among the three factors (depth, duration and habitat) and so they could not be interpreted in isolation (Tables 2 and 3).

In summer, above ground biomass followed a clear pattern (Figure 1), similarly found with below ground biomass data. Across all soil types and depths above ground biomass production peaked between 12 and 16 weeks, after which there was a significant decline
Flooding to a depth of 30cm delayed production in wetland and red gum habitat types with significantly less production at 30cm after 8 weeks of inundation, compared to the other flooded depth treatments (Figure 1). The black box habitat produced the greatest biomass followed by wetlands and then red gum, however this was not consistent across all depths and durations.

In winter there was little biomass either above or below ground, but there were still significant interactions between depth, duration and habitat types (Table 3). Saturated soils had significantly greater above and below ground production than flooded soils in black box and red gum habitat types but not in the wetland habitat. Black box had significantly less above and below ground biomass than wetland and red gum for the duration of the experiment and red gum and wetland habitats were only significantly different after 8 weeks (Figure 1).

Table 2 Summer sampling period F values, Pseudo-F values and associated significance levels for three-factor ANOVA and PERMANOVA with duration of inundation (‘Duration’), depth of inundation (‘Depth’) and floodplain habitat type (‘Habitat’) as factors. *P<0.05, **P<0.01, ***P<0.001

<table>
<thead>
<tr>
<th>DF</th>
<th>ABOVE GROUND BIOMASS</th>
<th>BELOW GROUND BIOMASS</th>
<th>ABUNDANCE (COUNT)</th>
<th>SPECIES RICHNESS</th>
<th>COMMUNITY STRUCTURE</th>
<th>BELOW GROUND AS % OF TOTAL</th>
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<td>Duration</td>
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<td>436.5***</td>
<td>260.4***</td>
<td>10.2***</td>
<td>13.7***</td>
<td>41.5***</td>
</tr>
<tr>
<td>Depth</td>
<td>3</td>
<td>5.6***</td>
<td>43.8***</td>
<td>69.9***</td>
<td>58.1***</td>
<td>51.7***</td>
</tr>
<tr>
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<td>2</td>
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<td>11.9***</td>
<td>27.8***</td>
<td>14.9***</td>
<td>52.2***</td>
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<td>4.8***</td>
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<td>0.8</td>
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<td>5.8***</td>
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<tr>
<td>Duration x Habitat</td>
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<td>2.5**</td>
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<td>2.2*</td>
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<tr>
<td>Depth x Habitat</td>
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<td>2.6*</td>
<td>2.2*</td>
<td>1.9</td>
<td>3.7**</td>
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<td>1.1</td>
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</tr>
<tr>
<td>Total</td>
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<td></td>
<td></td>
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</tr>
</tbody>
</table>
Table 3 Winter sampling period F values, Pseudo-F values and associated significance levels for three-factor ANOVA and PERMANOVA with duration of inundation ('Duration'), depth of inundation ('Depth') and floodplain habitat type ('Habitat') as factors. *=P<0.05, **=P<0.01, ***=P<0.001

<table>
<thead>
<tr>
<th></th>
<th>DF</th>
<th>ABOVE GROUND BIOMASS</th>
<th>BELOW GROUND BIOMASS</th>
<th>COUNT (ABUNDANCE)</th>
<th>SPECIES RICHNESS</th>
<th>COMMUNITY STRUCTURE</th>
<th>BELOW GROUND AS % OF TOTAL</th>
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<tr>
<td>Duration</td>
<td>2</td>
<td>22.1***</td>
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<td>115.9***</td>
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<td>16.0***</td>
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<td>32.4***</td>
<td>72.0***</td>
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<td>12.3***</td>
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<td>3.3*</td>
<td>2.9*</td>
<td>13.5***</td>
<td>10.0***</td>
<td>5.8***</td>
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<tr>
<td>Duration x Habitat</td>
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<td>3.0*</td>
<td>6.5***</td>
<td>17.2***</td>
<td>8.9***</td>
<td>5.0***</td>
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<tr>
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<td>6.2***</td>
<td>17.1***</td>
<td>14.4***</td>
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<td>1.3</td>
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<td>2.3*</td>
<td>1.8</td>
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<tr>
<td>Total</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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</tr>
</tbody>
</table>

The combination of depth, duration, and habitat resulted in a complex partitioning of production between above and below ground biomass (Tables 2 and 3, Figure 2). Overall there was a tendency for the understory vegetation community to have a greater proportion of biomass allocated below ground. In summer within the saturated treatment, the black box habitat had significantly lower proportion of biomass allocated to below ground than the red gum habitat at 12 weeks. Contrastingly, black box had significantly greater resources allocated to below ground biomass compared to wetlands at 20 weeks. The proportion of below ground to total biomass was relatively stable over time in saturated and 5cm flooded treatments in summer with no significant effect of duration, within habitats at 5cm but with some pairwise differences in saturated soils (e.g. a greater proportion of below ground biomass in saturated, black box at week 20 compared to weeks 8, 12 and 16). In soils flooded in summer to 15cm and 30cm, there was a significant decrease in the proportion of resources allocated to below ground biomass across habitat types over time (week 20 significantly lower than week 4, across all habitat types when flooded to 15 and 30cm). However the black box habitat followed a slightly different pattern compared to red gum and wetland habitats when flooded to 15 and 30 cm. When flooded in winter (-5cm and -30cm), the little biomass produced was in the form of roots, rather than above ground. Water depth changes the above ground to below ground biomass allocation in individual species (Rea and Ganf 1994) but little is known about how this might operate at the community level or between seasons. Below ground production is important to floodplain ecosystems, with shifts in production potentially having significant effects on energy stores/flow which is often overlooked in production estimates (Baldwin et al. 2013).
The understory vegetation community structure was affected by depth, habitat and duration, but like biomass these factors could not be interpreted independently due to the significant interaction between factors (Tables 2 and 3). The n-MDS ordination clearly showed a separation between summer and winter communities (Figure 3a). Within each season, there was a shift in community structure in response to the duration of inundation (Figure 3b). In winter this was significant for all habitat by depth combinations with the exceptions of black box habitat flooded to 30 cm where no effect of duration was observed and in the wetland habitat type where week 4 and 12 were not significantly different. In summer, the community structure at 4 weeks was different to any other duration across all habitat types and flood depths. After 4 weeks of flooding, the factors of habitat and depth were significant (Table 4). In the red gum habitat after 8 weeks, duration was only significant when flooding occurred to 30 cm depth. In the black box habitat duration was significant for the entire experiment when saturated and only weeks 16 and 20 were not significantly different in flooded treatments (5 cm, 15 cm and 30 cm). In the wetland habitat, duration was significant with most pairwise comparisons with a few exceptions (Table 4). In wetland at 30 cm although there are a number of pairwise comparisons that are not significant, week 12 is different to week 20 indicating there was still a shift in community structure at 30 cm with the increased duration.

The n-MDS showed a clear trajectory of change in community structure with depth in summer, which was not as clear in winter (Figure 3c). The pairwise comparison of the three way interaction showed that, across all habitat types, all depths were significantly different after 12 weeks of inundation in summer and winter. However, this was not consistent
across other habitat type and duration combinations. In summer, saturated soils produced a different community structure to flooded soil on every sampling occasion, across all habitat types (Figure 3c). On every sampling occasion, saturated soils produced a different community structure to flooded soil across all habitat types. Also across all habitats there were sampling occasions where individual depths were not significantly different. This was generally on a trajectory: where for example the community structure found in 5cm treatments was not different to that in 15cm but the community in 5cm and 15cm were different to that in 30cm.

The effect of habitat on community structure was less clearly defined in the n-MDS ordination (Figure 3d), however in both seasons, across all sampling weeks and inundation depths, the black box habitat type had a significantly different community structure, compared to the wetland and red gum habitats. There was some overlap in the community structure of red gum and wetland habitat types but this was dependant on season, depth and duration. Wetland and red gum habitat types were significantly different to each other on all occasions with some exceptions (Winter, after 4 weeks at 5cm and 15cm, Summer – 8 weeks at 30cm, 12 weeks at 5cm and 20 weeks at 30cm).

Table 4  Effect of duration on community structure. Pairwise significance of the tree way interaction of community structure PERMANOVA within each season, depth and habitat combination. All pairwise comparisons are significantly different to the p<0.05 except where indicated being equal (=) Depth treatments – winter (4, 8 and 12 weeks) – summer (4, 8, 12, 16 and 20 weeks)

<table>
<thead>
<tr>
<th>Season</th>
<th>Depth</th>
<th>Black Box</th>
<th>Red Gum</th>
<th>Wetland</th>
</tr>
</thead>
<tbody>
<tr>
<td>Winter</td>
<td>0.1</td>
<td>All different</td>
<td>All different</td>
<td>All different</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>4=12</td>
<td>All different</td>
<td>All different</td>
</tr>
<tr>
<td></td>
<td>30</td>
<td>4=8=12</td>
<td>All different</td>
<td>4=12</td>
</tr>
<tr>
<td>Summer</td>
<td>0.1</td>
<td>All different</td>
<td>12=16=20</td>
<td>12=20</td>
</tr>
<tr>
<td></td>
<td>5</td>
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<td></td>
<td>30</td>
<td>16=20</td>
<td>All different</td>
<td>12=16, 16=20</td>
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</tbody>
</table>
CONCLUSIONS

The results of the experiments suggest that diversity and productivity responses to inundation were influenced by interactions between habitat, depth, duration and timing of inundation. These complex interactions made quantification of the influence of individual factors difficult, however, in summer, biomass increased over the first three to four months and then declined. The species richness patterns were less pronounced and more variable, although the multivariate analysis suggested overlap between wetland and red gum communities with black box representing a different community.

One of the strongest influences was flow timing that influenced above ground and below ground biomass, abundance, species richness and community structure. Flow timing also influenced the influence of other factors reducing or eliminating the effects of depth changing the influence of duration. Further work is required to identify the specific causal factors (temperature, day length) that drive these differences. This finding is of particular
significance for the management of environmental flows as the timing of environmental flows can be controlled by managers.

Perhaps the most striking result was the complexity of vegetation community responses to environmental flows with significant interactions between depth, habitat type and duration for all vegetation communities. This complexity was manifest even though mesocosm experiments represent a simplified floodplain ecosystem. Our study eliminated many factors known to be important, including antecedent conditions, drying periods between floods (Smith and Brock 2007), rate of rise and fall, flood frequency (Casanova and Brock 2000), level fluctuations (Deegan et al. 2007; Smith and Brock 2007), nutrient availability (Deegan et al. 2012), transition zones between habitats, grazing (Blanch and Brock 1994; Crossle and Brock 2002), competition and changes in climatic zone. We also did not include biomass production from understory species that seldom germinate from seed banks (e.g. tangled lignum \textit{(Muehlenbeckia florulenta)} (Chong and Walker 2005), species like \textit{Eleocharis} which produce ribosomes or growth of plants which are already established at the time of an inundation event. It therefore appears likely that the situation is more complex in natural environments.

The complex interactions between depth, habitat type and duration meant that we were not able to develop statistical relationships between these factors and either rate of production or community responses. The objective of the project had been to develop these statistical relationships in order develop models capable of predicting productivity responses to environmental flows. As a consequence, the observed complexity does have implications for the development of predictive models of the response of systems to individual flows.

Floodplain ecosystems have long been recognised as a dynamic mosaic of habitat patches over multi-year time-scales (Junk et al. 1989; Ward and Stanford 1995). The results of this experiment suggest that from a productivity perspective, the most productive places on a floodplain are likely to vary between inundations events and over a single flow event. This implies that floodplains and wetlands are also dynamic mosaics of habitat and production over the course of individual inundation events. This suggests that developing the capacity to predict vegetation responses to environmental flows is unlikely to emerge from simple experiments at the scale of individual wetlands, but that flow is clearly a strong driver in these systems.

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2.13 Blackbox (*Eucalyptus largiflorens*) vegetation and bird communities in the Lowbidgee Floodplain – Flood regimes driving community transitions in semi-arid floodplain woodlands

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INTRODUCTION

Water resource development in south-eastern Australia has seriously reduced the frequency, extent and duration of inundation of floodplain woodlands, resulting in significant habitat change and loss of productivity (Kingsford, 2000, Horner et al., 2009, Alexander et al., 2008, Bren and Gibbs, 1986, Casanova and Brock, 2000). The effects of such changes on floodplain fauna are poorly understood. Woodland birds may be useful indicators of the effects of changing flood regimes on floodplain fauna because they are relatively numerous, diverse, easily surveyed, and responsive to change translated through the entire food web (McGinness et al., 2010). Flooding may affect birds through local and landscape-scale effects on primary productivity and food resources, habitat quality and configuration, or open water resources for drinking and nest construction. Differences in site factors can also influence woodland bird abundance through other mechanisms, such as competitive or invasive species interactions (Clarke and Oldland, 2007, Mac Nally et al., 2012, Maron, 2007). Different guilds or species groups may respond differently to spatial differences or temporal changes in flooding, and listed vulnerable or endangered species may also be sensitive to changes in water availability and its direct and indirect effects. Over time, the influence of differences in site flood history upon habitat, food and water availability is likely to be reflected most strongly by resident, sedentary species at a site, because these are the species most limited by the availability of local resources.

Terrestrial woodland birds have been in decline across Australia (Barrett et al., 2003, Ford et al., 2001, Olsen, 2008). In recent decades, local extinctions have become increasingly widespread, including previously common species (Ford et al., 2009, Mac Nally et al., 2009, Olsen, 2008). Generally, species that are resident, insectivorous, small-bodied and/or ground-foraging are most at risk (Reid, 1999). McGinness et al. (2010) suggested that floodplain woodlands and forests may be important refuges for woodland bird populations because a) floodplain woodlands and forests comprise some of the largest and most continuous vegetation remnants in south-east Australia; and b) floods intermittently supply water, sediment and nutrients that drive greater primary and secondary productivity than
found in woodlands not subject to flooding. They suggested that declining woodland bird species may be disproportionately affected by reduced productivity following changes in flood regime. Similarly, reductions in ground layer vegetation structure and primary production that flowed through the food web are considered key drivers of observed bird population declines (Reid and Fleming (1992)). Hence, the resources provided by flooding may be essential for persistence of declining woodland birds.

This research uses new data to explore the hypothesis that changes in flood regime drive transitions in vegetation structure and condition that in turn create dramatic shifts in woodland bird communities. Beginning with a set of conceptual models based on the links between flooding (frequency and single-event), resource availability (habitat and food) and woodland bird species presence, density and breeding success (Appendix 1), it examines the abundance of selected bird species and groups in remnant floodplain woodlands of a major floodplain and tests the following three predictions:

- vegetation condition will improve and structural complexity will increase with increasing flood frequency and with decreasing time since a site was last wet;
- terrestrial bird abundance will increase with improving vegetation condition and increasing structural complexity and;
- terrestrial bird abundance will increase with increasing flood frequency and with decreasing time since a site was last wet.

METHODS

Remnant black box (*Eucalyptus largiflorens*) woodlands in the lower Murrumbidgee river floodplain (Lowbidgee) in south-east Australia were surveyed in 2010 and 2011. Black box woodland communities in good condition are generally flooded every 2-10 years (George et al., 2005, Johns et al., 2009, Roberts and Marston, 2000, Taylor et al., 1996). Using a space-for-time substitution design, sites were selected across a gradient of water history characteristics, from rarely inundated or experiencing severe drought, to sites regularly inundated. Sites were also selected for contrasts between recently inundated and not recently inundated (time since last wet). Multiple inundation history, surface water proximity and landscape vegetation configuration variables were derived for each site from information provided by land managers, LANDSAT and SPOT imagery processed within CSIRO, and NSW OEH GIS mapping (Table 1), all of which were tested during modelling. All sites were in vegetation remnants greater than 10 ha in size, contained hollow-bearing trees, and were of similar topography and elevation.

Two intensive survey sessions were conducted in each of the years 2010 and 2011: Early spring (August-September) and spring-summer (November-December). These are in addition to pilot surveys at a subset of sites conducted in September and November 2009,
the data from which are being used to examine temporal changes over the 2009-2010-2011 period (from record drought to record wet years) separately.

Four transects 500m in length and 200m apart were surveyed at each site, covering approximately 56 ha at each site. Bird surveys comprised about 20 minutes walking observation per 500 m, recording all birds seen and heard and the transect location and distance and angle from the transect of each bird seen. The same two observers conducted each survey at each site, with each observer covering two transects. Each site was visited twice per survey trip: once in the morning, and once in the evening. Morning and evening data were added together for analysis. Thirty bird species were targeted in order to reduce observer bias. Selected species were predominantly sedentary or resident, considered to have strong reliance on the condition of the sites and their surrounds and to be reliable indicators of factors driving local population dynamics. The species selected ranged from common species to some that are considered vulnerable, threatened or declining, spanning insectivorous, nectivorous, granivorous and omnivorous groups. Analyses of bird responses to flood history and vegetation parameters were conducted first for all surveyed bird species combined, followed by analyses of various combinations of species in groups, e.g. social/non-social, granivorous/non-granivorous, patch-specialist/generalist, and excluding/including competitive miner species (noisy miner *Manorina melanocephala* and yellow-throated miner *Manorina flavigula*). Finally, analyses were conducted for selected individual species representing competitive and vulnerable groups, together with potential interactions between species. In this report, we focus on trends in abundance identified for the main bird groups tested in response to water and vegetation-related factors.

Photographic vegetation assessment was used to improve the efficiency and representativeness of data collection and reduce field-time. At each site, three standardised digital photographs were taken at 24 evenly distributed points, aligned with the bird survey transects: 1) a full-frame photo of the nearest unobscured entire single adult or mature tree, from base to top and full width, portrait or landscape view; 2) a landscape view community photograph with the horizon line at the middle of the image; and 3) a groundcover photograph taken at approximately 1.5 m perpendicular from the ground, using forced flash, no zoom, and moving away from shaded areas. Images were assessed in detail on-screen in the laboratory. The main variables recorded for each of the three photo types together with derivation of scores and indices are described in Table 2 and in McGinness et al. (2013).

Single-factor and multi-factor generalised linear models were fitted according to the data distribution (Poisson or negative binomial), and models compared using Akaike information criterion analysis for small sample sizes (AICc and Akaike weights). The AICc and Akaike weights measure the relative goodness of fit of individual models, and are used to compare relative support for the different models, with better models having lower AICc numbers.
Generally, models with an AICc within three points of the best supported model are also well supported, except where the null model is the better model (Burnham and Anderson, 2002). Zero inflated models were used when required (Zeileis et al., 2008). Models were fitted using water-related explanatory variables for vegetation responses, and both water-related and vegetation-related explanatory variables for bird responses. A null model was also fitted for each combination where response variables were not related to any factors (i.e. the mean of the sites). Counts of live, dead, and total numbers of trees and shrubs >1m tall were log transformed, and groundcover proportions were arcsine transformed. Rather than presenting AICc results for all models explored, statistical results were presented for strongly supported models in terms of likelihood ratio (Chi squared) tests between models with and without the term of interest. Model-predicted values were plotted for the best-supported models (as ranked by the AICc) and inferences made based on the size of the effects. All analyses were carried out in R, using the packages bbmle, nlme, pscl, and lmtest (Jackman, 2011, Pinheiro et al., 2013, Zeileis and Hothorn, 2002).

RESULTS

Models driven by site inundation history factors were consistently stronger than all other models, for both vegetation and bird response variables. Site inundation history was ultimately best represented in models by two primary categorical factors: 1) LowestARI5pccat: The lowest average recurrence interval (ARI) zone recorded that occupied more than 5% of the site, representing the frequency with which at least part of the site has received water (even if that water does not inundate the entire site); and 2) TSWW20pc: The time since the site was last wetted over more than 20% of its area. The LowestARI5pccat (ARI) categories used were one in <3, 4 to 9, 10 to 19, and >20 years; and the time since wet categories used were 0-2 years, 2-10 years, and >20 years. An ARI of <3 years means that a site has been flooded at least every 3 years on average, if not more often (frequent inundation), whereas an ARI of >20 years means that a site has been flooded less than once every 20 years on average (infrequent inundation).

Vegetation responses to flooding: shifts in condition and structure

Both vegetation condition and vegetation structure in the black box floodplain woodlands surveyed were clearly influenced by flood history and sometimes also influenced by the time since a site was last flooded. In general, the best supported models of tree condition (including crown density, crown death and flowering) were those driven by LowestARI5pccat or an additive interaction between LowestARI5pccat and TSWW20pc. Variables affecting habitat structure such as large shrub abundance and subshrub abundance were also strongly predicted by additive interactions between LowestARI5pccat and TSWW20pc. In contrast, the best supported models of groundcover variables were those driven by the time since a site was last flooded (TSWW20pc).
Lower flood frequencies at a site were associated with significantly lower average tree health (including decreased crown density and increased crown death) and reduced tree flowering. There were significantly fewer large shrubs where flooding occurred less than once every 20 years, together with a lower proportion of young trees present (demonstrating reduced regeneration and recruitment and lower vegetation structural complexity), increased abundance of dryland subshrubs, and increased numbers of dead trees.

Vegetation patterns in response to the time since a site was last wet were more complex and variable than those observed in response to flood frequency. Average tree health and tree flowering were significantly lower at sites that had not been wet for >20 years than other sites (including significantly reduced crown density and significantly increased crown death). Site vegetation complexity/structure was significantly greater at sites that had last been flooded between 2-10 years before, compared to other sites, partly driven by greater proportions of young and old trees at these sites. The number of live trees was also greater at these sites than at others. Groundcover was highly variable, but plant cover was reduced at sites that had been recently flooded (within two years), with relatively greater proportions of bare ground and organic litter and a significantly lower proportion of live plants present than other sites. Live plant cover was significantly greater at sites that had been flooded 2-10 years before compared to other sites.

**Bird responses to vegetation and flooding: shifts in relative abundance and community composition**

Woodland bird abundance in floodplain woodlands was significantly affected by flood history; however response patterns varied among different bird groups. Models of bird abundance directly related to flood history significantly outperformed models related to vegetation or abundance of competitive species such as miners. The strongest predictor of bird abundance was the lowest ARI recorded that occupied more than 5% of the site (LowestARI5pccat). In general, variables describing broad flood regime were better predictors of bird abundance than short-term variables such as the time since a site was last wet (TSWW20pc), however the latter was still significant and interacted with flood frequency (LowestARI5pccat) for some bird groups/guilds. The strongest vegetation predictors of bird abundance, over all analyses, were average site tree health and site vegetation complexity.

Low flood frequencies at a site were associated with significantly lower abundances of non-social bird species and patch specialist species (with granivores excluded), non-granivorous species, and small-bodied bird species than in other sites (e.g. Figure 1). There appeared to be a threshold where an ARI of less than one flood event in 10 years resulted in significantly reduced abundances in these bird groups at a site, whereas bird abundances in these groups at sites with ARIs of more than one event in 10 years were generally similar. The reverse
was true for granivorous species, with significantly greater abundances of birds in this group at sites with an ARI of less than one flood event in 10 years. No significant effect of flood frequency was apparent for social species (excluding miners), but the data trended toward increasing abundances with increasing ARI.

![Graph 1](image1.png)

**Figure 1.** Lower flood frequency at a site was associated with lower abundances of non-social bird species (with granivores excluded) and higher abundances of granivorous bird species. LowestARI5pccat is the lowest average recurrence interval (ARI) category recorded that occupied more than 5% of the site, representing the frequency with which at least part of the site has received water.

Bird abundance patterns in response to the time since a site was last wet were more variable than those observed in response to flood frequency. Increasing time since a site was last wet (particularly an interval of >20 years) was associated with significantly lower abundances of non-social, patch specialist and small-bodied bird species, when granivores were excluded (Figure 2). Most other bird groups were more abundant at sites that had been flooded within 2-10 years, however variability was much greater in this category. Overall, bird abundances were lower in sites that had not been flooded for more than 20 years, compared with sites that had been flooded within 10 years, except for social and granivorous species groups.

Increasing average tree health and increasing site vegetation complexity at a site were both associated with significantly increasing abundance of non-social bird species, patch specialist species, non-granivorous species, and small-bodied bird species. In contrast, greater tree health and vegetation complexity were associated with significantly lower abundances of granivorous species and social species.
DISCUSSION

These results suggest that black box floodplain woodlands that do not receive sufficient flooding undergo transitions in vegetation type or structure, rather than degradation in condition alone, and that this in turn affects woodland bird relative abundance and community composition. Black box sites receiving insufficient flooding appear to transition toward a more terrestrial, dryland state, with associated increases in relative abundance of dryland understorey species (e.g. subshrubs and grasses). With continued declines in tree condition the black box tree layer will probably eventually be lost entirely in the long term at these sites if a suitable flood regime is not reinstated. In the interim, vegetation condition (and potentially productivity) is reduced at both tree and understorey levels. Woodland bird community composition has also shifted at these sites – with greater abundance of more mobile granivorous and social or co-operative species at dry sites, and fewer small-bodied, non-social residents. Together, these data indicate that reduced flooding has changed resource availability, in terms of both habitat as structure changes and food type and abundance as productivity declines. These changes are culminating in significant shifts in vegetation and fauna community composition and will probably eventually result in an entirely different community type. Further analysis of species richness and community composition data across sites and over time will explore the nature of these shifts.

Such changes affect fauna populations and diversity at a site through multiple related mechanisms. Populations of species that require sites with greater flood frequency and associated productivity and habitat structure are more likely to decline and eventually become locally extinct. Increased competition for resources and changes in habitat...
structure such as increased openness and edge availability may advantage highly competitive or co-operative / social species. This may maintain or increase their population sizes while less effective competitors are reduced in abundance or eliminated. Co-operative social breeding may increase the chances of a population surviving at a site during dry years, and allow that population to take rapid advantage of boom conditions during high rainfall or flood years, quickly increasing population size and spreading to new areas, even where habitat structure and quality are poor. In contrast, small bodied non-social/non-co-operative species may be more susceptible to competitive and predatory attacks than large bodied social/co-operative species, and therefore their presence or population sizes may be disproportionally affected by such changes.

Alterations in flood regimes and associated changes in structure, productivity and condition of floodplain vegetation have probably contributed to observed declines in woodland bird populations in Australian drylands (McGinness et al., 2010). Declining bird species in these regions tend to be small-bodied, resident (or less mobile), insectivorous, and/or ground-foragers (Reid, 1999) – similar groups to those identified in this study as occurring in reduced abundance at sites with low flood frequency and reduced tree health and structural complexity. In south-east Australia, many of the most dramatic changes in flood regimes have occurred over the same period and across the same geographical areas in which significant declines in bird populations have been observed (Barrett et al., 2003, Mac Nally et al., 2009, Major et al., 2001, Reid, 1999). Woodland bird population declines have continued in these areas despite a recent general cessation of clearing and increasingly sensitive management of vegetation, prompting suggestions that continuing degradation of habitat (in particular food resources) and extinction debts are important drivers (Ford et al., 2009, Mac Nally et al., 2009).

This study demonstrates that changes in flooding frequency result in shifts in site character and ultimately transitions to different vegetation and fauna communities, even within the same broad vegetation type. Importantly, these shifts have a compounding effect resulting from interactions between vegetation changes, fauna habitat preferences and fauna behaviour (e.g. competition). Such transitions encompass changes in structure, composition, productivity and diversity of a community or site; with potentially far-reaching implications for ecosystem function at multiple scales and for the way a site is valued and managed.

ACKNOWLEDGEMENTS

This research was funded by the CSIRO Water for a Healthy Country Flagship. It would not have been possible without the generous support of the Yanga National Park NSW staff, the NSW Office of Environment and Heritage and the kind landholders on whose properties we worked. We gratefully acknowledge Murray Darling Freshwater Research Centre staff
including Darren Baldwin and Jessica Wilson for introducing us to the study area and sharing information, and Nick Nicholls (CSIRO) for statistical advice.

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Johns C, Reid CJ, Roberts J, Sims N, Doody TM, Overton IC, McGinness HM, Rogers K, Campbell C and Gawne B (2009). Native trees of the River Murray floodplain:
Literature review and experimental designs to examine effects of flow enhancement and floodwater retention. Final report to the Murray-Darling Basin Authority. Wodonga, Murray-Darling Freshwater Research Centre.


Table 1 Water-related variables used in analyses

<table>
<thead>
<tr>
<th>Flood frequency</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>&quot;ARI_0p5&quot;</td>
<td>Percentage of the site inundated at an average recurrence interval of 2 floods per year</td>
</tr>
<tr>
<td>&quot;ARI_1p5&quot;</td>
<td>Percentage of the site inundated at an average recurrence interval of 1.5 floods per year</td>
</tr>
<tr>
<td>&quot;ARI&gt;20&quot;</td>
<td>Percentage of the site inundated at an average recurrence interval of &lt;1 flood every 20 years</td>
</tr>
<tr>
<td>&quot;ARI10&quot;</td>
<td>Percentage of the site inundated at an average recurrence interval of 1 flood every 10 years</td>
</tr>
<tr>
<td>&quot;ARI15&quot;</td>
<td>Percentage of the site inundated at an average recurrence interval of 1 flood every 15 years</td>
</tr>
<tr>
<td>&quot;ARI2&quot;</td>
<td>Percentage of the site inundated at an average recurrence interval of 1 flood every 2 years</td>
</tr>
<tr>
<td>&quot;ARI20&quot;</td>
<td>Percentage of the site inundated at an average recurrence interval of 1 flood every 20 years</td>
</tr>
<tr>
<td>&quot;ARI3&quot;</td>
<td>Percentage of the site inundated at an average recurrence interval of 1 flood every 3 years</td>
</tr>
<tr>
<td>&quot;ARI4&quot;</td>
<td>Percentage of the site inundated at an average recurrence interval of 1 flood every 4 years</td>
</tr>
<tr>
<td>&quot;ARI5&quot;</td>
<td>Percentage of the site inundated at an average recurrence interval of 1 flood every 5 years</td>
</tr>
<tr>
<td>&quot;GARI_0p5to5&quot;</td>
<td>Percentage of the site inundated at an average recurrence interval of 1 flood every 0.5 to 5 years</td>
</tr>
<tr>
<td>&quot;GARI10to20&quot;</td>
<td>Percentage of the site inundated at an average recurrence interval of 1 flood every 10 to 20 years</td>
</tr>
<tr>
<td>&quot;LowestARI5pca&quot;</td>
<td>The lowest average recurrence interval (ARI) recorded that occupied more than 5% of the site, representing the frequency with which at least part of the site has received water (even if that water does not inundate the entire site)</td>
</tr>
<tr>
<td>&quot;LowestARI5pccat&quot;</td>
<td>The lowest average recurrence interval (ARI) category recorded that occupied more than 5% of the site, representing the frequency with which at least part of the site has received water (even if that water does not inundate the entire site)</td>
</tr>
<tr>
<td>&quot;ARICAT2&quot;</td>
<td>A two-category version of LowestARI5pccat</td>
</tr>
<tr>
<td>&quot;MinARI&quot;</td>
<td>The lowest average recurrence interval at the site</td>
</tr>
<tr>
<td>&quot;MaxARI&quot;</td>
<td>The highest average recurrence interval zone recorded at the site</td>
</tr>
<tr>
<td>&quot;ARIRange&quot;</td>
<td>The range of average recurrence intervals at the site (categorical groups)</td>
</tr>
<tr>
<td>&quot;Ctwaterpres_2006_2011&quot;</td>
<td>The number of times water was recorded as present at a site between the years 2006 and 2011</td>
</tr>
<tr>
<td>&quot;Ctwaterpres_3yr_NS&quot;</td>
<td>The number of times water was recorded as present within the site during the months September and November over the preceding three years</td>
</tr>
<tr>
<td>&quot;Ctwaterpres_3yr_sm&quot;</td>
<td>The number of times water was recorded as present at a site during the same month as the survey over the preceding three years</td>
</tr>
<tr>
<td>&quot;Ctwaterpres20pc_2006_2011&quot;</td>
<td>The number of times water was recorded as occupying &gt;20% of the site between the years 2006 and 2011</td>
</tr>
<tr>
<td>&quot;Ctwaterpres20pc_3yrNS&quot;</td>
<td>The number of times water was recorded as occupying &gt;20% of the area of the site during the months September and November over the preceding three years</td>
</tr>
<tr>
<td>&quot;DomARI&quot;</td>
<td>The average recurrence interval category that covers most of the site</td>
</tr>
</tbody>
</table>

Recent flood extents and time since wet

| "TSW20pc"    | The time elapsed since >20% of the site was inundated |
| "TSW2"       | A two-category version of TSW20pc |
| "pcFlooded"  | Percentage of the site inundated during survey |
| "Water_ha"   | Area of water present within site during survey |
| "Waterores20pc_1_0" | Presence or absence of water inundating >20% of the site during survey |
| "Waterpres_1_0" | Presence or absence of water within the site during survey |
| "Waterpres_YN" | Presence or absence of water within the site during survey |
| "Waterpres20pc_YN" | Presence or absence of water inundating >20% of the site during survey |
| "Cumpcflood_3yrNS" | The sum of the percentage of the site inundated during the months of September and November over the preceding three years |
| "Cumpcflood_3yr_sm" | The sum of the percentage of the site inundated within the same month as the survey over the preceding three years |
| "Maxextent_3yrNNS" | The maximum percentage of the site inundated during the months of September and November during the preceding 3 years |

Water in the surrounding landscape

| "DistAnyChan"   | Distance from the centre of the survey site to the nearest channel of any kind (m) |
| "DistBidgee"    | Distance from the centre of the survey site to the Murrumbidgee River |
| "DistFarmDam"   | Distance from the centre of the survey site to the nearest farm dam |
| "DistPerWater"  | Distance from the centre of the survey site to the nearest perennial water |
| "FarmDamCt5km"  | Number of farm dams within a 5km radius of the centre of the survey site |
Table 2 Vegetation variables used in analyses. Each variable was either averaged to site level, or analysed as proportions of photos on which they were present per site.

<table>
<thead>
<tr>
<th>Single tree photo</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Crown death score</td>
<td>Percentage of the total crown completely defoliated (0 = 0%; 1 = 1-10%; 2 = 11-20%; 3 = 21-40%; 4 = 41-60%; 5 = 61-80%; 6 = 81-90%; 7 = 91-100%)</td>
</tr>
<tr>
<td>Crown density score</td>
<td>Percentage of skylight blocked by those portions of the tree crown that were foliated (0 = 0%; 1 = 1-10%; 2 = 11-20%; 3 = 21-40%; 4 = 41-60%; 5 = 61-80%; 6 = 81-90%; 7 = 91-100%).</td>
</tr>
<tr>
<td>Live or dead</td>
<td>Tree alive (1) or dead (0)</td>
</tr>
<tr>
<td>Frequency of tree flowering</td>
<td>Flowers visible on tree (Yes=1/No=0).</td>
</tr>
<tr>
<td>Frequency of new buds or new leaves</td>
<td>New buds or new leaves visible on tree (Yes=1/No=0).</td>
</tr>
<tr>
<td>Tree health score</td>
<td>The sum of the above scores (maximum score 17; scores for crown death reversed)</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Landscape photo</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Live tree count</td>
<td>Number of individual live trees visible in each image, excluding those that formed part of the blurred horizon line, were indistinct because they were too far away or too close to other trees, or that were &lt;50% within the image.</td>
</tr>
<tr>
<td>Dead tree count</td>
<td>Number of individual dead trees visible in each image, excluding those that formed part of the blurred horizon line, were indistinct because they were too far away or too close to other trees, or that were &lt;50% within the image.</td>
</tr>
<tr>
<td>Total tree count</td>
<td>Total number of individual trees visible in each image, excluding those that formed part of the blurred horizon line, were indistinct because they were too far away or too close to other trees, or that were &lt;50% within the image.</td>
</tr>
<tr>
<td>Frequency of old trees</td>
<td>Number of images in which old trees are visible (mature or aged-mature).</td>
</tr>
<tr>
<td>Frequency of young trees</td>
<td>Number of images in which young trees are visible (seedling or sapling).</td>
</tr>
<tr>
<td>Presence of old trees</td>
<td>Old trees (mature or aged-mature) present at site (Yes=1/No=0)</td>
</tr>
<tr>
<td>Presence of young trees</td>
<td>Young trees (seedling or sapling) present at site (Yes=1/No=0)</td>
</tr>
<tr>
<td>Number of tree size classes</td>
<td>Of 6: Seedling, sapling, pole, adult, mature, aged-mature.</td>
</tr>
<tr>
<td>Shrub &lt;1m count</td>
<td>Total number of individual subshrubs &lt;1m tall visible in each image, excluding those that formed part of the blurred horizon line, or that were &lt;50% within the image.</td>
</tr>
<tr>
<td>Shrub &gt;1m count</td>
<td>Total number of individual large shrubs &gt;1m tall visible in each image, excluding those that formed part of the blurred horizon line, or that were &lt;50% within the image.</td>
</tr>
<tr>
<td>Large woody debris (LWD) score</td>
<td>Count of all pieces of woody debris &gt;50% within the image estimated at &gt;10cm diameter. If a complex fallen branch was present, the number of points touching the ground was counted and included in the overall score.</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Groundcover photo</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bare %</td>
<td>Bare soil, rocks and stones.</td>
</tr>
<tr>
<td>Live plants %</td>
<td>Any living plant, including trunks of living trees and upright dormant plants.</td>
</tr>
<tr>
<td>Dead plants %</td>
<td>Standing dead plants.</td>
</tr>
<tr>
<td>Organic litter %</td>
<td>Dead, detached plant material &gt;2cm diameter.</td>
</tr>
<tr>
<td>Woody ground cover %</td>
<td>Dead, detached woody plant material &gt;2cm diameter.</td>
</tr>
<tr>
<td>Cryptogams %</td>
<td>Any visible cryptogams, e.g. lichen.</td>
</tr>
<tr>
<td>Frequency of Sclerolaena spp.</td>
<td>Number of images in which Sclerolaena is visible</td>
</tr>
<tr>
<td>Frequency of Hordeum spp.</td>
<td>Number of images in which Hordeum is visible</td>
</tr>
<tr>
<td>Frequency of Muehlenbeckia</td>
<td>Number of images in which Lignum (Muehlenbeckia) is visible</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>GIS-based</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>&quot;Wood2a&quot;</td>
<td>The area of River Red Gum tall gallery forest (adjacent to rivers) within a 5km radius of the centre of the survey site</td>
</tr>
<tr>
<td>&quot;Wood2c&quot;</td>
<td>The area of Black Box with Lignum / Nitre Goosefoot understorey within a 5km radius of the centre of the survey site</td>
</tr>
<tr>
<td>&quot;Wood2f&quot;</td>
<td>The area of Black Box with grass / chenopod shrub groundcover within a 5km radius of the centre of the survey site</td>
</tr>
<tr>
<td>&quot;Wood1b&quot;</td>
<td>The area of River Red Gum forest with Spike-rush ground cover within a 5km radius of the centre of the survey site</td>
</tr>
<tr>
<td>&quot;Wood1d&quot;</td>
<td>The area of River Red Gum forest with shrubby (Lignum / River Cooba) understorey within a 5km radius of the centre of the survey site</td>
</tr>
<tr>
<td>&quot;Wood2b&quot;</td>
<td>The area of Black Box with grass / chenopod shrub groundcover within a 5km radius of the centre of the survey site</td>
</tr>
<tr>
<td>&quot;Alwood25km&quot;</td>
<td>The area of woodland of any type within a 5km radius of the centre of the survey site</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Composite site-based variables</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>&quot;SITECOMPLEXITYVA&quot;</td>
<td>All variables rescaled to values between 0 and 1 before summing</td>
</tr>
<tr>
<td>&quot;SITECOMPLEXITYVB&quot;</td>
<td>The sum of: Shrubs &lt;1m count, Shrubs &gt;1m count, Large woody debris (LWD) score, Live plants %, Organic litter %, Presence of old trees, Presence of young trees</td>
</tr>
<tr>
<td>&quot;SITESCORE&quot;</td>
<td>The sum of Crown death score, Crown density score, Shrubs &lt;1m count, Shrubs &gt;1m count, Large woody debris (LWD) score, Live plants %, Organic litter %, Presence of old trees, Presence of young trees, Total tree count, Number of tree size classes, and Woody ground cover</td>
</tr>
<tr>
<td>&quot;SUMSCOREALL&quot;</td>
<td>After rescaling scores to values between 0 and 1, the sum of all photo-derived vegetation variables</td>
</tr>
</tbody>
</table>
Antecedent flow and juvenile fish abundance in floodplain wetlands of the mid-Murray River

L. Beesley\textsuperscript{1,2}, A. Price\textsuperscript{3}, A.J. King\textsuperscript{14}, J.D. Koehn\textsuperscript{1}, B. Gawne\textsuperscript{3}, D. Nielsen\textsuperscript{3} & D.C. Gwinn\textsuperscript{5}

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INTRODUCTION

One of the greatest threats to lotic ecosystems is flow regulation. The impacts of flow regulation on native fish are often mitigated using periodic water allocations, termed environmental flows. The effectiveness of environmental flows has been studied in some systems, but the role of flow conditions prior to water allocation (i.e. antecedent conditions) has rarely been quantified. This is somewhat surprising because research on an array of biota, including fish, suggest that antecedent flows, particularly episodes of flood and drought, can affect: (i) the dispersal of biota (Labbe and Fausch 2000; Wen et al. 2011), (ii) the recruitment and abundance of fish (Freeman et al. 2001; Puckridge, Costelloe and Reid 2010; Balcombe et al. 2012), (iii) the productivity of ecosystems (Puckridge, Costelloe and Reid 2010; Leigh et al. 2010; Wen et al. 2011), (iv) the number of species (Balcombe and Arthington 2009; Puckridge, Costelloe and Reid 2010; Leigh 2013), (v) the condition of individuals (Abujanra, Agostinho and Hahn 2009; Balcombe et al. 2012), and (vi) the condition of refuge habitats (Labbe and Fausch 2000; Leigh et al. 2010).

A significant challenge to informing how antecedent conditions might guide the use of environmental flows for the benefit of native fishes is the difficulty collecting reliable long-term community data. Field data on fish assemblages are always imperfect and can be highly variable. Variation in the sampling methods, the behaviour of the study organisms and the environment, can lead to variation in detection probability, potentially resulting in spurious conclusions (Hangsleban, Allen and Gwinn 2013; Archaux, Henry and Gimenez 2011). In spite of these sampling issues, few investigations of environmental flows and fish have attempted to account for incomplete or variable detection (but see Bradford et al. 2011). Fortunately, there have been many recent advances in the applications of Bayesian hierarchical models that account for incomplete and variable detection (Royle and Dorazio 2008).
We developed a Bayesian hierarchical multiple-species abundance model for six wetlands in the Murray River (Australia), a flow-regulated system that received variable levels of inundation, and whose fish populations were sampled seasonally, over five years. We investigated the relative importance of short-term, medium-term and long-term antecedent flow conditions on juvenile fish abundance. We also evaluated the factors that affect the detection probability of wetland fish species. Lastly, we discuss the implications of our results for informing environmental flow management aimed at enhancing native fish communities in floodplain wetlands.

**METHODS**

This study was conducted in six floodplain wetlands of the mid-Murray River, a heavily flow-regulated system in south-eastern Australia (Close 1990), sampling three times a year, for five years (October 2007 to April 2012). Each wetland varied in river-wetland commence-to-fill values (Figure 1). Intra-annual sampling was related to season (late October: Spring; late January: Summer; April: Autumn). The drying of one wetland prevented sampling twice, and poor access prevented sampling of three wetlands once. Consequently, a total of 85 samples were collected. Further detailed descriptions of study wetlands exist (Beesley et al. 2012).

![Figure 1 Average daily discharge from June 2002 to June 2012 for two gauging stations on the Murray River (Yarrawonga (grey) and downstream Corowa (dark). Horizontal dashed lines showed the flow threshold](image-url)
Fish were sampled using a passive method, single-wing fyke nets, and an active method, beach seine. Sampling effort was scaled to wetland size to keep sample coverage similar among wetlands. Generally, four fyke nets (range 2 to 5) were set overnight on each sampling occasion (1.5-mm mesh, six hoops, two funnels, 5-m wing 0.6m drop); and on average 4.5 seine hauls (range 3 to 5) were conducted during the day (0.5mm-mesh, 7m long, 1.5-m drop with a small purse). Fish collected were identified to species, counted and released. The majority of all specimens collected (80-100%) were ≤ age 1 (Beesley et al. 2012) with the exception of oriental weatherloach (*Misgurnus anguillicaudatus*) which were mainly age 1+. A detailed description of the study wetlands and fish sampling methods is provided in Beesley et al. (2012).

We summarized the indicators of wetland inundation into three flow metrics representing antecedent flows on three different time scales. This was achieved by summing the number of days that a wetland was inundated for each time scale. The time scales were defined as short-term (three months prior = 1 to 91 days), medium-term (four to twelve months prior = 92 to 365 days), and long-term (one year to five years prior = 366 to 1822 days). These time periods were deliberately not nested as to ease interpretation and avoid issues of correlation among antecedent flow metrics. Together the short and medium-term metrics describe wetland connection over the year prior to sampling, and together with the long-term metric, describe wetland connection over five years prior to sampling. All flow metrics were determined by using average daily discharge data from the nearest gauging station (Figure 1).

**Statistical Analyses**

We performed our analysis of antecedent flow and juvenile fish abundance with a multi-species occupancy model (Royle and Dorazio 2008), an extension of the single-species occupancy models. These models were essentially zero-inflated logistic regressions that accounted for imperfect detection of individuals, allowing for variation in sampling efficiency. We hypothesized that flow and seasonal covariates may influence the mean abundance of juvenile fish and incorporated them into the model with a log link function (McCullagh and Nelder 1989). We also hypothesized that the detection probability may be influenced by the type of sampling gear used and the wetland sampled. We incorporated these covariates into the detection model using a logit link (McCullagh and Nelder 1989).

Finally, the effect of site (wetland) was modelled as a random effect across wetlands, representing the cumulative influences of the unique characteristics of each wetland impacting on sampling efficiency (e.g. area, depth, or plant cover).
Our model assumes that the abundance of fish is a latent random variable $N_{ij}$ described by a Poisson distribution as $N_{ij} \sim \text{Poisson}(\lambda_{ij})$, where $\lambda_{ij}$ is the Poisson mean for species $i$ at site $j$. Our data $y_{ij}$ is the total number of replicate samples where species $i$ was observed at site $j$. We assume that $y_{ij}$ is the result of multiple binomial outcomes as, $y_{ij} \sim \text{Binomial}(p_{ij}, n_j)$, where $p_{ij}$ is the probability of detecting at least one individual of species $i$ at site $j$ and $n_j$ is the number of replicate samples collected at site $j$. We specified the relationship between $p_{ij}$ and $N_{ij}$ per Royle and Nichols (2003) as, $p_{ij} = \frac{1}{1 + \exp(-r_{ij}N_{ij})}$, where $r_{ij}$ represents the detection probability on the individual level as opposed to $p_{ij}$ which is the probability of detecting one or more individuals of species $i$ at site $j$. This formulation essentially models the detection probability $p_{ij}$ as a random effect defined by the relationship between $p_{ij}$ and $N_{ij}$ and the mixing distribution of $N_{ij}$ (Poisson) to account for variation in $p_{ij}$ due to variation in abundance of fish among sites.

We incorporated antecedent-flow and seasonal covariates that may influence the mean abundance of fish ($\lambda_{ij}$) into the model with a log link (McCullagh and Nelder 1989) as:

$$\log(\lambda_{ij}) = \beta_1 + \beta_2 \text{long}_j + \beta_3 \text{medium}_j + \beta_4 \text{short}_j + \beta_5 \text{long}_j \text{short}_j + \beta_6 \text{medium}_j \text{short}_j + \beta_7 \text{season2}_j + \beta_8 \text{season3}_j + \beta_9 i_k \text{weland}$$

where, $\beta_1$ represents the species-specific intercept of the abundance sub-model, $\beta_2, \beta_3, \beta_4$ represent the effects of each antecedent-flow variable on the abundance of $i$ species, $\beta_5$ and $\beta_6$ represent the interaction effects of short, medium and long-term antecedent flows, and $\beta_7$ and $\beta_8$ represent species-specific seasonal differences in abundance. The parameters represented by $\beta_9 i_k$ were random effects across $i$ species and $k$ wetlands to account for differences in the abundance of fish related to each wetland’s unique characteristics and the non-independence of samples collected through time in the same wetland.

We hypothesized that the detection probability $r_{ij}$ was influenced by sampling gear, wetland area, and wetland sampled, and incorporated them into the detection model using a logit link as:

$$\logit(r_{ij}) = \alpha_1 + \alpha_2 \text{gear}_j + \alpha_3 \text{area}_j + \alpha_4 \text{gear}_j \text{area}_j + \alpha_5 i_k \text{weland}$$

where $\alpha_1$ represents the species-specific intercept and $\alpha_2$ represents the species-specific gear effect. The parameter $\alpha_3$ represents the species-specific effect of the wetland area on detection as an index of overall wetland size. The parameter $\alpha_4$ represents the interaction between the gear and the wetland area to evaluate the possibility that different sampling gears are affected by the size of the wetland differently. The parameters represented by $\alpha_5 i_k$ were modelled as random effects across $i$ species and $k$ wetlands and represent the cumulative influences of the unique characteristics of each wetland that could impact sampling efficiency.
All species-specific parameters were specified as random effects drawn from hyper-distributions governed by community level hyper-parameters. All hyper-distributions were specified as normal distributions. The random effects of wetland on abundance ($\beta_{9i,k}$) and detection ($\alpha_{5i,k}$) were also assumed to be drawn from normal distributions with means equal to zero and species-specific standard deviations. We evaluated the importance of covariates on species-specific abundance and detection by sampling the posterior distributions of the full model. We considered covariates important when 90% credible intervals did not include zero.

**Flow scenarios**

We evaluated native and non-native fish responses to wetland inundation to aid in the interpretation of species-specific results and gain insight into flow characteristics that result in fish communities dominated by native species or non-native species. We achieved this by, first, defining five generic flow scenarios based on intervals of wetland inundation as: (i) zero days of inundation during a five-year period, (ii) 60 days of inundation once at the end of five years, (iii) 60 days of inundations once every year, (iv) 60 days of inundation once every six months, and (v) 60 days of inundation every three months (see Figure 2). We generated simulated flow data based on each flow scenario and summarized it into the wetland inundation metrics for the long-term, medium-term, and short-term time scales. We then utilized our fitted model to predict the ratio of total abundance of native fish to non-native fish for each hypothetical flow scenario.

**RESULTS AND DISCUSSION**

Our results offer insight into the relative influence of multiple temporal scales of antecedent flows on the structure of a wetland fish assemblage. The hierarchical multi-species modelling approach identified patterns across the entire assemblage and highlighted
species-specific variation. For some species, juvenile fish abundance in these floodplain wetlands was significantly related to antecedent flow conditions (Table 1). The short-term responses found by this study, were in general agreement with the flow-related life history groupings put forward by Humphries et al. (1999). For example, our finding that flathead gudgeon, carp gudgeon and Australian smelt, showed little to no response to recent high flows corroborates the findings of King et al. (2003) and is consistent with Humphries et al. (1999) categorisation of these species as flow generalists.

Of particular interest though, was our finding that medium and longer-term antecedent flows affected the response to short-term flows for other species (i.e. common carp, gambusia and oriental weatherloach) (see interaction terms in Table 1). These interactions are important for management, because they suggest that past flow conditions can moderate the impact of current environmental watering events on these non-native species. That common carp juvenile abundance was greatest when recent flows were high and previous flows were low is probably driven by the fact that recently inundated, shallow habitats with abundant plant material are ideal carp spawning habitat (Koehn et al. 2000), and that drying of the floodplain promotes a dense growth of macrophytes and understorey terrestrial grasses (Briggs and Maher 1985) – a perfect spawning substrate when inundated.

Our evaluation of hypothetical flow scenarios suggests that policies that ensure the frequent inundation of wetlands will promote native fish and suppress non-native fish (Figure 2). This prediction agrees with the findings of a recent study by Ho, Bond and Thompson (2013) who also studied wetland fish in south-eastern Australia, and found that regularly flooded wetlands supported higher abundances of carp gudgeon (native), and irregularly flooded wetlands supported higher abundances of eastern gambusia (non-native). In the southern Murray-Darling Basin, river regulation has reduced the frequency of floodplain inundation (Maheshwari, Walker and McMahon 2006); so, an improvement for native species as the frequency of flow increases is in accordance with general expectations (Poff et al. 1997). The restoration of flow regimes in regulated rivers has benefited native fish elsewhere in the world (see Travnichek, Bain and Maceina 1995; Brown and Ford 2002; Kiernan, Moyle and Crain 2012). In the southern Murray-Darling Basin, our results suggest that policies aimed at avoiding long drying periods by frequent watering will benefit the native fish community.
Table 1 The significance of antecedent flow covariates at different time scales (short, medium and long) on species-specific juvenile abundance. The symbol, $+$ represents a significant positive affect on abundance and the symbol $-$ represents a significant negative affect on abundance. Significance was determined by 90% credible intervals that do not overlap zero. LT:ST = the interaction between long-term and short-term wetland inundation; MT:ST = the interaction between medium-term and short-term wetland inundation.

<table>
<thead>
<tr>
<th>SPECIES</th>
<th>SHORT-TERM</th>
<th>MEDIUM-TERM</th>
<th>LONG-TERM</th>
<th>LT:ST</th>
<th>MT:ST</th>
</tr>
</thead>
<tbody>
<tr>
<td>Australian smelt</td>
<td></td>
<td>$+$</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Flathead gudgeon</td>
<td>$+$</td>
<td></td>
<td>$+$</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Carp gudgeon</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Unspecked hardyhead</td>
<td></td>
<td>$-$</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Native species</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>European perch</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Oriental weatherloach</td>
<td>$+$</td>
<td></td>
<td>$-$</td>
<td></td>
<td>$-$</td>
</tr>
<tr>
<td>Eastern gambusia</td>
<td>$+$</td>
<td></td>
<td>$-$</td>
<td></td>
<td>$-$</td>
</tr>
<tr>
<td>Common carp</td>
<td>$+$</td>
<td></td>
<td>$-$</td>
<td></td>
<td>$-$</td>
</tr>
<tr>
<td>Goldfish</td>
<td>$+$</td>
<td></td>
<td>$-$</td>
<td></td>
<td>$-$</td>
</tr>
<tr>
<td>Non-native species</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Our analysis revealed multiple sources of heterogeneity in the detection process that could bias analyses that do not account for variable detection. We found that detection probability varied randomly among species and wetlands, and systematically with gears and wetland areas (Figure 3). Firstly, our model revealed an aspect of our sampling design that imparted significant heterogeneity in detection probability, i.e. the use of different gear types. The use of multiple gears is common when sampling fish communities because it expands detection opportunities across species and individuals with variable vulnerability to different detection methods (e.g. Lauretta et al. 2013). However, the use of statistically valid methods to combine data from multiple gears is rare in the literature (but see Haynes et al. 2013).
Figure 2. Hypothetical flow scenario’s i – v where, (i) zero days of inundation during a five-year period (ii) is 60 days of inundation once at the end of five years, (iii) is 60 days of inundations once every year, (iv) is 60 days of inundation once every six months, and (v) is 60 days of inundation every three months. The y-axis is the proportion of the total possible number of days of inundation for each time-scale (long-term, medium-term, and short-term). Nat/Non represents the resulting ratio of total native fish abundance to total non-native fish abundance of each flow scenario, where higher numbers indicate more natives relative to non-natives.

One common method of sampling with multiple gears is to standardize the relative sampling effort of both gears (e.g. Rayner, Jenkins and Kingsford 2009); however, at the end of the survey it remains unknown how detection varied for each method. Our hierarchical model combined the data from both gears in a statistically valid way by estimating the detection probability of each gear. This analysis indicated that the detection probability tended to be higher for fykes than seines, but that fyke detection probability declined as the area of a given wetland increased. Variation in detection of this nature can easily lead to spurious trends and incorrect conclusions. Indeed, in a separate analysis not reported here, we analysed these data with a Zero-inflated Poisson GLM that ignored variable and incomplete detections. This analysis resulted in unsubstantiated parameter estimates for most species that were clearly unreliable (Beesley unpub. data). Thus, sampling designs for evaluating the effects of future environmental flows in the Murray-Darling River basin (and elsewhere) will benefit from careful consideration of the detection biases indicated by this analysis.
CONCLUSIONS

Our hierarchical model of juvenile fish abundance revealed that antecedent flows are important in determining the structure of the wetland fish community. We observed that native and non-native fishes tended to differ in their response to antecedent flows, and that the response of some non-native species to recent flow was affected by prior medium and longer-term conditions. Furthermore, species-specific detection probabilities demonstrated significant spatial and temporal variation indicating that future research investigating environmental flow policies for enhancing native fish communities will benefit from accounting for variable detection. This knowledge will allow managers to develop effective environmental flow policies that promote the conservation of native fish communities.
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2.15 Hydrological and biophysical predictors of frog occupancy patterns across the Murray-Darling Basin

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INTRODUCTION

Frogs are important components of wetland ecosystems in the Murray–Darling Basin (MDB). However, the relative importance of hydrology, water quality and habitat features in driving species occupancy patterns are poorly described. In addition, habitat occupancy modelling for frogs is typically conducted at relatively small spatial scales, within a single catchment or wetland complex, with transferability poorly known.

Hydrological and biophysical habitat characteristics are important predictors of frog distributions (see conceptual model in section 6). Hydrology (e.g. flow characteristics, water permanence) plays a vital role in driving aquatic ecological processes and hence species distributions (Poff and Ward, 1989). Both aquatic and terrestrial ecosystem characteristics influence the quality of habitat for frogs, due to their complex life cycle (Wilbur, 1980). Hydrology is commonly identified as a predictor of frog occupancy and species richness (Gulve, 1994, Kolozsvary and Swihart, 1999, Jakob et al., 2003, Weyrauch and Grubb, 2004, Rubbo and Kiesecker, 2005, Ball, 1975, Baldwin et al., 2006). Hydrological variability may affecting timing of successful reproduction for different groups of frog species (Jakob et al., 2003). Altered flow regimes causing ecological decline may influence habitat suitability for frogs (Poff and Zimmerman, 2010). Distributions of amphibian species are correlated to vegetation characteristics (Vos and Stumpel, 1996, Healey et al., 1997, Hazell et al., 2001, Jansen and Healey, 2003, Bailey et al., 2004, Hazell et al., 2004, Rubbo and Kiesecker, 2005, Lane et al., 2007, Wassens et al., 2010a), as have water quality measures (Gulve, 1994, Weyrauch and Grubb, 2004, Lane et al., 2007, Wassens et al., 2007, McKibbin et al., 2008, Wassens et al., 2010a).

Occupancy modelling is a relatively powerful statistical technique that uses presence–absence data in relating these to habitat characteristics. The comprehensive incorporation of detection probabilities into occupancy predictions, as opposed to using simple presence–absence values, renders occupancy modelling uniquely suited when combining datasets with unequal survey effort.

The aims of this study were to describe key drivers of frog occupancy at local, regional and basin-wide levels, and to test the suitability of occupancy modelling for basin-wide frog distribution models.
METHODS

Species’ detection and habitat data were drawn from 173 sites from the mid-Lachlan (2006-07) (Wassens and Maher, 2011), mid-Murrumbidgee (2010-12) (Wassens and Amos, 2011, Wassens et al., 2012), Lowbidgee (2008-2010) (Spencer et al., 2011, Spencer and Wassens, 2009), Murray (2008-11) (Wassens et al., 2010b), and Wakool (2010-11) (Griese, 2011). To increase coverage of wetland complexes in the northern basin, the Gwydir and Gingham wetlands were also surveyed in 2011-2012. Sites surveyed in more than one season were counted as separate records, giving a total of 216 unique records, or site–season combinations.

The frog data used for analysis were in the form of Boolean presence–absence values for each site–season–species combination. The original data collected were discrete counts of individuals on each sampling occasion. Tadpole and fish surveys were carried out during the day, consisting of a sweep net survey in each 5m–wide transect, with at least three transect sweeps completed in total. Adult frog surveys were conducted as soon after dark as possible by two teams of two people. Each team surveyed frogs along a meandering transect through a site for 15 to 30 minutes, using a 25-watt spotlight. All individuals observed were identified to species and recorded. The number of calling individuals of each species was estimated at 5- to 10-minute intervals.

Adequate and reliable data across regions were only available for 27 variables in (Table 1) included for modelling. Flood return data were extracted from the Murray–Darling Basin Aquatic Assets and Environmental Attributes GeoDatabases v2.0 (Ward et al., 2012). Standard freshwater ecosystem measurements were carried out according to methods developed by Spencer et al. (1998).

Detection histories were created for each record for occupancy modelling (MacKenzie et al., 2005). Data were collected for seven species, but modelling was only completed for four species Limnodynastes fletcheri, Limnodynastes tasmaniensis, Litoria peronii, and Crinia parinsignifera with known ranges across all study regions.

There were two key modeling steps. (1) Single site covariate models, or simple models, (with survey region as a covariate) were developed and graphed. (2) Individual covariates of high predictive value were combined in complex models (Table 2). Akaike information criterion AIC, model weightings (see Mackenzie and Bailey (2004)) were used to rank models. Goodness of Fit tests were carried out using 100 parametric bootstraps and a model considered to be a poor fit to the data if the p-value (probability of obtaining a test statistic ≥ observed) ≤ 0.05. A p-value approaching 1 indicated over-fitting (MacKenzie et al., 2006).
Table 1. Descriptions of 27 variables included in univariate models for The four frog species. Variables included in the top three ranked multivariate models for each species are highlighted in bold. Variables classified as broad scale describe characteristics of the landscape and hydrological classifications of the wetland complex drawn from (Ward et al., 2012). Fine scale variables describe vegetation and water quality variables within 100m of the frog survey point.

<table>
<thead>
<tr>
<th>SCALE</th>
<th>VARIABLE</th>
<th>MODELLING ABBREVIATION</th>
<th>TYPE</th>
<th>DESCRIPTION</th>
</tr>
</thead>
<tbody>
<tr>
<td>Broad</td>
<td>Region</td>
<td>reg</td>
<td>Categorical</td>
<td>Region that site was located in (e.g. Lachlan or Gwydir)</td>
</tr>
<tr>
<td></td>
<td>System type</td>
<td>type</td>
<td>Categorical</td>
<td>(e.g. open wetland or minor stream)</td>
</tr>
<tr>
<td></td>
<td>Connection type</td>
<td>conn</td>
<td>Categorical</td>
<td>Manner in which the site was filled (e.g. ground water-fed, overbank, rain-fed)</td>
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<tr>
<td></td>
<td>Surrounding land use</td>
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<td>Categorical</td>
<td>Land use(s) occurring within 50 m of site</td>
</tr>
<tr>
<td></td>
<td>Hydrology/water permanence</td>
<td>hyd</td>
<td>Categorical</td>
<td>Permanent waterbodies flood return 5 in 5 year, seasonally flooded wetlands (1-2 in 5 years), and ephemeral wetlands (&gt;3 in 5 years)</td>
</tr>
<tr>
<td></td>
<td>Flood return 1 in 1 year</td>
<td>fr1</td>
<td>Continuous</td>
<td>Proportion of 1km-radius site zone expected to flood each year.</td>
</tr>
<tr>
<td></td>
<td>Flood return 1 in 2 years</td>
<td>fr2</td>
<td>Continuous</td>
<td>Proportion of 1km-radius site zone expected to flood every 2 years.</td>
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<tr>
<td></td>
<td>Flood return 1 in 10 years</td>
<td>fr10</td>
<td>Continuous</td>
<td>Proportion of 1km-radius site zone expected to flood every 10 years.</td>
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<td>friTallGrass</td>
<td>Continuous</td>
<td>Average percent cover of tall grasses (&gt;0.1 m) in the fringing zone.</td>
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<tr>
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<td>Fringing short grass</td>
<td>friShortGrass</td>
<td>Continuous</td>
<td>Average percent cover of short grasses in the fringing zone.</td>
</tr>
<tr>
<td></td>
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<td>friTallHerb</td>
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<td>Average percent cover of tall herbs in the fringing zone.</td>
</tr>
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<td>friShortHerb</td>
<td>Continuous</td>
<td>Average percent cover of short herbs in the fringing zone.</td>
</tr>
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<td></td>
<td>Fringing cover</td>
<td>friCover</td>
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<td>Average percent total ground cover provided by all fringing vegetation combined</td>
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<td>Fringing layers/complexity</td>
<td>friLayers</td>
<td>Continuous; discrete</td>
<td>Count of fringing vegetation types present at a site in a season.</td>
</tr>
<tr>
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<td>Aquatic tall emergent</td>
<td>aquTallEm</td>
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<td>Average percent cover of tall emergent vegetation (&gt;0.5 m) in the aquatic zone</td>
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<td>aquBL</td>
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<td>Average percent cover of broadleaf emergent vegetation</td>
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<td></td>
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<td>aquFloatAttach</td>
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<td>Average percent cover of short attached floating vegetation</td>
</tr>
<tr>
<td></td>
<td>Aquatic free floating</td>
<td>aquFloatFree</td>
<td>Continuous</td>
<td>Average percent cover of short free floating vegetation</td>
</tr>
<tr>
<td></td>
<td>Aquatic submerged</td>
<td>aquSub</td>
<td>Continuous</td>
<td>Average percent cover of submerged aquatic vegetation</td>
</tr>
<tr>
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<td>Aquatic cover</td>
<td>aquCover</td>
<td>Continuous</td>
<td>Average total percent of water covered by all aquatic vegetation combined</td>
</tr>
<tr>
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<td>Aquatic layers/complexity</td>
<td>aquLayers</td>
<td>Continuous; discrete</td>
<td>Count of aquatic vegetation types present at a site in a season.</td>
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<td>pH</td>
<td>wPH</td>
<td>Continuous</td>
<td>Average water pH at 1 m from water’s edge</td>
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<tr>
<td></td>
<td>Temperature</td>
<td>wTemp</td>
<td>Continuous</td>
<td>Average water temperature at 1 m from water’s edge</td>
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<tr>
<td></td>
<td>Conductivity</td>
<td>wCond</td>
<td>Continuous</td>
<td>Average water conductivity at 1 m from water’s edge</td>
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<td>Turbidity</td>
<td>wTurb</td>
<td>Continuous</td>
<td>Average water turbidity at 1 m from water’s edge</td>
</tr>
</tbody>
</table>
RESULTS

For all four species, *C. parinsignifera*, *L. tasmaniensis*, *L. peronii*, and *L. fletcheri*, occupancy modelling was likely to be reliable and produce unbiased results using the available data. There were clear differences in detection probability estimates between regions (Figure 1) which supports the inclusion of region as a survey covariate in all models. AIC values for complex models were lower than those for simple models, implying an advantage to using more than one variable to model occupancy for these species.

![Figure 1 Estimated detection probabilities (± 95% credibility intervals) (n=153) for six regions and four frog species. *indicated species were always detected, resulting in a detection probability of 1 for which credibility intervals cannot be calculated.](image)

Of the simple models developed for *Limnodynastes tasmaniensis*, the categorical variables of connection type and system type ranked highly, with some aquatic and fringing vegetation measures. The best complex model (lowest AIC value) included the variables aquatic vegetation layers and connection type (Table 2). Nearly all of the best candidate models contained the aquatic layers variable. For all complex models, p-values were ≤ 0.05, evidence of lack of fit.

Of the simple models developed for *Litoria peronii*, broad-scale categorical variables ranked highly, specifically including, connection type, system type, hydrology, surrounding land use, and 1 in 10 year flood return proportion. All the complex models listed had p-values > 0.05, indicating adequate fit. Many of the categorical variables were highly correlated, limiting the options for complex model development because the best individual predictors were categorical. The p-value for two of the best models was 1.0, indicating overfitting and so these models were excluded from further consideration. The best viable complex model included four variables: system type, surrounding land use, water turbidity, and aquatic layers (Table 2). All of the top ranking complex models included surrounding land use and either system type or connection type.
Fine-scale variables associated with aquatic vegetation and water quality ranked highly for *Limnodynastes fletcheri* in simple models. A positive relationship between predicted occupancy and short emergent, tall emergent and floating attached vegetation was evident, although variation was only present at a limited portion of the total range and credibility intervals were large. Some broad variables ranked (Table 2) including surrounding land use, connection type, and flood return period, but the rankings indicated they were not as important as the fine-scale variables. The fine-scale variables of aquatic short emergent vegetation, aquatic vegetation layers count, and water pH all featured consistently in the best complex models for *L. fletcheri*. The categorical variables of connection type and surrounding land use also improved models. There was evidence of lack of fit for several of the best complex models ($p$-value < 0.05).

For *Crinia parinsignifera*, the broad system variables of connection type and system type were the most informative of the simple models. There was evidence of lack of fit for all complex models ($p$-values were ≤ 0.05). Nonetheless, the variables present in the high-ranked complex models included connection type, aquatic layers, flood return, and aquatic free-floating vegetation cover (Table 2).

**Table 2** Top 3 Complex (> 1 site covariate) models ranked from best to worst according to AIC. Model fit assessed using Goodness of fit test (Mackenzie and Bailey 2004), modified Pearson’s Chi-square statistic; $p$ < 0.05 indicates lack of fit. Refer to Table 1 for description of variables.
DISCUSSION

Robust models were developed for *Litoria peronii* and *Limnodynastes fletcheri*, but we were less successful in developing models for two other common and widespread basin species, *Limnodynastes tasmaniensis* and *Crinia parinsignifera*. Model development for these latter species was difficult due to their broad habitat requirements and apparent insensitivity to the hydrological and biophysical variables included, which meant that key drivers of their distributions could not be described with confidence.

Broad scale hydrological variables influenced occupancy for the species modelled. At fine scales, vegetation variables were also important, consistent with previous studies (Wassens et al. 2010a). The predicted relationships with habitat variables were weaker at the basin-wide scale than at fine scales, suggesting that region-specific occupancy relationships cannot be applied to other regions reliably.

For all four modelled species, the key finding was that regional differences in detection probability far outweighed the influence of site-specific habitat variables. These regional differences suggest that Basin level assessment of frog communities and their expected response to flow will be more robust if they incorporate regional variability. For frogs at least, the Murray–Darling Basin is not homogeneous, so broad-scale management of the basin should also incorporate region-specific frog habitat management, if species are to be effectively conserved.

Clear relationships were revealed between predicted occupancy and measured variables, while broad scale hydrological variables were generally not as important as fine scale habitat characteristics, flow plays an important role in shaping habitat at finer scales. The value of the broad scale flood return classifications could have been improved if complimented by fine-scale hydrological data for each region. For example, models to predict species’ distribution and persistence with respect to hydrological composition of floodplains provide opportunities for modelling across the Lowbidgee floodplain.
REFERENCES


2.16 The role of antecedent conditions in determining responses to environmental flows

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INTRODUCTION

There are considerable challenges in understanding and managing flows to ecosystems, given the background of impacts to natural flow regimes. Natural flow regimes in rivers are highly variable, particularly in Australia, where sequences of floods are critical in determining ecosystem responses (Leigh et al. 2010). For example, flows of rivers in the Lake Eyre Basin variably reach different parts of the river system, often depending on whether a series of floods has provided the requisite amount of water to reach downstream rivers channels and floodplains (Kingsford et al. 1999; Puckridge et al. 2000). Correspondingly, antecedent dry periods are critically important in determining the effects of a particular flow event on in-stream and floodplain ecosystems. In regulated rivers, there are managed environmental flows which represent part of the flow regime and are often targeted at particular ecological outcomes. Ecological outcomes can be diverse (e.g. bird numbers, fish condition, ecosystem respiration) and we will describe responses generically in this section. We will also use the term ‘ecological condition’ as an indicator of the underlying state of an ecosystem, with systems in poor condition less able to show positive ecological responses to watering events.

Early research on environmental flow research tended to ignore the role of temporal and spatial antecedent conditions as well as interactions between flows and other stressors in influencing ecological condition (Postel and Richter 2003; Poff et al. 1997). Ignoring these factors is unwise for management and research on the ecological responses to flows, given their importance in dictating ecological condition. Understanding how flow responses vary with antecedent conditions can help water managers understand their relative importance of their environmental flow management in delivering on ecological outcomes, including when to capitalise on previous conditions. There are also the often intractable challenges of dealing with the confounding factors affecting ecological responses. For example, native fish populations in the Murray-Darling Basin have declined significantly over time with regulation of flows identified as a major stressor (Gehrke et al. 1995) but many other
stressors confound this impact in different ways including exotic species, barriers and harvesting. Ultimately, an environmental flow manager may have a target to improve native fish population but fail because of these other factors. Understanding long-term trends in condition and the relationship to non-flow related stressors can provide water managers with critical information on where and when to prioritise environmental flow delivery, and what level of response magnitude may be expected.

Provision of environmental flows is best considered in the context of restoration ecology, which seeks to reverse habitat degradation through active intervention (Jordan 1994). Restoration seeks to take biodiversity values and/or ecosystem functions (such as productivity) back towards the levels found in the non-degraded ecosystem (Hobbs and Norton 1996). Increasingly restoration ecology as a discipline is recognising the difficulties of defining restoration end-points and in determining efficacy against natural background variability in condition, and the impacts of unrelated changes such as natural or anthropogenic climate change (Pickett and Parker 1994; Hey and Philippi 1995). Similarly, it is increasingly clear that restoration in a river management context requires a landscape-scale, rather than site-scale, approach (George et al. 1995). Hobbs and Norton (1996) summarised the broad conceptual basis of restoration ecology and recognised the importance of determining all degrading processes and assessing which of these management interventions are addressing. This is particularly important in systems which are subject to multiple degrading processes.

The provision of environmental flows occurs against a background of short and medium term trends in flow regime and ecological condition which naturally differ between different ecosystems, and which usually interact with flow regimes. The attributes of a particular flow event (e.g. timing, duration, frequency, magnitude) will also influence the timing and scale of ecological responses. The intention of this section is to discuss the ways in which antecedent conditions may influence the potential of particular ecological systems to respond to environmental flows at two time scales: short (within year) and medium (years). We aim to provide information on the likely importance of antecedent conditions on likely response to environmental flows. We also discuss the role of trends in condition which result from non-flow related stresses (legacies) which may interact with flow impacts.

THE INITIAL CONDITION AND NATURAL VARIABILITY

Ecological responses to environmental flows will depend on an interaction between the type of ecosystem to which they are being applied and the initial condition of that ecosystem. The natural resilience of ecosystems, which is a function of historical water regimes (reflecting climate), over evolutionary time will determine how sensitive systems are to drying over various timescales, and how responsive they will be to environmental flows after dry periods. Many Australian ecosystems are highly adapted to prolonged dry
spells with intermittent water. Systems which have evolved with long term drying may still
be in good condition and able to respond to environmental watering in situations even
when antecedent conditions are very dry (Figure 1). Systems that have evolved with regular
wetting are likely to lose ecological condition as the length of the dry period increases, and
be less able to respond to watering (Figure 1). At an extreme, naturally perennial wetlands,
waterholes or streams which have dried completely will respond differently to the provision
of flows than will systems that have retained some water. For example, a wetland system
adapted to long dry periods with occasional wet periods may respond to the provision of
environmental flows with very large ecological responses that rapidly restore condition.
Systems which are adapted to more regular watering may show large ecological responses
to water if they are already in good condition due to previous watering events, but much
smaller and slower responses if environmental water is provided after unusually long dry
periods. In studying responses of riverine and wetland ecosystems to environmental
watering it is important to take into account natural spatial variability in environmental
conditions as a factor in predicting likely ecological responses to water.

Figure 1. Responses to environmental flows depending on the natural flow characteristics of the ecosystem
and sensitivity to the length of time since last flows.
There may be a range of different conditions for any particular site which will be dependent on the site’s natural flow regime and effects of different stressors, including river regulation. For river regulation, sites may be broadly categorised into those where the flow regime is considerably reduced leading to increased drying and a few other areas where water is kept artificially and often constantly high (Kingsford 2000; Kingsford et al. 2004). Sites where there is decreased flooding compared to natural (Kingsford and Thomas 1995, 2004) are likely to be in poor ecological condition and when provided with environmental flows may show a slow response, compared to sites where this impact is not so dramatic (Figure 2). Importantly, this will likely also affect the effects of the flow in terms of duration and magnitude of flooding. Parched soils will take considerably longer and require more flow to become saturated and inundated. The actual magnitude of the response will also be influenced by initial ecological condition. Sites in good condition may have limited capacity to improve further, but can maintain their condition (Figure 2a). Sites in poor condition may respond slowly, but may have greater capacity to show improvement in condition (Figure 2b). Sites in very poor condition, compared to natural, may be very slow and have limited capacity to respond at annual time scales (Figure 2c). Responses will also vary in terms of life history. A key aim of restoration should be to establish self-sustaining populations which can grow, survive, reproduce and recruit. It will not be sufficient to simply maintain except if managing for particular dry periods. The actual nature of these relationships will depend on the traits of the constituent biota, the landscape context (e.g. relationships to nearby refugia to provide colonists) and the time scales involved (Bond et al. 2012). Environmental flows should provide the greatest responses in ecological condition where sites are in poor or declining condition, relative to natural but extreme dry conditions.
THE ROLE OF SHORT TERM DISTURBANCE HISTORY

Effects of recent flow conditions (within the year), in determining the condition of ecological communities, and thus their potential to respond to environmental flows are poorly known. Flows supplemented by a high degree of local variability in terms of flow and cease-to-flow events explained regional ecological condition of macroinvertebrate communities in Victorian streams (Bond et al. 2012). The recent history of cease-to-flow events strongly causes distribution of macroinvertebrate taxa to decline (Boulton and Lake 1992; Chessman 2009; Bond et al. 2012). In delivering environmental flows, it is critical to know the natural flooding regimes of sites to understand any response to environmental flows.
High flow disturbance similarly may negatively influence community response to environmental flows at one point but be positively impacted downstream. Sites in poor ecological condition may respond slowly to environmental flows (similar to Figure 2b). Alternately, sites which have been subjected to high flows and may have responded to those flows may have limited capacity to respond further to any additional flows (similar to Figure 2a). Thus it is important to have an understanding of recent flow history in predicting likely responses to environmental flows.

THE ROLE OF MEDIUM TERM DISTURBANCE HISTORY

Short term event-based antecedent conditions such as drying may be nested within medium term (years) flow trends that impact on the initial condition of communities and their potential to respond to environmental flows. Over the period 2000-2010, south eastern Australia was subjected to intensifying drying due to the Millenium drought. This contributed to long-term declines in condition of freshwater ecosystems across the region (Chessman et al. 2009; Kingsford et al. 2011; Thomson et al. 2012) until the drought broke with extremely wet years in 2010 and 2011. This backdrop of increasing flow stress (Bond et al. 2012) may have affected the potential for communities at a location to respond to the provision of environmental flows. Hypothetically, a site one year into the drought may have remained in relatively good condition with potential to respond to the provision of flows (Figure 2a), but as the drought progressed, condition and potential to respond to flows may have reduced (moving from Figure 2b to 2c). The time lags involved in these declines in ability to respond are likely to be taxa dependent, and are currently little understood.

In providing environmental flows against a backdrop of downwards trending condition due to medium term factors such as drought or climate-change induced drying, managers need to be aware of the rate of decline in condition of target taxa, and the ability of target taxa to respond to provision of flows. Very resilient taxa (such as short lived invertebrates) may require the provision of single flows at relatively long intervals to restore condition to levels which are consistent with those that may be predicted in the absence of water abstraction. However, long-lived, slow responding taxa such as River Red Gums may need provision of water more regularly.

THE ROLE OF LONG TERM DISTURBANCES

The provision of environmental flows against a background trend of drying is particularly challenging, but represents an important challenge for environmental flow management. Long term changes in ecological condition as a result of drying are will occur at scales of decades and more. Aridification of south-eastern Australia has been occurred over the last several thousand years, more recently compounded by additional drying generated by climate change. The ecological response to environmental flows will depend on the
interaction between the rate of decline in ecological condition due to medium term drying trends, the rate of decline due to anthropogenic causes such as abstraction, and the ability of taxa to respond to any provision of environmental water. Systems where ecological condition would be declining due to medium term trends in climate, may respond to the provision of water and thus on average, exhibit similar trends to those that might have been expected in the absence of water abstractions (Figure 3a). However, systems where trends in condition are very rapid and responses of biota to environmental flows are relatively small or slow may exhibit steep declines in condition even when environmental flows are provided (Figure 3b).

![Figure 3. Responses to environmental flows depending on background trends in condition caused by medium term (years) processes such as drought.](image)

Similar patterns may be expected for other, long term trends in stressors, even when they do not directly influence flow. Land use impacts on stream ecosystems can be pervasive and play out over many decades (Thomson et al. 2012). These existing stressors can result in biota which have less capacity to respond to changes in hydrologic regimes (Palmer et al. 2008; Mac Nally et al. 2011). Land use change may also be having long term negative
impacts on ecological condition similar to those seen due to drying in Figure 3a, and with similar effects on responses to provision of flows. For example in central Victoria, sand slugs as a result of land clearance reduce the potential for stream biota to respond to flows, even if a fully natural flow regime was to be restored (Atkinson et al. 2008). This is made more complex by the fact the responses of many taxa are lagged by varying degrees from months to decades, and that these responses are also influenced by superimposed lagged responses to a variety of other stressors. Recent studies of urban streams have shown that biota responses to urbanisation of agricultural land are strongly influenced by lagged responses to initial land clearance from forested to agricultural landscapes, even though this took place decades earlier (Roy et al. 2003). In an environmental flows context, responses to flow provision will occur against a shifting baseline of condition responses to a variety of stressors that have occurred over decades.

CONCLUSION

Assessing the effects of environmental flows is difficult because responses are likely to be contingent on antecedent flow conditions, and play out on a complex landscape of background trends, legacies from past impacts and with lagged responses by some biota. However, sophisticated analyses are now capable to disentangling these effects (e.g. Thomson et al. 2012; Bond et al. 2012), but it is important to note that flow regimes do not operate in isolation from long-term and large scale effects of other impacts. The responses to environmental flows described in the remainder of this report occur against a range of hydrologic backgrounds from relatively wet (for studies which took place after the exceptionally wet years in 2010/2011), to extremely dry (for studies which occurred during the Millenium Drought. Studies where environmental flows were provided against a hydrologic background of natural high flows may have reduced the total magnitude of the responses seen, but may also have ‘primed’ natural systems to be able to respond to environmental flow provision. Environmental flow responses need to be considered in terms of the ability of taxa to respond, which is a product of the traits of the target taxa and the antecedent flow conditions that precede the environmental flow. In addition, it is important to recognise that longer term trends in ecological condition may underlie and even obscure effects of environmental flows in some contexts.

REFERENCES


3 Summary of research implications

Assessing the responses of ecosystems to in-channel flows can be difficult because there is limited understanding of flow-ecology relationships for many aquatic species and for important ecosystem processes a relatively small number of examples studies of in-channel pulsed flows (Watts et al. 2009). In addition, in-channel flow pulses can be short-lived and responses to these flows are likely to be influenced by antecedent flow conditions and past impacts, and there may be lagged responses by some biota (see Section 2). However controlled field-based studies of environmental flows can account for these complexities and contribute to improving predictive models.

Field-based experiments assessing ecosystem responses to in-channel flows as well as analysis and synthesis of existing datasets were undertaken as part of this subproject. We sought to improve our understanding of ecosystem responses to individual flow events and improve the capacity to predict the outcomes of environmental flows within in-channel ecosystems. However, important knowledge gaps remain, and our research has raised further questions and identified some areas for future research. Addressing some of these knowledge gaps will help us improve our understanding of responses to in-channel environmental flows and will assist managers better use environmental water to help restore riverine ecosystems.

CHANGES IN BENTHIC WETTED AREA AND AVAILABILITY OF SLACKWATER IN RESPONSE TO IN-CHANNEL FLOWS

We investigated lateral connectivity and availability of slackwater habitat in the Edward-Wakool system during in-channel flows using hydrodynamic modelling (Section 5.2). Many different organisms depend on these habitats. We showed that the relationship between discharge and wetted surface area and the area of slackwater in rivers in this system was not linear and most likely strongly influenced by geomorphology. It may be more appropriate to use area of inundation, instead of daily discharge, to better understand the relationship between in-channel flows and ecosystem responses. Future research could focus on examining the nature of this relationship in other river systems to improve models for predicting the responses of in-channel flows on slackwater dependent biota and ecosystem functions.

WHOLE STREAM METABOLISM

Our investigation of whole instream metabolism in the Edward-Wakool system (Section 5.3) demonstrated that small managed flow pulses did not stimulate primary production. This clearly raised the possibility that larger flows may be needed to test the hypothesis that more inundation of riverbanks and backwaters may provide greater stimulation of primary
production and respiration. This will increase the biomass of primary producers and provide important food resources for high trophic levels, including macroinvertebrates and fish.

**ORGANIC MATTER BREAKDOWN**

There were generally low organic matter (leaf-litter) breakdown rates in relation to changes in flow regime among four rivers in the Edward-Wakool system (Section 5.4). This implies that such rates may not be a sensitive indicator for assessing environmental watering, within in-channel ecosystems where shredder consumers are in low densities. This may not be a general finding across other river systems. Also, other mechanisms may possibly alter breakdown rates.

**INVERTEBRATE RESPONSE TO IN-CHANNEL FLOW PULSES**

We also investigated responses of macroinvertebrate biomass in the Edward-Wakool system (Section 5.5) following delivery of small environmental flows that occurred after large magnitude unregulated flow pulses. Zooplankton abundance, biomass and richness were highest directly after large unregulated flow pulses, whereas small environmental flow events alone did not initiate zooplankton response, possibly due to minimal inundation of riverbanks during these small events (see section 5.2). Increased macroinvertebrate biomass, following unregulated events, provided indirect evidence of benefits for higher trophic levels, such as fish and frogs. The interlinkages among components of the foodweb in response to environmental flows require further investigation.

**FISH SPAWNING**

We investigated fish spawning in two separate studies. In the Edward-Wakool river system, opportunistic spawning and recruitment of carp gudgeon occurred during and after in-channel environmental flow events (Section 5.6). However, the timing of spawning for Murray cod, Australian smelt, common carp and native floodplain-spawning species was independent of these flow events. Widespread abundance of opportunistic spawning species, such as carp gudgeon, may reflect their ability to successfully spawn and recruit under variable in-channel flow conditions. In the Murray River at Barmah-Millewa Forest, temperature was the dominant and overriding environmental parameter influencing spawning occurrence for all four species (Murray cod, trout cod, silver perch and golden perch), although attributes of flow were also important and in particular affected the spawning intensity of the latter three species (Section 5.7). Our studies demonstrated the significance of timing of water application in the design and management of environmental flows and could be used to create a stronger conceptual or analytical framework for flow management for improved conditions for native fish spawning.
PREDICTING THE CONDITION OF YOUNG-OF-YEAR FISH

We also retrospectively investigated juvenile body condition of two small-bodied native species (Australian smelt and unspecked hardyhead) in the mid-Murray River, using six years of data with differing antecedent flow conditions (Section 5.8). Juveniles have limited capacity to store energy and do not use it for reproduction, and so their condition probably reflects current system energetics. This study provided insight into the longevity of flow-related energy pulses, rather than the capacity of organisms to store energy from previous energy pulses. There was preliminary evidence that antecedent flow conditions altered system energetics and fish condition, The importance of flows a year before fish were spawned, suggests that antecedent conditions may affect the energetics of the system in excess of a year later. The relationship between antecedent flow and juvenile fish body condition, however, differed markedly between the two species studied. For Australian smelt, body condition was positively related to short-term flow and negatively related to long-term flow, while for unspecked hardyhead, body condition was unrelated to short-term flow, and negatively (but mildly) related to long-term flow. The different responses among species with similar life histories and habitat preferences, suggests it is unwise to make generalisations about how the body condition of different species will respond to flow. As we relied on a relatively small dataset with limited capacity to detect relationships and how different components of flow interacted, we caution against extrapolation of these findings and recommend additional investigation in this area to further determine how such sequencing of flow may benefit native fishes.

HYPOXIC BLACKWATER FISH KILLS

We also focused on the role of hypoxia and tolerances of juvenile stages of four lowland river fishes native to the Murray-Darling Basin (Section 5.9). Despite the natural occurrence of hypoxia and blackwater in lowland rivers of the Murray-Darling Basin, large bodied predatory fish in this ecosystem are vulnerable to acute mortality induced by low oxygen concentration and associated water chemistry changes. Logistic models predicted that hypoxic blackwater mortalities of golden perch, silver perch, Murray cod and freshwater catfish may occur at oxygen concentrations as high as 4.54 mg L⁻¹ and sub-lethal stress, as indicated by onset of aquatic surface respiration, may occur above 5.00 mg L⁻¹ at 25–26 °C. The thresholds reported in our study provided a starting point for managers to develop hypoxia mitigation strategies but must be carefully interpreted, given potential sub-lethal effects, and ambient and antecedent environmental conditions. Consequently, a better understanding how these variables interact will be essential in further developing hypoxia management plans to prevent fish kills and the loss of aquatic biodiversity.
FLOW AND INUNDATION MODELS

A key aspect of understanding the effects of flow on ecosystems in wetlands and floodplains is understanding the relationship between flow regimes and flooding regimes (i.e. height, frequency, duration, timing). There are few data available for flooding, but classification of inundation from satellite imagery can be linked to flows through modelling. This can be enhanced by improving the availability of flow data for flow gauges near wetlands. Development of integrated flow and flood models allow sub-regional predictions of area inundated to be made on a daily basis (Sections 5.10 and 5.11). Models from this project exist for the Macquarie Marshes, Murrumbidgee River and Lower Murrumbidgee which are helping link to ecosystem responses. Such linking will greatly increase our understanding of flood regimes and the link to river flows. By linking flood regimes to floodplain-dependent biota and ecosystem processes should help guide environmental flow management.

WETLAND AND FLOODPLAIN VEGETATION

Variations in seasonal flow timing, duration, depth and habitat type were all found to affect riparian understory vegetation production and community composition (Section 5.12). The responses were, however, complex and no single variable (season, flood duration, depth or habitat type) can be used to predict production or community structure after inundation. One of the outcomes of the research was that productivity and diversity were not well correlated with Black Box wetlands supporting the greatest number of species while wetland habitats supported the greatest increase in plant biomass. This suggests that ecosystem water requirements to sustain productivity may differ from the water requirements to sustain biodiversity. The results clearly demonstrate that flow has a significant influence on species richness both within wetlands and at a landscape scale. This suggests that achieving environmental flow objectives may require strategies to create a habitat mosaic to promote both diversity and productivity.

Changes in flooding frequency can shift vegetation communities, ultimately transitioning them into different communities, consequently affecting their dependent fauna communities (Section 5.13). Managers of environmental flows need to understand the individual nature of vegetation communities and their reliance on different flooding regimes so that they can ensure resilience across the spectrum of floodplain vegetation communities (e.g. redgum-wetland, black box habitats). This approach may not maximise overall vegetation productivity, but will increase diversity and ensure productive patches, reflecting the gradient of flooding regimes within the managed area. Flow timing is also complex and amenable to management and variation in timing of inundation may increase long-term species diversity. From a simple productivity perspective, flows in warm months increase productivity. Flows delivered in cool months, however, may not result in low rates of
production, if the water temperature or soil moisture remains high with the onset of warmer conditions.

Knowledge of dependencies between vegetation communities and flooding regimes can also inform management aimed at restoration to a former state, using flooding or environmental flows. For aquatic and flood-dependent vegetation, seed bank longevity is a critical limiting factor, with extended dry periods reducing opportunity for recovery. Both long-term flood regimes and short-term flood events significantly affect vegetation and woodland bird communities in floodplain woodlands – therefore both must be managed for short-term and long-term biodiversity outcomes.

Inundation of the whole site may not always be necessary to maintain site value and biodiversity during droughts, provided flooding occurs with sufficient frequency over long periods of time. Floodplain woodlands are important productivity refuges from both drought and land clearing, and the use of environmental water and natural flooding must be considered to maintain or restore floodplain woodland condition.

**ANTECEDENT FLOWS AND THE FISH COMMUNITY**

Relatively few studies have attempted to quantify importance of antecedent conditions which can alter flow-ecology relationships. Our study of six floodplain wetlands in the mid-Murray, revealed that antecedent flows are important in determining the structure of the wetland fish community (Section 5.14). We investigated the relative importance of short-term (3 month prior), medium-term (3 month to 1 year prior) and long-term (1 to 5 years prior) antecedent flow conditions on juvenile fish abundance and developed a Bayesian hierarchical multiple-species model. We observed that native and non-native fishes tended to differ in their response to antecedent flows, and that the response of some non-native species to recent flow was affected by prior medium and longer-term conditions. Native fish generally responded positively to frequent watering of wetlands, while non-native species generally responded positively to long dry periods followed by short-term watering events. For some non-native species (common carp), long dry periods not only generated a positive response in abundance, but enhanced their positive response to short-term watering events. This divergence between native and non-native fishes’ response to antecedent flows provides opportunities for managers to allocate flows to favour native fish assemblages. Our evaluation of hypothetical flow scenarios suggests that frequent inundation of wetlands will promote native fish over non-native fish. Future research and management of environmental flows for fish assemblages should consider the role of antecedent conditions and be mindful of different species’ responses to varying flow characteristics.
FROGS IN THE MURRAY-DARLING BASIN

For four species of frogs (*Limnodynastes fletcheri, Limnodynastes tasmaniensis, Litoria peronii* and *Crinia parinsignifera*), there were no common drivers of occupancy across the sites (Section 5.15). Further, significant flow and habitat drivers varied for species across the basin. In particular, the two hydrological variables of water permanence and flood return were not identified as particularly informative at a basin-wide level for any species. Of the variables considered, region was overwhelmingly the best predictor in all models. These findings indicate that these widespread species are unlikely to be responding consistently to the same hydrological and biophysical variable across the basin, with the implication that management for frog species will likely need to be localised.