Conceptual modelling of the ecological responses from a flood event in the Lower River Murray
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Executive Summary

Despite the importance of the River Murray as an iconic aquatic ecosystem in Australia, our lack of knowledge regarding response to floods following drought is a significant limitation in our ability to appropriately manage that ecosystem. The Murray Flood Ecology (MFE) project provided an opportunity to redress this gap, focusing on the responses of primary productivity, vegetation, and fish to returning flows in the Lower River Murray. This presented a further opportunity to collate these responses to glean a more holistic view of that response at an ecosystem-scale. This report aims to provide a framework for such a synthesis, by presenting a generic conceptual model of biotic responses to flooding events, and populating that with responses measured during the MFE. We intend that this conceptual model be used as the basis of future attempts to develop qualitative and quantitative models of responses to flow in the Lower River Murray.

A basic conceptual model was developed prior to the inception of MFE. This initial model used our understanding of the effect of flow on the processes occurring in the river channel, floodplain and in connected wetlands based on ecological first principles. The structure of this model was discussed with MFE project members and then refined. Following the completion of data collection as a part of MFE, we then incorporated the key findings into the draft model, and refined the structure of the model further. MFE project members and other stakeholders were again given the opportunity to comment on the ability of the model to represent those findings accurately. Nonetheless, it is important to note that the models presented herein represent the authors’ interpretation of the findings of MFE sub-projects. The model represents both in-channel and floodplain and wetland processes, as previous attempts to separate these systems illustrated the similarity of the underlying processes, albeit with distinct differences in the relative importance and extent of each.

The initial generic model performed well in capturing the responses as measured by the various sub-projects, with the range of drivers able to be tailored to represent those identified as drivers. Task-specific models were combined to develop species-specific models, functional group-specific models and a revised ecosystem-wide response model. Despite the focus on measuring response to flooding flows, in most instances, there remains insufficient data to describe the shape and magnitude of those relationships, highlighting the need for ongoing research in this system. Synergies across the taxa were also apparent, with similarities in response identified for nutrients, primary productivity and habitat complexity, for example.

In developing these models, we deliberately focused on ecological processes as better reflecting the nature of response to flows, allowing ecosystem-scale interactions to be represented and to avoid underestimating the complexity of the Lower River Murray ecosystem. The models are also developed to represent a range of spatial and temporal scales, which will depend on the taxonomic group and event of interest. The biotic functions included (e.g. survivorship, reproduction), as well as habitat and food resource boxes are intended to be used to link various biota via their interspecific interactions, thus enabling the model to be applied at an ecosystem scale. A sophisticated application of the model may include nesting a series of taxon-specific models, or incorporating multiple feedback loops within that interaction section of the model. This would allow emergent ecosystem properties to become apparent where they may not be if using a single taxonomic group.

There are a number of limitations associated with using these models. We have not attempted to represent the relationship between flow and water level, due to the ‘chain of weir-pools’ nature of the Lower River Murray. Thus, clear flow-ecology relationships may be difficult to identify using this tool. The model has not been extended to include the Coorong and Lower Lakes, nor involve groundwater interactions, and has not been linked to other management programs (e.g. environmental watering programs). As yet, limited testing of the model has occurred, and its value to managers and other stakeholders is also untried to date, although feedback from managers has been promising. Suggested uses by stakeholders include comparing responses of flows across various functional groups and ecological components to identify conflicts and explicitly consider trade-offs. Also, it should be possible to apply the model from the bottom up, to identify the conditions required to achieve a given ecological
outcome and could be used to develop hypotheses to enable further scientific research to be undertaken to fill knowledge gaps.
Introduction

The River Murray channel is recognised by the MDBA as a significant ecological asset to be targeted for environmental flows, and many of the associated wetlands are also of high ecological value and can be affected by water management in the channel. Nevertheless, our current knowledge of environmental water requirements is limited in the Lower River Murray, and little is known regarding the capacity of the ecosystem to recover from recent drought conditions. This seriously limits our ability to manage the system in an optimal fashion through the provision of environmental water.

In particular, very little is known about the relative importance of different ecological components and processes in the Lower River Murray channel, floodplains and floodplain wetlands and their contribution to the overall function and resilience of river ecosystems, particularly under moderate to high flow conditions, given that many of the recent advances in our ecological understanding were made during severe drought in the Lower River Murray. This means, for example, that our knowledge of the links between the floodplain, floodplain wetlands and the river channel is limited.

Our current knowledge of environmental water requirements is limited in the Lower River Murray, and little is known regarding the ability of the ecosystem to recover from recent drought conditions. Murray Flood Ecology was a research project designed to take advantage of the recent high river flows (2010/2011) and the refilling of the channel and wetlands along the River. The Murray Flood Ecology project took advantage of recent flow events by investigating the ecological response of key components and processes and testing some of the relevant management concepts and scientific hypotheses. While this project was specifically focused on the Lower River Murray, it is likely that many of the findings would be relevant to other floodplain rivers with highly variable flow regimes, particularly where there is now significant manipulation of flow regimes. The research undertaken as a part of this project, along with ecological knowledge gained in the last ten years in particular, have then been combined to develop a framework for proposed models for assessing the ecological response of the entire system to various flow events and future management tools in the region. The Murray Flood Ecology project included 11 tasks, with this report completing Task 2: Conceptual Modelling.

Figure 1 illustrates our conceptual understanding at the beginning of the overall Murray Flood Ecology study. This diagram, which was developed at the inception of the project, illustrates how the various components of the project are potentially interlinked and how river ecosystems may be affected by changes in flow regime, whether they be increases or decreases. It is likely that main channel ecosystems may respond differently from the floodplain or connected wetlands, and aspects of each were thus included in the investigations within the Murray Flood Ecology project. The diagram represents a significant simplification of river ecosystems (i.e. floodplain ecosystems in particular), but our intention in developing the diagram was to include those processes likely to be affected by flow regimes of the magnitude being studied in this project.

The recent (2010-2011) large-volume over-bank flow provides a unique opportunity to conduct structured, targeted investigations on flow related ecology. This will improve our conceptual understanding of the responses of constituent biota and ecological processes (Figure 1), providing critical knowledge to underpin the prediction of responses to the delivery of environmental flows. The integrated data collected across a range of ecological components and processes through this study and knowledge generated could then be used to refine and develop more sophisticated models of ecological recovery (resilience) from drought events, and ecological response to moderately-high flow events.

In determining what the impact of flow is likely to be on ecological assemblages, there is much theory from which to draw. For example, the flood pulse concept (Junk et al., 1989) emphasises the significance of high flow events across the aquatic-terrestrial transition zone, which is likely to be particularly relevant to large floodplain rivers like the Murray. This concept proposes that the pulsing of
river discharge, the so-called flood pulse, is the major driving force for the existence, productivity and interactions of the major biota within riverine ecosystems. The annual timing, duration, amplitude and rates of rise and fall in water levels and the regularity of flood pulses are important factors for biota when considering the flood pulse (Junk et al., 1989). Life cycles of biota that utilise the floodplain habitat are often related to the timing and duration of the flood pulses (Junk et al., 1989). Aquatic organisms colonise the floodplains during high water levels to utilise the increased habitat and food resources, whereas terrestrial biota occupy the various floodplain habitats during low water levels (Junk et al., 1989).

It should be noted that the flood pulse concept was developed with large rivers with predictable and prolonged flood pulses in mind. In low-order streams higher in the catchment the level of adaptation of biota to flooding can be low. In these cases, unpredictable flood pulses are important mechanisms, acting to reset the physical and environmental conditions. Also, in temperate systems, the effects of the pulse may be influenced by the light and/or temperature regime (Junk et al., 1989) and the degree of river regulation can affect the links between the floodplain and in-channel ecosystems. Later models treat riverine ecosystems as hydrogeomorphic patches that are likely to have similar ecosystem functioning, with patches based on geomorphology and hydrology (Thorpe et al., 2006).

New theories specifically around the identification of environmental water requirements have also been developed (Arthington, 2012). While environmental flows and the notion of providing water for ecological purposes has been under consideration for more than 30 years (Petts, 2009), the application of these theories in practice has been largely piecemeal, and environmental flows in the Murray-Darling Basin, for example, were suspended during the recent drought, when they were arguably most important. Theories such as the Ecological Limits of Hydrologic Alteration (ELOHA; Poff et al., 2010)
provide a framework for the best-practice design and implementation of flows for ecological benefit. ELOHA uses a process of determining the degree to which a range of aspects of a flow regime can be changed by human activities before there is an unacceptable, negative impact on the waterway’s associated ecosystems (Poff et al., 2010). In theory, understanding these limits should guide decisions regarding water extraction and environmental flows, but this particular concept is in its infancy, with example applications only beginning to appear, but no widespread application of the model to date.

Many tools, either based on ELOHA or one of a range of other theories, currently exist for assisting river managers (in South Australia and elsewhere; Arthington, 2012) in their task of managing river ecosystems, and environmental flows in particular (e.g. the Murray Flow Assessment Tool [Young et al., 2003], platforms such as EcoModeller [Marsh 2007]). To date, however, no tools exist for South Australia that enable managers to predict the relative benefits of competing strategies and optimize the delivery of environmental water to the various channel, wetland and floodplain environments. Such a tool would need to be developed based on our understanding of how the river system as a whole responds to flow, across the various ecological components (e.g. vegetation, fish), processes (e.g. carbon and nutrient cycling) and habitat types (e.g. channel, wetland, floodplain). The form that such a tool would take is outside the scope of this short-term project, but the data that are collected during the Murray Flood Ecology project should be used to inform that process in the future.

A first step in the process of developing such a tool was to ensure the integration of data collection and hypothesis testing among tasks in the Murray Flood Ecology project, as far as was possible. A second step was to collate those hypotheses, and others that are not currently being tested, into a conceptual model of how the Lower River Murray as a whole responds to flow events (both high and low). The purpose of this report is to describe the conceptual model diagram that was compiled to capture those hypotheses.
Model objectives

When conceptual models of this sort are developed, often no explicit model objectives are specified. We have attempted to avoid this lack of clarity by explicitly stating objectives for the use and role of the conceptual model developed below.

The objective for this model is to provide a framework within which we can capture our current understanding of the impact of high flows and floods on the River Murray ecology, as at the start of the Murray Flood Ecology project (i.e. in the first incarnation of the model, Figure 1) and then during the project (Figure 2), and to allow for refinement following the completion of the other tasks associated with the project. Thus, the scope of the model allows for assessment of some management intervention (e.g. includes manipulating weir-pool levels) in river operations, but is primarily focussed on our understanding of the ecological processes that occur in the River Murray as it current exists, as a result of high flows and flood. The Lower River Murray consists almost entirely of a series of weir pools, with very few sections that flow freely, particularly under low-flow conditions. As a result, we assume that the processes occur in the context of weir pools for the purposes of this report, with flooding of those weir pools likely at high flows.

Furthermore, we also have the objective that this model could be used as a basis for the future development of tools to assist in the management of the River Murray, by providing a mechanism for quantifying the expected impact of managed and natural flow events in the future. At this time, there is no management application built into the model, but by developing a simple model that captures the majority of processes occurring, in as consistent a manner as possible across ecological components (e.g. fish, vegetation, zooplankton), the development of such a tool in the future should be a simpler task. Thus, in developing this model, we have taken a holistic approach to the ecology of the River Murray. The model is developed specifically for the South Australian section of the River Murray, but would also apply downstream of the Darling confluence. The model is designed to apply equally well to a range of ecological components, with a view to interlinking models for multiple components to present a whole-of-system model.

By developing the models presented in this report, we address the primary aim of the conceptual-modelling task (Task 2) within the Murray Flood Ecology project, which was to develop a conceptual model for the response of river ecosystems to changing flows that incorporates the knowledge and understanding of the project members. In developing the model, we have taken an adaptive management approach, where we have captured our knowledge at various times during the Murray Flood Ecology project, updating that knowledge as new data became available. The process involved the development of a conceptual model, refinement of that model based on the project priorities, application of the model to the tasks within the project and then assessment of the results to refine the original conceptual model. We intend that this process should be ongoing beyond the life of Murray Flood Ecology, and that the models contained herein could be a starting point for future projects modelling ecological response in the Lower River Murray or other similar lowland floodplain rivers.
Figure 2. Floodplain and in-channel conceptual model (including connected wetlands). Coloured box types are defined in the key, with additional information on page 13.
Floodplain and in-channel conceptual model development

The conceptual model presented in Figure 2 was developed based on our understanding of the effect of flow on the processes occurring within river, floodplain and connected wetland ecosystems, with special reference to ecological first principles and to the circumstances of the Lower River Murray (e.g. the presence of locks, weirs and barrages regulating the flow of water) before the research of other aspects of the Murray Flood Ecology project had been undertaken. Based on those considerations, we developed a draft conceptual model.

The draft conceptual model was then circulated to all Murray Flood Ecology project members for comment. We discussed the structure and content of the draft model with at least one member of each task within the project, to ensure that the linkages that were there were meaningful with reference to the area of expertise of that researcher, and that no critical links were missing. Following these discussions, the model was refined to better reflect the various ecological components and to remove a number of terms that had different meanings for different groups. The structure of the model was also altered at that time.

A second draft model was then produced and circulated for comment (and is presented here; Figure 2). Minor changes based on colleague feedback were made, resulting in the model that is presented here. Thus, we are reasonably confident that this model is credible, and that it represents the relationships between flow and river ecology as were understood by the project team at the beginning of the project.
Floodplain and in-channel conceptual model description

In keeping with the purpose of using the model as the basis for developing future management tools, we have attempted to draft a relatively generic process-based model that can be applied to a wide range of components of an ecosystem (or the ecosystem as a whole), focused specifically on the Lower River Murray (Figure 2). Thus, it is relatively simple but also quite different from many of the species- or assemblage-specific models that have previously been developed. Processes occurring in the floodplain and within the channel are different, but are inextricably interconnected during times of flow, so a single model has been developed for both parts of the ecology of a floodplain river such as the Lower River Murray.

Some context is of value to assist in the interpretation of the model that was developed (Figure 2). In developing the model with a view to applying it to different groups of organisms within the Murray ecosystem, we expect that different components will be more or less useful for different applications. We do not expect all biotic components to respond in the same way to each lever and environmental condition. Furthermore, there may be some applications for which boxes can be deleted, and others where additional factors that are not currently included may be important. We do not necessarily assume a linear response among ecosystem components, and various thresholds or categorical responses may be needed.

The definitions of the boxes may vary somewhat among ecological components. Growth of plants, for example, is encompassed by survivorship while germination for plants is assumed to be part of reproduction. For many taxa, including vegetation and fish, there are likely to be multiple stages to reproduction (e.g. pollination, seed set, germination for plants), but for simplicity we capture them as a part of the same process. The term ‘reproduction’ is used because of inconsistencies across disciplines as to the use of the word ‘recruitment’. For abundance, no density-dependent processes are included in the generic model, but this does not exclude them from being included for a specific application, where warranted by empirical evidence. The box labelled survivorship is intended to encompass general loss factors within a population (e.g. cell death in phytoplankton), while water quality will include a range of physicochemical factors that may differ among target taxonomic groups. Phytoplankton and plants may be most susceptible to light availability and the source of water so these may be the parameters of focus for ‘water quality’ for that group, while other parameters like salinity or dissolved oxygen would be more critical for other groups. Water temperature is also intended to be included in the ‘water quality’ factor. The flow/flooding regime and habitat boxes will also encompass a range of concepts depending on the group(s) being modelled. For example, hydraulic complexity is known to be important in determining available fish habitat, but may act differently, or only indirectly, for other groups. Flow/flooding regime can also include concepts such as flood recession characteristics, which are important for floodplain and riparian vegetation. Flow and flooding cues are relatively poorly understood for many species. Flow/flooding regime may also be able to be considered to be a driver, as much as a lever. Here, we have included it as a lever, because of the highly-regulated nature of the Lower River Murray. Factors other than flow may also be important for triggering recruitment, particularly for individual taxa. The diagram is intended to broadly represent our current understanding of how spawning and recruitment are triggered, but is likely to need updating as our knowledge improves.

In colour coding the boxes, we hoped to illustrate the links between external drivers or modifiers, levers operating within the system, the intermediate effects of those two, and their subsequent impact on ecological components or taxa. External drivers are those that operate at larger scales than the model encompasses (e.g. climate). Modifiers influence the effects of those external drivers (e.g. upstream water extraction or infrastructure management). Levers include those factors that can be changed most easily by river operators, at least in theory. The impact of manipulating those levers on the target ecological component is the endpoint of the model, while intermediate effects represent the links
between the two (i.e. how the levers change the river environment that will then influence the biota). For example, climate (external driver) will influence the flood extent (lever) which is also able to be manipulated by changing flows at the South Australian border. This, in turn, will affect the available habitat (intermediate effect), stimulating food resource production (intermediate effect) which will increase fish survivorship (impact on target taxa). Thus, the impacts act on the specific taxonomic group, or collection of groups, for which the model is being applied.

We have, in all areas, attempted to keep the diagrams as simple as possible. Thus, many potential links may not be shown (e.g. climate is likely to influence infrastructure management, but there is no link shown). The diagram represents potentially complex systems, with many interdependencies and feedback loops. Similarly, other factors may be important in different systems. For example, land use is likely to influence both flow regimes and water quality, but is not shown in this generic diagram. Thus, we intend that individual users will tailor the diagrams to include those links that are most important in a given context.
Floodplain and in-channel conceptual model refinement

Following the development of the initial conceptual model, the project members for each task undertook the sampling activities associated with those tasks to yield new datasets. This provided us with an opportunity to test the initial conceptual model for the range of taxa and processes targeted by those tasks and assess the utility of the model across a range of spatial and temporal scales.

The floodplain and in-channel conceptual model (Figure 2) was applied to each of the tasks within the Murray Flood Ecology project. Key findings for each task were summarised and used to populate the model. These models were then circulated to the relevant project teams for comment and discussion. Based on those discussions, the task-specific models were adjusted to accurately reflect the main findings for that task.

We then attempted to synthesise the main findings across tasks, in accordance with our objective to capture the knowledge and understanding across the project, rather than on a task-by-task basis. Here, we developed synthesis models at multiple scales. These models were presented to the project team for comment, and were also reviewed by the expert reference group convened for the Murray Flood Ecology project. Following further review, the models were finally presented to a stakeholder group in a workshop setting. The models presented here are those arrived at by incorporating the feedback given at each of those stages.
Refined floodplain and in-channel conceptual models

Ecological processes occur on different scales of space, time and organisational complexity (Levin 1992). Understanding the resultant patterns in terms of the processes that produce them is key to the development of principles for management and, furthermore, is the essence of science (Levin 1992). Different processes are likely to be important on different scales. For example, for fish, hydraulics are important at the small scale, because they structure habitat, but flow regimes are important on a larger scale in providing access to floodplain and wetland environments and spawning cues for some species.

For this project we have used a hierarchical modelling approach to characterise the responses of the Lower River Murray to the flood that occurred in 2010 (Figure 3). This approach allows modelling at various organisational and spatial scales. The highest step of the hierarchical model consists of one overarching model which demonstrates the broad-scale links that were identified throughout this study and thus incorporates all aspects of the project (Figure 4). At the middle level, a collection of models was developed for the various functional components of the study (Figures 5-10). These models included three functional groupings of fish assemblages (small-bodied, medium-bodied and apex predators), two functional models for vegetation (floodplain and wetland), and one model for the phytoplankton, water quality and metabolism components, combined. To then capture the detail that is occurring at a finer scale, species-specific models have been produced for Murray cod (*Maccullochella peelii*) and golden perch (*Macquaria ambigua ambigua*) (Figures 11 & 12), which were the subject of multiple tasks within the Murray Flood Ecology project. Lastly, we also present the task-specific models that were the starting point for these synthesis models (Figures 13-20). For most models, high-flow processes are explicitly separated from low-flow processes, as different drivers are likely to be of importance in times of high versus low flow (e.g. with extreme events likely to structure biotic assemblages via re-assembly; Poff and Zimmerman, 2010).

![Figure 3. Hierarchical organisation of the models developed for the Murray Flood Ecology project](image)

**Overall model**

The overall model (Figure 4) draws together the relationships identified by the Murray Flood Ecology group between high flow events and the response of the various biotic components studied. We have omitted low flows from this overall model because high flows were the focus on the Murray Flood Ecology project, and the additional information provided regarding low flows was inconsistent with regard to amount and type among the individual tasks, so was difficult to consolidate. However, please note that both low- and high-flow conditions are included in all of the smaller-scale models presented.
Figure 4. Overall conceptual model for ecological response to high flows in the Lower River Murray. A dotted line indicates an indirect interaction. Fish species mentioned include flat-headed gudgeon complex (Philypnodon spp.), carp gudgeon complex (Hypseleotris spp.), bony herring (Nematalosa erebi), silver perch (Bidyanus bidyanus), freshwater catfish (Tandanus tandanus), Murray cod (Maccullochella peelii) and golden perch (Macquaria ambigua ambigua), and the non-native common carp (Cyprinus carpio), goldfish (Carassius auratus auratus) and redfin perch (Perca fluviatilis). Arrows inside boxes indicate the response to high-flow events. Where there is some idea of the direction of response, that is included beside the relevant arrow (e.g. +ve for a positive relationship).

In creating a synthesised model for the ecological response of the Lower River Murray as a whole, we have selectively included the drivers, levers and impacts from the generic model, based on the response of each group represented. In most cases, there was insufficient information to describe the shape and nature of the relationships among the drivers and the impacts, or the relationship was likely to vary among different functional groups. Where possible, we have included additional information about how each driver or impact would respond, under high flow conditions. Simplification of complex relationships, where understood, was needed to capture the overall response of the ecosystem to high flow events.
For most groups, flooding flows were thought to have an overall positive impact. Increased lateral connectivity would import nutrients from the floodplain into the river, increasing both net primary productivity and community respiration rates, indicating that the in-stream productivity of the ecosystem would increase. Some parts of the phytoplankton assemblage, such as diatoms, were likely to experience increased survivorship, but cyanobacteria were likely to decline with flooding flows. Lateral bank recharge would increase the survivorship of floodplain river red gums (*Eucalyptus camaldulensis*) and other flood-dependent floodplain vegetation, while flood waters themselves would increase the coverage of amphibious floodplain vegetation, river red gums and understorey plants. In-stream submerged macrophytes were likely to decline in extent with high or flooding flows. Changing water temperature and other flow characteristics would provide migration and spawning cues for fish species such as silver perch (*Bidyanus bidyanus*), golden perch and Murray cod. These cues, and increases in access to floodplain and wetland vegetation, would lead to recruitment events for those taxa, but also freshwater catfish (*Tandanus tandanus*) and the introduced redfin perch (*Perca fluviatilis*). Increases in the diversity of habitat, particularly on the floodplain, would lead to increased survivorship for Murray cod and increased abundance of small-bodied taxa on the floodplain, apex predators and medium-bodied fish on both the floodplain and in the channel, but decreased abundance of small-bodied fish in the channel.

The generic model performed well in allowing the relationships across a range of taxa to be represented at the scale of the flow events surveyed. Synergies were apparent across the various taxa, with links apparent between nutrient concentrations, primary productivity and habitat complexity, for example. Very little information was available, however, to describe the shape of the relationships. This is, perhaps, not surprising, given that only one flood event could be sampled as a part of this project, and more will need to be studied to understand how each taxon and each group respond functionally to high flows with different characteristics.

### Functional-group models

The functional-group models (Figures 5-10), provide the link between the individual task- and species-specific models and the response of the system as a whole, as represented by the overall model above (Figure 4). We have included composite models for the response of phytoplankton, water quality and metabolism (Figure 5), for wetland and floodplain vegetation (Figures 6 & 7, respectively), and for small-bodied, medium-bodied and apex-predator fish (Figures 8-10, respectively) in order to synthesise responses among groups likely to be responding to the same variables in the environment. The development of these composite models was based on the knowledge gathered during the Murray Flood Ecology project, as well as the background material provided by task leaders, so these are not necessarily comprehensive reviews of all knowledge of the response of a floodplain river to high flows. However, as a part of the review during the various project workshops, project participants, the expert reference group and stakeholders were given the opportunity to identify any missing links, which have since been included in the models that are presented here. For each of the functional-group models, we have included the identified response of that functional group under both high/flooding flows and low flows to capture differences in the responses under different hydrologic conditions.
Phytoplankton, water quality and metabolism

The phytoplankton, water quality and metabolic components of the Lower River Murray are important components of the ecological status of the River to capture when comparing responses to flow events. For the water quality and phytoplankton, results were based on the results of sampling that was conducted before the flood event during June 2008 and August 2009 and during that flood, during June 2010 to August 2011 (Aldridge et al. 2012). Nine sites were sampled, from Lock 9 to Tailem Bend. Metabolic activity within the River was sampled at various times from 2006 to 2009 prior to the flood and between February and December 2011 for the flood period (Oliver and Lorenz 2013), with the flood period defined separately within each task. Sampling locations for the metabolic activity were at Locks 1 through to 5 and at Swan Reach, with upstream weir-pool sites and downstream running water sites sampled at each.

A threshold of 3,000 ML day$^{-1}$ was identified as differentiating between high- and low-flow responses in metabolic processes in-stream. Below that threshold, low water levels, nutrient concentrations and turbidity led to increased macrophyte production and decreased phytoplankton abundance, with gross primary productivity and respiration occurring at low overall rates. Above the threshold of 3,000 ML day$^{-1}$, high water levels and turbidity, along with increased lateral connectivity and the import of carbon from the floodplain, increased gross primary production in the main channel, with diatoms in particular increasing in abundance. High flows also had the capacity to mobilise resting stages of some species of phytoplankton, completing the recruitment cycle for those taxa.

Figure 5. Conceptual model for the phytoplankton, water quality and metabolism in the Lower River Murray during high and low flows
The generic model was relatively difficult to apply to metabolism, water quality and phytoplankton, partly because of the diverse range of taxa and responses to be represented, but also because of differences in the manner in which those responses were measured, compared to the representation in the generic model (e.g. survivorship and abundance in the generic model versus measured gross primary productivity and respiration). In order to account for this, the impact on the target ecosystem component boxes from the generic model were replaced with ones more suited to this fraction of the ecosystem. Time frames and spatial scales for response in this functional group are also likely to be smallest relative to all other groups investigated.

**Aquatic vegetation**

The conceptual model for aquatic vegetation in the Lower River Murray (Figure 6) was developed using data from Bice et al. (2014) and Nicol et al. (2013). The former study surveyed vegetation at 14 sites along the Lower River Murray: seven sites in the floodplain (Locks 3 to 6) and seven sites in the so-called Gorge region of the River (i.e. between Locks 1 and 3). Vegetation for this study was quantified using percent coverage of aquatic microhabitat types with vegetation categorised into functional groups. Nicol et al. (2013) sampled the submerged and emergent aquatic plant communities in two regions downstream of Lock 1: the Gorge region (Lock 1 to Mannum) and the Lower Lakes. Sampling was conducted in spring 2008 and autumn 2009, during the drought period, and then in spring 2011 and autumn 2012 following the high flow period. This study investigated both the submergent and emergent vegetation within the main channel, wetland areas and the Lower Lakes.

![Conceptual model for the aquatic vegetation in the Lower River Murray](image)

During low-flow periods, low values for water levels, turbidity and shear forces resulted in an increase in submerged macrophytes in the main channel, but a decline in submerged macrophytes in wetlands, in emergent taxa and in the variability of habitats across the main channel. The recruitment of terrestrial and floodplain species increased via colonisation processes in dry wetlands and in riparian zones during the period of low flow. During high-flow or flooding events, increased shear forces, turbidity and water levels resulted in declines in macrophyte abundance in the main channel, but increased coverage of emergent and amphibious species on the floodplain, with a loss of terrestrial taxa in those areas.
Floodplain vegetation

The conceptual model for the floodplain vegetation response (Figure 7) was developed using data from Holland et al. (2013). Vegetation was quantified from transects on the Bookpurnong floodplain near Loxton, focussing on the dominant tree species (black box *Eucalyptus largiflorens*, river red gum, and river cooba *Acacia stenophylla*). Understorey vegetation was also measured on the Chowilla and Pike floodplains, using quadrats to estimate percent coverage.

![Diagram of conceptual model for floodplain vegetation response](image)

**Figure 7.** Conceptual model for the response of floodplain vegetation to high flows following a period of drought in the Lower River Murray.

Under low-flow conditions, low water levels and shear forces resulted in increases in terrestrial and floodplain species, with lower abundances of wetland and emergent taxa and lower variability in habitats in the main channel. Under moderate and high flow conditions, lateral bank recharge of more than 90 to 120 m distant from the main channel is likely to increase survivorship for river red gums and, combined with high water levels, increase the abundance of amphibious taxa, river red gums and understorey species on the floodplain.

Small-bodied fish

The following model was developed for the abundance of both larval and adult small-bodied fish in the Lower River Murray and the interaction between those fish, vegetation and other habitat components (Figure 8). This model was developed based on the results of sampling which was conducted twice during the Murray Flood Ecology study. Larval fish were sampled using plankton tows on six occasions during the spring/summer period in each of 2005 – 2008 and 2010 (Cheshire et al. 2011). Larval fish samples were collected from both Lock 1 and Lock 6. Sampling for adult fish was carried out during the low-flow period between March and May 2008 and in the high-flow period in April 2012. Both floodplain (Locks 3 to 6 inclusive) and Gorge (Locks 1 to 3 inclusive) sections of the River were sampled for adult fish. The small-bodied fish present in the Lower River Murray include the threatened
unspecked hardyhead (*Craterocephalus stercusmuscarum fulvus*), carp gudgeons (*Hypseleotris* spp.), Murray rainbowfish (*Melanotaenia fluviatilis*), flat-headed gudgeon (*Philypnodon grandiceps*) and Australian smelt (*Retropinna semoni*).

During times of low flow, low water levels, turbidity and shear forces combined to decrease the variability in microhabitats and increase the abundance of submerged vegetation cover. This, in turn, tended to increase abundance of small-bodied fish in the main channel, and also increase the recruitment of carp and flat-headed gudgeon. At times of high and flooding flows, increases in shear force, turbidity and water levels resulted in decreased cover of submerged vegetation in the main channel, but increased cover of emergent, amphibious and terrestrial vegetation on the floodplain. As a result, abundances of small-bodied fish declined in the main channel but increased on the floodplain and in associated wetlands.

**Medium/large-bodied fish**

The following model was developed for the abundance of both the larval and adult life stages of medium- to large-bodied fish in the Lower River Murray and their interaction with the vegetation and other habitat components (Figure 9). The model was developed based on the results of sampling of larval fish assemblages at two sites (Locks 1 and 6) on six occasions, spaced fortnightly during October to December between 2005 and 2008 and in 2010 (Cheshire et al., 2011). Samples were also collected in January of 2005, 2006 and 2010. To assess habitat interactions, sampling was undertaken on two occasions, both in autumn. Habitat interaction sampling was carried out both during the low-flow period in March to May 2008 and in the high-flow period in April 2012 in floodplain (Locks 3 to 6 inclusive) and Gorge (Locks 1 to 3 inclusive) sections of the River (Bice et al., 2014). The medium-bodied fish present in the Lower River Murray included the native bony herring (*Nematalosa erebi*), freshwater catfish, Australian smelt and silver perch, and the non-native common carp (*Cyprinus carpio*), goldfish (*Carassius auratus auratus*) and redfin perch.
During times of low flow, increased conductivity had an impact on recruitment of Australian smelt. Under high-flow conditions, increased water levels, lower conductivity and more available habitat, along with spawning cues for some species tended to increase recruitment. Additional habitat is also likely to increase the amount of food available for larvae and juveniles (see Figure 11 below). This led to an increase in abundance of medium-bodied species in the floodplain and in the main channel.

**Apex predators – Murray cod and golden perch**

The apex predators of the Lower River Murray include Murray cod and golden perch. The larvae of the apex predators were collected between 2005 and 2008 and in 2010, with sampling occasions occurring fortnightly over the spring/summer period at Locks 1 and 6 (Cheshire et al., 2011). The recruitment and abundance of golden perch was also studied from 2005 to 2011 at 128 different sites in the River Murray main channel, the Chowilla and Katarapko Anabranch systems and the littoral zones of Lake Alexandrina (Zampatti and Leigh, 2013). Finally, movement of Murray cod was documented over the period from November 2010 until April 2011 (Bice et al., 2014). This study was conducted both in the main channel of the River Murray and in the Chowilla Anabranch system.
Figure 10. Conceptual model for the apex predators within the Lower River Murray: Murray cod and golden perch. \(^{a}\) flows of 10,000 ML per day are required to induce spawning of *Macquaria ambigua ambigua*. ? denotes possible interactions. CWD indicates coarse woody debris and the dotted line indicates an indirect interaction. Fish species include Murray cod (*Maccullochella peelii*) and golden perch (*Macquaria ambigua ambigua*).

High flows are thought to be required for response in apex predators in the River Murray. During those high flows, increased water levels led to increased habitat diversity (including hydraulic diversity) but also increased available habitat as the floodplain inundates, which increases recruitment and survivorship of apex predators and so increases the abundance of those predators on the floodplain and in the main channel. Declining conductivity and water temperature and flow-related spawning cues are also thought to contribute to recruitment, particularly of golden perch. As floodwaters recede, low dissolved oxygen concentrations can result in lower survivorship of apex predators (although there are likely to be other effects such as an increase of food resources in-channel).

**Species-specific models**

Two species were the subject of tasks designed specifically to focus on individual species, and so warranted the production of species-specific models. These are included below, along with details of the various tasks used to develop these models.
Effects of flooding and abundance of golden perch (*Macquaria ambigua ambigua*) in the Lower River Murray (Task MF2)

Golden perch is one of two native fish species in the Murray Darling Basin that is considered to require high-flow events to initiate spawning. Previous investigations of the spawning of golden perch have been restricted to the mid-reaches of the River Murray and thus, investigations into their spawning in the Lower Murray River were made for this study. The objectives of Task MF2 were to assess the recruitment of golden perch post-flooding in the Lower River Murray and to use otolith microchemistry to determine the origin of any larvae captured. The researchers hypothesised that increased discharge and floodplain inundation would promote golden perch recruitment and abundance in the Lower River Murray. It should be noted that this task originally also aimed to quantify the recruitment of Murray cod in the Lower River Murray but the results of this aim cannot be evaluated because so few Murray cod were captured.

The age-structure of adult golden perch was also studied from 2005 to 2011 at 128 different sites in the Lower River Murray (Zampatti and Leigh, 2013). Sites were sampled in three separate regions: swamplands (downstream of Mannum), the Gorge (Mannum to Lock 3) and floodplain (Locks 3 to 6). Abundance of golden perch was also studied in the Chowilla Anabranch system and the adjacent River Murray channel. The conceptual model developed (Figure 11) demonstrates the response of golden perch to flow. For this study, recruitment was determined as survival to at least young-of-year. Sampling was conducted using electrofishing during daylight hours in all available littoral habitats. The total length (±1 mm) of each individual was also measured.

![Figure 11. Conceptual model developed for the response of golden perch populations to flows after a period of drought in the Lower River Murray.](image-url)

WC F: within channel flows; OB F: overbank flows * Golden perch may not spawn on the floodplain but the inundated floodplain may provide a rearing habitat for juvenile golden perch.
The abundance of golden perch in the Lower River Murray was significantly higher in 2011 than in previous years. From the study period, three distinct broad size-classes of golden perch could be identified. The modes of these classes in 2011 were 110 mm, 200-210 mm and 410 mm. These sizes suggested distinct recruitment events, in 2005 and in both the year before and year of the 2010/2011 flood period. There was an observed difference in age-classes of golden perch between the different regions of the Murray River. High abundances of low age-classes of golden perch were frequently captured in the swanpland region and older, larger fish were concentrated in the lower regions of the River Murray, particularly in the Lower Lakes.

The otolith microchemistry employed in this study was able to identify the origin of golden perch larvae in the Lower River Murray. The strontium signature was used because it is able to differentiate between different geomorphic regions, and the River Murray has distinct strontium concentrations in the different regions. The strontium signature from the golden perch that spawned in 2005 indicated that those fish were spawned in the River Murray, and aligned with a small flow pulse that occurred within the channel in that year. The 2009 cohort of golden perch spawned in the year before the 2010/2011 flood. The strontium signature from that cohort indicated that those fish spawned in the Darling River. High flows occurred in the Darling River at the time of purported spawning, possibly reaching bankfull levels. The final cohort aligned with the 2010/2011 flood event and the strontium signature indicated that those fish spawned at a range of locations, consistent with widespread high flows at that time. These findings are consistent with those of previous studies that indicate that golden perch is a flood-cued spawner (e.g. Mallen-Cooper and Stuart, 2003).

Previous studies have suggested that golden perch require flows to initiate spawning. This study supports these findings, and has also identified the significance of tributaries, such as the Darling River, to golden perch populations in the Lower River Murray. As a result, the longitudinal connectivity of flows is essential for the spawning of golden perch in the Lower River Murray.

The findings of this task supplement the findings from the larval fish component (Task MF1) of the Murray Flood Ecology project, which also identified a large abundance of golden perch larvae in the Lower River Murray following the flood event. The findings of the phytoplankton and nutrient dynamics (RM2) indicate that during the flood event, the abundance of food (i.e. via increased production) and nutrients was increased, and would be available for larval fish.

Movement and mortality of Murray cod (*Maccullochella peelli*) during a flood in the Lower River Murray, Australia (Task MF3)

Murray cod are an iconic species in the River Murray and have declined in abundance in recent years. The aim of Task MF3 was to document the movements of Murray cod within the Lower River Murray during the flood period and identify the mesohabitats used. The conceptual model for the movement of Murray cod in response to high flows following a period of drought in the Lower River Murray (Figure 11) was developed using data from Leigh and Zampatti (2013).

Sampling was conducted in the River Murray channel and the Chowilla Anabranch system. A total of 36 Murray cod were tagged between October 2007 and January 2009, and were tracked on five occasions between November 2010 and April 2011. Six remote fixed logging stations were also positioned at the junction of Chowilla Creek and the River Murray and on the major tributaries of the Chowilla Creek. Time and direction of travel were recorded for any individual travelling past a logging station. Data from these loggers was downloaded during each of the five tracking trips. Finally, aerial tracking to locate fish that had travelled large distances upstream was carried out in March 2011.

The movements of the 36 Murray cod tagged as a part of this study can be categorized into four groups dependent on the extent of movements recorded:
1) small-scale movements (<2 km; \( n = 7 \));
2) broad-scale movements within the Chowilla region system (\( n = 7 \));
3) movements between the Chowilla system and the main channel (\( n = 16 \)); and
4) large-scale riverine movements (>50 km; \( n = 6 \) but could have been up to 11 due to the loss of signal from another five fish) (Figure 12).

The majority of the Murray cod moved between the River Murray channel and the Chowilla region. Five additional fish were not located after the flood event and are thought to have moved upstream. There were no significant differences observed in fish movements relating to either the age or sex of the fish. All Murray cod tracked within this study were located in the main channel of the River Murray; they were never found on the floodplain or in ephemeral flood runners unless the mortality signal was activated on the tag (i.e. initiated by no movement for an extended period). During the period between March and April in 2011, nine of the tagged fish (equating to 25%) began emitting the mortality signal. The death of these fish coincided with an extensive blackwater event that was initiated by the high-flow event. All of the fish that died during this event were older fish moving upstream.

Figure 12. Conceptual model developed for the response of Murray cod to high flows following a drought period in the Lower River Murray. HF: high flow; LF: low flow; FP: floodplain; MC: main channel; CWR: coarse woody debris.
Murray cod have previously been observed moving during high flows, often within the Chowilla region. This study supports this finding, with initiation of large movements observed after the flood event. Cod have also often been found in flowing regions that contain structural habitat elements, including snags. It is important to ensure the maintenance and, where possible, enhancement of this structural complexity in the River to support current and future populations of Murray cod. The long-distance movements exhibited by Murray cod in this study also highlighted the importance of considering Murray cod on a river-wide scale. Focusing on single sections of the River Murray, such as the Lower River Murray alone, risks leaving the population picture incomplete.

**Task-specific models**

Models for each of the tasks associated with the Murray Flood Ecology project were the basis for the synthesised models that have been presented above (Figures 4-12). Each of these models attempted to summarise the main interactions and findings of the respective task. We have included summaries of the findings of each task, as well as the model developed from those summaries here (Figures 13-20). For each task, the spatial and temporal scales of the data used to create each of the individual models have been described. Figure 1 illustrates the links between tasks and the focus of each.

**From drought to flood: annual variation in larval fish assemblages in a heavily regulated lowland river (Task MF1)**

The spawning and recruitment of various fish species are dependent on flows. The objective of Task MF1 was to determine what the influence of high flows was on larval fish assemblages in the Lower River Murray. Specifically, the task team aimed to compare annual variability in larval assemblages between a within-channel flow pulse year, a series of low-flow years and a high-flow/overbank-flooding year and attempted to correlate any observed differences with changes in hydrology and other environmental variables.

The model (Figure 13) was developed based on the results of sampling of larval fish assemblages at two sites (Locks 1 and 6) on six occasions per year spaced fortnightly between October to December between 2005 and 2008 and also in 2010 (Cheshire et al., 2011). Samples were also collected in January of 2005, 2006 and 2010. Larval fish assemblages were captured by plankton tows, (determined as the single best method for determining larval fish assemblages [Cheshire, 2010]). Three day and night plankton tows were conducted at each site.

Eleven species were identified throughout the study, nine of which were native. The most abundant fish in all years were the small- to medium-bodied native species, Australian smelt, bony herring, carp gudgeon complex and flat-headed gudgeon complex. Hardyheads (Craterocephalus spp.), Murray cod and freshwater catfish were also collected in all years. Silver perch and golden perch larvae were only found in 2005 and 2010. The non-native common carp and goldfish were also collected in all years at low to moderate abundances.

The larval fish assemblage was significantly different among years, sites and trips. The larval fish assemblage was significantly different in 2010 compared with all other years. The 2010 assemblage was characterised by golden perch, freshwater catfish and Murray cod larvae and the presence of perch eggs and hatchlings. The key environmental drivers for the differences observed between 2010 and all other years were identified as flow and water level. Water temperature was also identified as a driver, highlighting the seasonal differences between spawning and recruitment of fishes (although migration was not measured as a part of this task).
Small- to medium-bodied fish spawned during both the low- and high-flow periods, but high flows may benefit the survival of larval fish assemblages. The spawning of both golden and silver perch were linked to flow events in the river channel and continued low flow was identified as a potential risk to large-bodied fish in the River Murray.

Increased nutrients and altered phytoplankton dynamics were identified during and following the high flow event (see Task RM2 below). These alterations may be contributing to the survivorship of larval fish by providing an extensive food source (e.g. via carbon flow to zooplankton). Golden perch were also identified as a flow-spawner in this study, which supports the findings of Task MF2 (see below).

**Figure 13.** Conceptual model developed for the response of larval fish to flows after a drought in the Lower River Murray. LF: low flow; HF: high flow. * Abundance was positively correlated with discharge and water level; and negatively correlated with EC for *M. peelii*, *M. a. ambigua*, *B. bidyanus*, perch eggs and hatchlings and *P. fluviatilis*. Abundance was negatively correlated with discharge and water level; and positively correlated with EC for *Retropinna semoni*. # Abundance was negatively correlated with temperature for *R. semoni* and *P. fluviatilis*, and positively correlated with *Nemataolsa erebi*, *Hypseleotris* spp. and *Craterocephalus* spp. Thick lines indicate statistically-significant relationships within the model.

**Fish-habitat associations (Task MF4)**

The fish and habitat of the Lower River Murray were investigated by Bice *et al.* (2014) to identify any associations between fish and habitat both during the drought period and the subsequent high-flow period. The researchers undertaking the task hypothesised that high flows would affect microhabitat availability and that those changes may be associated with changes in fish assemblage structure.
Sampling was conducted at 14 sites along the Lower River Murray: seven sites in the floodplain (Locks 3 to 6) and seven sites in the so-called Gorge region of the River (Locks 1 to 3). Fish were sampled using electrofishing techniques. Vegetation for this study was quantified using percent coverage of in-stream microhabitat types for vegetation (categorised into functional groups) and structural elements (such as coarse woody debris [CWD], tree roots, rock, and man-made structures). Data were collected in both 2008 (during the drought period) and in 2012 (after the high flow event). The conceptual model below highlights the findings from the survey (Figure 14). Fish identified during the study included the native golden perch, Murray cod, bony herring, silver perch and freshwater catfish, and the non-native common carp, goldfish and redfin perch. The small-bodied fish identified included the unspecked hardyhead, carp gudgeon, Murray rainbowfish, flat-headed gudgeon, dwarf flat-headed gudgeon (*Philypnodon macrostomus*), Australian smelt and non-native eastern gambusia (*Gambusia holbrooki*).

Throughout the course of this study, there were more species of fish identified from the sampling in the drought period (2008) compared with after the high-flow period (2012). There was no difference in the assemblage observed between different regions of the River Murray, but significant differences among years. In 2008, the small-bodied fish dominated the assemblage observed, but in 2012, large-bodied fish
dominated the catch in the River, likely due to spawning and recruitment events during the high-flow period. The vegetation in the River Murray also showed significant changes among the two years. In 2008 there was a variety of different habitats present, and submergent species dominated the system. In 2012, following the high-flow event, the submergent species were lost from the system in the areas sampled and there was an increase in open water habitats, with the cover of emergent and structural habitat partly a function of increased stage height of the river.

Some associations between different fish species and habitat types were observed during this study. Small-bodied fish species had an association with at least one, but sometimes many, species of submergent macrophytes. The subsequent loss of submergent vegetation following the high-flow event coincided with a decreased abundance of small-bodied fish observed. The small-bodied fish may have moved into the wetland habitats during the time of high flows. There were fewer associations between habitat and the large-bodied species of fish and these were less consistent between the low- and high-flow periods. The increase in abundance of the large-bodied fish was thought to be better associated with flow rather than habitat characteristics, at least at the scale studied here.

**Resilience of wetland fish communities (Task WR1)**

The resilience of wetland fish communities was investigated before and after the 2010/2011 flood in the Murray River by Thwaites and Fredberg (submitted). The construction of the barrages in the 1940s resulted in a relatively constant water level in wetland habitats in the Lower River Murray in subsequent years. Following an extensive drought from 1996, water levels in the Lower River Murray were greatly reduced, resulting in many of the associated wetland habitats drying completely from late 2007 onwards. Flows returned to the basin in late 2010, which resulted in the refilling of wetlands. This sequence of events provided an opportunity to investigate the resilience of fish that inhabit wetlands in the Lower River Murray, and to determine how fish communities responded to the refilling of wetlands after being dry for more than two years. This task aimed to document short- to medium-term spatial and temporal recovery trajectories of individual fish species and wetland fish communities following inundation of previously-dry wetland habitats. This included assessing how exotic species responded compared with native species and whether wetlands had the capacity to recover compared with historical data (2004-2009).

Sampling was conducted before the drying of the wetlands in autumn during 2004 and 2007 and spring of 2005 and 2006. Following the refilling event, sampling was conducted in spring of 2011 and autumn of 2012. Sampling sites were concentrated within a range of wetlands below Lock 1, but three wetlands above Lock 1 were also sampled.

Following the high-flow event in 2010/11, the abundance of fish captured in wetlands increased (Figure 15). A change in the proportions of native, relative to non-native, fish species was also observed, with the wetlands being dominated by native fish during the drought period, but non-native species dominating the wetlands following the high-flow period. Common carp showed the greatest response to the high-flows, with a substantial increase in abundance following the flows. Bony herring also showed a positive response to the high-flow period. Eastern gambusia showed a negative response to returning flows in the system, with lower abundances recorded during the high-flow period.
The findings from this study are consistent with the results observed in other parts of the Murray Flood Ecology project, including the larval fish assemblages (see MF1 above) and habitat-fish associations (see MF4 above).

**Resilience and resistance of aquatic plant communities downstream of Lock 1 (Task WR2)**

The aim of this task was to assess the resistance and resilience of aquatic plant communities in the Lower River Murray. The conceptual model for aquatic vegetation in the Lower River Murray was developed using data from Nicol et al. (2013, see Figure 16). This study investigated both the submergent and emergent vegetation within the main channel, wetland areas and the Lower Lakes. The researchers compared data collected during a period of low water levels (2007-2010) with those from after higher water levels were reinstated (2011-2012). An earlier period of high water levels was also used for comparative purposes (2004-2007) to assess whether vegetation assemblages resembled those of the earlier time.

Nicol et al. (2013) sampled the aquatic plant communities in two regions downstream of Lock 1: the Gorge region (Lock 1 to Mannum) and the Lower Lakes. Sampling was conducted in spring 2008 and autumn 2009, during the drought period, and in spring 2011 and autumn 2012 following the high flow period.

During the low-flow period, many of the wetlands dried up and the waters receded in the Lake beds. Subsequently, the submergent plants were extirpated from the Lakes system and the exposed sediment was colonised by terrestrial taxa (which were often weeds). The emergent species persisted throughout the drought although the condition of the emergent stands declined.
After the high-flow event, emergent taxa increased in abundance substantially. All of the terrestrial taxa that had colonised the exposed sediment were extirpated. The response of submergent vegetation following the flows was mixed. In the main channel and in Lake Albert, submergent species did not recruit but recruitment was seen in Lake Alexandrina and the Goolwa Channel.

Figure 16. Conceptual model of the response of aquatic plant communities to high flows following a period of drought in the Lower River Murray.

This study highlighted that emergent vegetation tended to be resistant to the low-flow period and responded well to the high-flow event in 2011. Submergent taxa were resilient in the Goolwa Channel and Lake Alexandrina regions, due to a viable seed bank and good dispersal mechanisms. However, it was less resilient in the main channel and in Lake Albert. Historically, Lake Albert has had a poor submergent vegetation community due to the habitat and geomorphology not being ideal. The increased turbidity and water depth within the main channel during the after-flow sampling period was thought to restrict the re-colonisation of submergent taxa.

Changes in metabolic activity of a regulated lowland river during a flood that followed a decadal drought (Task RM1)

The aims of Task RM1 were to assess an important aspect of the functional ecology of the Lower River Murray both during a decadal drought and then following a high-flow event. This was achieved by assessing the metabolic activity in the Murray River both before and after the high-flow event (Oliver and Lorenz 2013). The authors tested a number of hypotheses, including that:

- an extended period regulated flows would result in transport of carbon from upstream being the major food source for phytoplankton (i.e. compared with allochthonous floodplain sources);
• during flooding, allochthonous sources of carbon would increase respiration within the water column, but that water depth, colour and turbidity would limit production at increased flows;
• that coarse particulate organic material from the floodplain would accumulate in the channel and contribute to metabolic activity; and
• following the flood, planktonic metabolism would return to pre-flood levels, but with enhanced metabolism in the sediments due to storage of allochthonous organic material.

River metabolism in the Lower River Murray was measured at six sites from Lock 5 to Swan Reach. At each of these sites, photosynthesis and respiration rates were estimated using a daily time series of dissolved oxygen concentrations and light intensities. From the measurements of productivity and respiration, gross productivity and net productivity were also determined. To determine the difference between planktonic and non-planktonic primary productivity, incubation chambers suspended in the water column were used to estimate the planktonic component. The non-planktonic component was then calculated as the difference between total productivity and planktonic productivity.

The high-flow event caused a substantial change in the metabolic activity in the Lower River Murray (Figure 17). Increases were observed in the rates of open water production, plankton, respiration, net production and open water respiration. The non-planktonic respiration also increased substantially, although this change was not expected. Many peaks in oxygen levels were observed at the various sites along the Lower River Murray, but these peaks were not aligned with daylight. Instead, the peak was shifted downstream and thus could be sourced back to where the oxygen peaks originated. At each site, the oxygen in the Lower River Murray was able to be sourced back to large floodplains upstream. The cause of these peaks was hypothesised to be phytoplankton because there was no vegetation in the source locations. Respiration was also suggested to be occurring on the floodplain.

Figure 17. Conceptual model for the response of metabolic activity to high flows following a period of drought in the Lower River Murray.
Changes in water quality and phytoplankton communities in the Lower River Murray in response to a drought-flood sequence (Task RM2)

Changes in nutrient concentrations and phytoplankton community structure from a low-flow period to a subsequent high-flow period were investigated in Task RM2 (Aldridge et al., 2012). The water quality and phytoplankton communities were investigated at six sites in the Lower River Murray, between Lock 5 and Tailem Bend. This project used historical data on river flow, nutrients and dissolved organic carbon concentrations and phytoplankton. Again, a number of hypotheses were tested. These included that:

- low-flow conditions would result in limited water mixing, resulting in a community dominated by mobile taxa;
- inundation of the floodplain would increase mobilisation of nutrients in the Basin which would then be incorporated into phytoplankton biomass; and
- high-flow conditions would increase water mixing and so the phytoplankton community would be dominated by immobile taxa.

Before the high-flow event came down the Lower River Murray, the system was in a nutrient-limited state (Figure 18). The high-flow event in 2010/2011 changed nutrient and phytoplankton dynamics of the Lower River Murray substantially. Following the high-flow period, the electrical conductivity of the Lower River Murray decreased, dissolved organic carbon (DOC) increased, due to floodplain inputs, and the dissolved oxygen concentration decreased, as a result of microbes consuming the DOC. Nutrient concentrations also increased following the high-flow event, with forms of nitrogen, phosphorus, silica and chlorophyll a all increasing from levels measured during the drought.
Figure 18. Conceptual model for the responses to high flows following a period of drought for the water quality and phytoplankton communities in the Lower River Murray. LF: low flow; HF: high flow. *Potentially driven by evapo-concentration and groundwater inputs. Concentrations of NOX, FRP, TKN, TN, TP and Si concentrations were higher downstream of Lock 1 during the low flow period, suggesting a local nutrient input, most likely from evapo-concentration, irrigation returns from diaries, groundwater or inputs from Lake Alexandrina.

The changes in nutrient concentrations were largely thought to be governed by flow. Nutrients were sourced largely from upstream regions, with only 10% being sourced locally. During the low-flow period when nutrients were limited, cyanobacteria dominated the system but increased nutrient concentrations following the high-flow event supported a substantial increase in phytoplankton abundance. The hydrodynamics of the system governed the community composition and the nutrients controlled the abundances of each taxonomic group present.

The response of river red gums to bankfull flows (Task T1)

The objectives of Task T1 were to determine the relationship between bankfull flows and river red gum health. More specifically, this project aimed to determine the duration of time that the river red gum community was inundated for and determine the relationship between that duration and the health of river red gums (Doody et al. submitted). The authors hypothesised that sites with greater access to overbank flows and lateral recharge would exhibit higher levels of physiological response (e.g. improvement in tree condition) than those with less access to water. This effect was expected to decrease with distance from channel.
Remote sensing was used to investigate inundation extent along the Lower River Murray. The vegetation growth of the river red gums was determined using the Normalised Difference Vegetation Index (NDVI). NDVI values range from -1 to +1, with live vegetation having a positive NDVI value and water having a negative NDVI value. The health is estimated using the densities of trees, with denser trees giving a higher NDVI value.

This project highlighted the importance of lateral recharge and flooding in the Lower River Murray (Figure 19). The health of river red gums increased in response to flooding. Measured health was 30% higher in the river channel compared to the floodplain regions. High flows were also determined to increase river red gum health (when spring and summer flows were investigated).

The lateral recharge zone was identified to be between 90 and 120 m from the river bank. Two of five sites showed increases in river red gum health following the high-flow event and the authors indicated that a lag in response time was likely, and that river red gum health may also increase at the remaining sites through time. This study also identified that inundation of at least seven days was required for a positive response in river red gums to be observed, but river red gum health decreased once inundation exceeded 60 days. These findings were not the same as those of others including Roberts and Marston.
(2011), who recommended inundation of between 5 and 7 months to improve river red gum tree health, but are within similar ranges.

Floodplain response and recovery: comparison between natural and artificial floods (Task T2)

The final Task, T2, assessed the response of the floodplain and understorey vegetation to the high flow event in the Lower River Murray (Holland et al. 2013). It also assessed what differences there were between floodplains that had been artificially altered during the drought period, compared with floodplains that had not been. Changes to soil, groundwater, tree condition and understorey vegetation were all documented. No specific hypotheses were presented by the authors.

Three floodplains were studied for this task, the Bookpurnong (which was artificially watered), Pike and Chowilla (also artificially watered) floodplains. Existing data were used for the drought period, with the floodplains revisited after the recession of flooding flows. Groundwater and surface water levels were determined for the Bookpurnong floodplain. Surface water was collected using a grab sample and measurements of various components of the water chemistry were determined (including Na⁺, K⁺, Ca²⁺, Mg²⁺, HCO₃⁻, Cl⁻ and total dissolved solids). Piezometers were used for groundwater sampling at a depth of 1 to 3 m below the water table. Soil profiles were taken near each piezometer. Vegetation response was also measured at Bookpurnong, using six vegetation transects perpendicular to the River. Observations of each tree along established transects were made (including presence of tip growth, reproductive status and canopy cover) and stem diameters of a subset of trees were measured.

At Pike and Chowilla floodplains, understorey vegetation surveys were undertaken at a range of sites. Quadrats (15 m x 1 m) were used at each site, with the presence of each species of live, rooted plant recorded. Quadrats were given a score out of 15 for vegetation complexity, with quadrats of only bare soil given a score of one.

The groundwater assessment was undertaken only at the Bookpurnong floodplain. Both the artificial watering and the natural high-flow event in the Lower River Murray reduced soil salinity (Figure 20). Chloride levels in the soil were reduced between 40 and 55% after the flow event. The groundwater was substantially fresher following the flow events, although the quantities of water varied among events.
Figure 20. Conceptual model for the floodplain response to high flows following a period of drought in the Lower River Murray.
Discussion

Using ecological processes

In developing this model, we focused on the use of ecological processes as opposed to merely describing structural components. Ecological processes are useful as indicators as they are flexible and tend to integrate responses across multiple species. This can be particularly beneficial when assessing large-scale ecological function, such as across the Lower River Murray. Ecological processes also have the advantages of being easier to measure, can more directly reflect the consequences of ecological change and can provide an early warning of changes in ecological character before long-lived organisms have been affected (Fairweather, 1999a, b). Ecological processes are a key component of ecological condition and function. Using ecological processes as indicators includes the interactions between the living and non-living components of an ecosystem. Using a species-based approach has the potential of missing key components that are not identified by individual species. Thus, using ecological processes allows for broad ecosystem-scale interactions to be modelled and so does not underestimate the full complexity of an ecosystem (Lester et al., 2011).

Spatial and temporal scales

The models are intended to be applied at several spatial and temporal scales, depending on the target ecological component. To effectively use the models, that scale must be specified in advance. It is likely that relevant scales will depend on the size of the flow event being considered, the ecological component being modelled and the likely lag time between the flow and any response. For example, it would be expected that phytoplankton would respond much more quickly than riparian vegetation assemblages, but links between flow and fish may be mediated through a response in vegetation, and so may involve a lag in the response of fish. Assessments involving multiple taxonomic groups (e.g. at ecosystem scales), such as the overall model presented here (Figure 4), require consideration at multiple spatial and temporal scales, and recognition of these interacting scales is needed to accurately interpret the results of the conceptual diagrams. By explicitly considering scale in advance of applying any of the models presented here plausible hypotheses can be generated and then tested. This could be done through the use of a Stommel diagram, for instance, (see Wilkinson et al., 2007 for such an application), and would allow the user to refine his/her notions of how scale may influence ecological responses to flow and floods.

Assessing ecosystem-scale responses

In assessing the responses of multiple taxonomic groups, the intention was to link multiple sets of biotic functions (e.g. survivorship) through their interspecific interactions, available habitat and food resource boxes (i.e. depending on the nature of the links among species). In doing so, we define our model as describing an ecosystem scale, because it encompasses the abiotic climatic and hydrologic components and their impact on a range of biota within the Lower River Murray, rather than limiting the assessment to one or more taxonomic groups. Using this approach, for example, flow- or flood-related impacts on vegetation, for example, are able to feed through the model to influence fish that require the vegetation for habitat, as well as those birds that may directly feed on the macrophytes, for example. Increases in piscivorous birds would affect fish populations through predation encapsulated within the interspecific interactions box. Sophisticated application of the model may include the nesting of a series of taxon-specific models within an overarching ecosystem-scale model, or multiple feedback loops within the impact section of the model (i.e. abundance, survivorship, reproduction). This would enable new and emergent properties of the ecosystem to become apparent where they may not in a single-taxon application. Thus, complex, interacting and potentially-contradictory responses should be able to
be captured by the model. The overall model shows some of these relationships where they were explicitly considered in the Murray Flow Ecology project, but many other possible links are also likely to be important, and are not yet captured in this model. For example, links involving macroinvertebrates and zooplankton are not currently represented in the models.

Model limitations

One of the major limitations of this approach is that the relationship between flow and water level in the Lower Murray is complex, due partly to the influences of the weirs. For example, it is possible to have a high river water level but zero flow. This means that, while flow is a relevant currency for management, water level often may be more significant within this system for the ecological components. This issue makes it very difficult to identify clear flow-ecology relationships in any highly-regulated river such as the Murray.

Identifying ecosystem-scale responses remains a goal of the model, but as yet additional testing is needed to ensure that it is capable of representing those links adequately. The overall model presented here is a first attempt to do that, but this has yet to be applied either by researchers, managers or other stakeholders, so the value of such a model has not yet been tested independently. In addition, linking the model to the Lower Murray Lakes and the Coorong has also not yet been attempted. The model, as it stands, is intended to describe the links between flows, floods and river ecosystems, but both flow and floods will also affect the Lower Lakes and Coorong. Other models do exist to describe these links (e.g. Lester and Fairweather, 2011), but this model should also eventually be linked to those extant downstream models (or to their replacements in time), to enable state-wide responses to be assessed simultaneously.

Other limitations, such as the lack of groundwater in the model (see above) and the need for further testing and links to other management programs (see below), are also relevant. The point was made during the stakeholder workshop that scientists need to move beyond their own specialisations and so study (or at least consider) the ecosystem as a whole, with the recognition that all components and processes will potentially be influenced by each watering decision. These models still reflect the preoccupation of science with particular species and ecological components, and so are limited in their ability to describe the response to flow more generally. However, if used in an adaptive management framework, where the model is refined through time as additional evidence is collected to inform management, these limitations can be quantified and minimised through time.

Utility of the models developed

The utility of the models developed was a key topic of conversation at the stakeholder and reference group workshops at the completion of the Murray Flood Ecology project. One of the key benefits of the models developed, from both scientific and managerial perspectives, is that they are able to compare the response of flows across various functional groups and ecological components. This enables conflicts and trade-offs to be explicitly considered and hence the optimal outcomes to be identified. It is also possible to work from the bottom of the models (i.e. the functional responses of various components of the ecosystem) up to the top in an attempt to identify how to achieve a given outcome, which would be of value when planning environmental flow releases, for example. Using the models in this manner should allow potential ‘road-blocks’ to desirable outcomes to be identified and thence avoided where possible. The form and content of the models provides a mechanism for identifying knowledge gaps, and developing and prioritising monitoring hypotheses. In particular, providing guidance to managers about what should be monitored following an environmental watering event is a valuable way in which these diagrams could be applied.
The whole-of-system approach was seen as a key benefit to the manner in which the models had been developed. This enabled any positives and negatives (from a management or stakeholder perspective) to be identified without any unjustified prioritising of some over others, as will occur following any watering event. The models were seen, therefore, as a valuable way of considering the impact of environmental watering. A key expectation arose from discussion of the models that our current knowledge gaps mean that unexpected outcomes as a result of watering are highly likely and that managers, stakeholders and the general public should expect some surprises as our knowledge develops. Identifying the key areas of uncertainty was seen as a priority.

The conceptual models were also seen as a method for communicating the complexity of the system in a simple way. The models in their present form were not seen as suitable for direct communication with the general public (nor were they intended to fulfil that role), but simple cartoon animations could show changes in ecological response to flows through time, as hypothesised by the models. These models need to be considered in the framework of other conceptual models for the Murray-Darling Basin (e.g. the CEW cause and effect diagrams; CEW, 2011), but the synthesis provided by the models presented here, and Murray Flood Ecology as a whole, illustrates the value of multidisciplinary, multi-agency research projects that makes the most of monitoring data from the past.

Further development of the model

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

Links to other management programs

The model currently does not link directly with agency approaches to model ecological responses. This was done deliberately, to ensure that the model best represented our current ecological understanding of the links between flow, flooding and the Murray ecosystem, but efforts can now be made to explicitly link the model to other approaches being used elsewhere. For example, the Commonwealth Environmental Water Holder has developed a system of classifying ecological responses to flow conditions, including ‘extreme dry’, ‘dry’, ‘median’ and ‘wet’ flow conditions (CEW, 2011). Thus, they effectively classify the flow into separate ‘scenarios’ and these could be used as the basis for further model testing and hypothesis generation relating to the impact of those flow scenarios on Lower Murray ecosystems. Managers using these models should use them as a base upon which to build, recognising, as stated above, that not all ecological knowledge for each group has been reviewed and incorporated into the models as presented.
Furthermore, once further testing has occurred, it would be prudent to develop explicit links to ecological monitoring in the region (Downes et al., 2002; Lester et al., 2011). Where hypothesised responses are developed from the model, recommendations can be made as to useful variables to monitor in order to measure responses to flow and floods, to ensure that tests of model hypotheses are realised upon subsequent flows. This monitoring may be addressed by existing programs in place through government agencies and researchers, or novel monitoring may be required, depending on the component being considered and the hypotheses generated.
References


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