

Restoration of Fish Populations in Semi-Arid Ecosystems

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GENERAL ABSTRACT

*An abundance of ecological theory highlights the importance of taking temporal and spatial scale into account when managing fish populations. However, in heavily modified riverine systems that can cross many social, economic and political boundaries, the links between scientific results and the day-to-day realities of managing for fishery and biodiversity outcomes, can be difficult. Australia is the world's driest continent, and in our largest and most productive water catchment (Murray-Darling Basin), many different interventions are occurring in an attempt to strike a balance in a system where both agricultural and environmental outcomes are prioritised. While measuring agricultural outputs is relatively easy, it is much more difficult to quantify the outcomes of river restoration on fish species that have life-history processes spanning huge spatial and temporal scales. In this thesis, I present case studies providing both lines of evidence on the success of restoration programs, and additionally outline linkages with theory that frames this evidence of success within a conceptual framework built on restoration theory. In **Chapter 1**, I outline why linking ecological concepts to management objectives is important, as it provides managers with an understanding of 'how' their intervention will lead to a tangible outcome, and this is significant in riverine systems where pressures on restoration resources are large. Next, I quantify connectivity (measured as rates and timing of fish movements) between floodplain and main-channel habitats, and describe how these are affected by differing connection regimes (**Chapter 2**). With altered flow regimes common in most large waterways in the Murray-Darling Basin, data linking rates of fish movement to hydrological change are useful when setting water-delivery schedules. Using a case study from the Ovens River, I show that re-introduction of fish is a valid conservation action (**Chapter 3**). My results show that the survival of stocked cohorts is highly variable, so that ensuring a re-introduction program that is sufficient in spatial and temporal scale to overcome a range of environmental conditions (such as changes to water quality and quantity) is necessary to be successful. I also provide the first published data of histology of the endangered trout cod (*Maccullochella macquariensis*) from a natural riverine system, necessary information for those charged with conserving this species. Demonstrating positive outcomes from restoration is necessary for investors of waterway restoration means that data reliability is essential.*

*In **Chapter 4**, I describe a field-based study of electrofishing efficiency, where I test the influence of turbidity, depth and species identity on detection rates of target species. Increasing depth, turbidity, and changes in species and size of fish, all influenced electrofishing detection probability at my study site. The major implication here is that if one does not account for imperfect detection, sampling can either fail to identify successful restoration, or over-estimate its change to the system. Using a range of data sources, and measuring population processes rather than just abundances, are ways to overcome variable efficiency over time. I measured the response of native fish species to a habitat-restoration trial by collecting data on immigration, emigration, and survival to determine how fish populations responded following a habitat restoration program in the Murray River (**Chapter 5**). I found that populations of the target species (*Maccullochella peelii*) and golden perch (*Macquaria ambigua*) increased following restoration, while staying stable in reference reaches, and that this increase was primarily driven by immigration from a nearby source population. In my general discussion, I provide several recommendations for managers and researchers that I have shown will increase the probability of successful river restoration (**Chapter 6**). In particular, by linking our knowledge of the scale of the life-history processes, in particular movement and migration, of target fish species, and investing specifically at these scales, the probability of successful restoration increases.*

STATEMENT OF ORIGINALITY

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

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Jarod Lyon

Melbourne, 24/12/2017

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Chapter 1

General Introduction

General Introduction

The increase in global human population size over the past 200 years has brought about unprecedented degradation of natural environments (Myers *et al.* 2000; Brooks *et al.* 2006; Bradshaw and Brook 2014). Riverine environments, as low points in landscapes, can be particularly susceptible to human-induced changes (Dudgeon *et al.* 2006; Vörösmarty *et al.* 2010). In addition to changes in form and function (induced by a range of interventions, such as the construction of dams and levees, or the removal of instream habitats), rivers are also impacted by changes in surrounding catchments, both locally or in upstream or downstream sections. Such change includes reduced water quality, changed water quantity, or introduction of barriers to ecological connectivity (Wohl *et al.* 2005; Collen *et al.* 2014), and increased demands for the range of ecosystem services provided by rivers. The environmental, economic, and social/cultural value of rivers is large, with rivers now supporting extensive agriculture, natural purification of water, biodiverse ecosystems, and recreational pursuits (Loomis *et al.* 2000; Vörösmarty *et al.* 2010).

Aside from Antarctica, Australia is the world's driest continent, and this scarcity of run-off means that its river systems are possibly even more important for people and biodiversity than they are in areas where water is abundant (Davis *et al.* 2013). The Australian climate is characterised by intense extremes — from long periods of drought to large floods (Letnic and Dickman 2006) — and this 'boom and bust' aspect of the landscape has ultimately sculpted a biota that is both adapted to respond quickly to changes in available resources, and robust enough to survive in a patchy, resource-poor environment when resources become scarce (Bradshaw and Ehrlich 2015). Like the rest of the world, Australia's river systems have become heavily degraded as a result of anthropogenic impacts from mining, intensive agriculture, and water-resource management (Bunn *et al.* 1999; Arthington *et al.* 2006).

One of the most important regions in Australia in terms of agricultural production and ecological value is the Murray-Darling Basin. The Murray-Darling Basin has a catchment area of 1.07 million km² — about the same size as France and Germany combined (Walker 1992). The Murray River, the main southern tributary, drains 300,000 km² before its confluence with the Darling River at

Wentworth. It rises at 1430 m in the south of the Murray-Darling Basin and receives run-off from the western and northern sides of the Great Dividing Range. However, most of its run-off comes from < 5% of this area in the upland regions (Figure 1). Flowing west, the Murray River drains increasingly warmer and drier regions, and evaporation generally exceeds precipitation downstream from Albury such that the river receives no appreciable run-off after the first 500 km of its full 2600-km length (Walker 1992). Flow is highly regulated, with large impoundments on the Murray River and its tributaries (Walker 1992). Although some variability remains (minimum flow is 25% of mean, maximum is > 200% of mean), irrigation requirements of the impounded reaches lead to the natural seasonal pattern becoming largely reversed, with peak flows now in summer and lowest flows in winter (Rutherford 1991). The Murray-Darling Basin has relatively few species of freshwater fishes (Lintermans 2007) compared to those on other continents, and ultimately, an endemic fish community that has evolved only 46 fish species for the entire catchment (compared with the Amazon basin where 5600 extant endemic fish species have evolved (Albert and Reis 2011)).

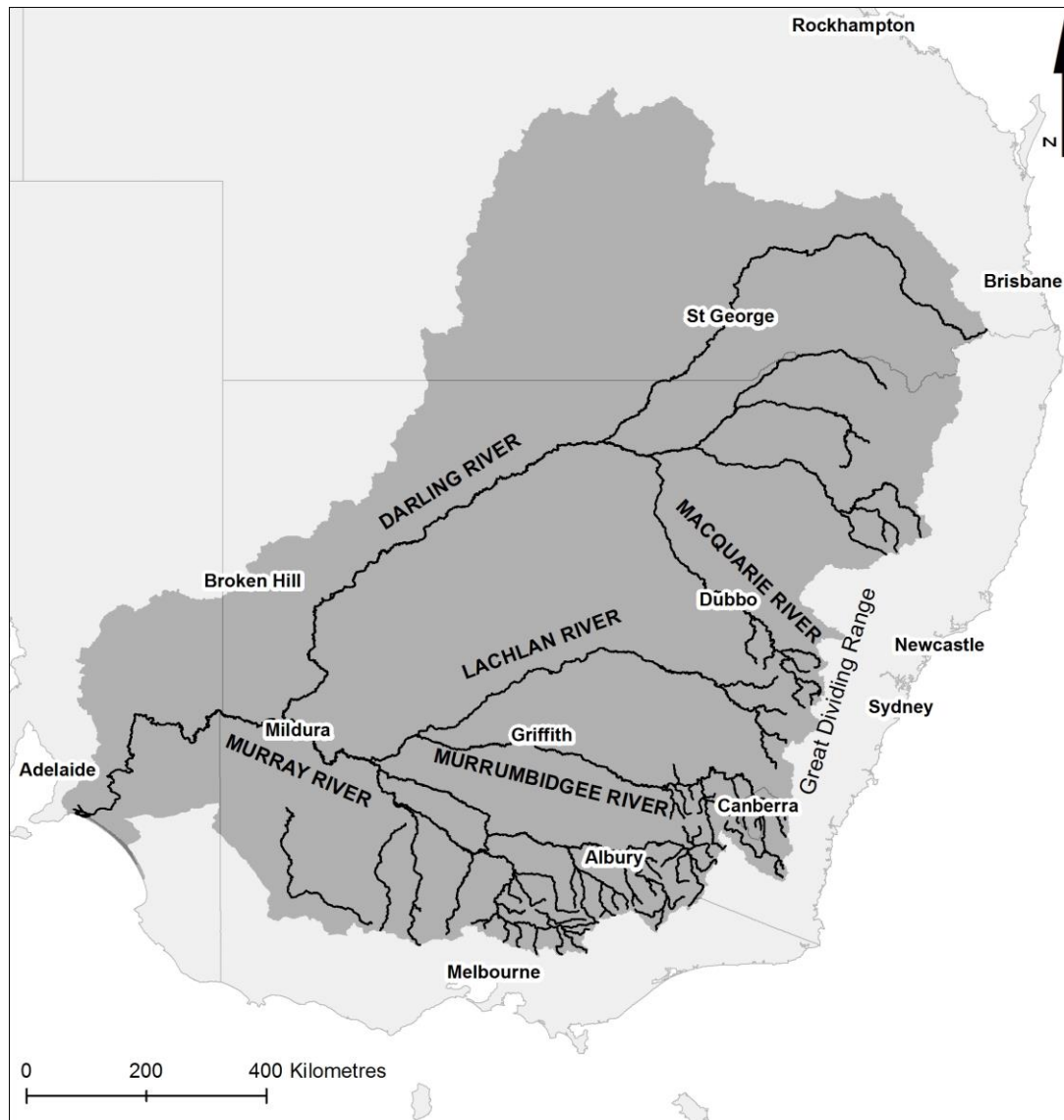


Figure 1. The Murray Darling Basin

For fishes inhabiting the Murray-Darling Basin, impacts of river degradation, such as altered flow regimes (including unseasonal wetting and drying cycles), barriers to migration, thermal pollution from stratified dams, exotic fishes, loss of instream habitat, loss of flow variability, and decreases in primary productivity are all well-documented (Murray-Darling Basin Commission 2004). In many areas throughout the Murray-Darling Basin, fish stocks are now estimated to be at 5-10% of their pre-European abundance (Murray-Darling Basin Commission 2004). Indeed, in many of the larger Murray-Darling Basin rivers, combinations of these stressors have impeded actions to increase native fish populations (Murray-Darling Basin Commission 2004). As a consequence, over half of the

46 native freshwater fish species within the Murray-Darling Basin are considered threatened (Lintermans 2007). These include several large-bodied, culturally important, long-lived species such as trout cod (*Maccullochella macquariensis*) and Murray cod (*M. peelii*).

River Restoration

Restoring rivers and catchments to provide ‘natural’ ecosystem function costs billions of dollars per annum globally (Pelley 2000; Bernhardt *et al.* 2005). The overarching goal of such investments is to provide healthy catchments and waterways that deliver ecosystem services (such as the provision of clean water for drinking and agriculture) vital to human society (Naiman 2013). The methods and techniques used in river restoration are varied, and depend on the target outcome chosen for restoration, and the ‘guiding vision’ of the local community of river stakeholders (*sensu* Palmer *et al.* 2005). Most often, river rehabilitation is done to re-establish lost or diminished components of natural ecosystem functions (Loomis *et al.* 2000), such as the regeneration of catchment and riparian vegetation, restoring water for the environment or floods to maintain floodplain processes, rebuilding meanders in channelised systems, restoring habitat heterogeneity, stocking threatened species, removing redundant instream structures, and providing fish passage past instream barriers (Roni *et al.* 2002; Bernhardt *et al.* 2005). Of course, many factors can influence the effectiveness of restoration attempts, including the amount of degradation that has already occurred, the other threats impeding recovery, the size of the system to rehabilitate, and the current and future operational needs of the system for irrigation or water supply (Palmer *et al.* 2005).

Palmer *et al.* (2005) suggested five criteria for measuring ecological success of restoration projects that provide a ‘common sense’ approach for researchers and managers: (i) projects should be done with a clear guiding image for the restored river reach, based on input from managers, scientists, and community stakeholders; (ii) the river’s ecological condition should be assessed to confirm a measurable improvement; (iii) the scale, type and longevity of the interventions should allow restored habitats to become increasingly self-sustaining and resilient to external perturbations; (iv) during implementation phases, no lasting harm should be inflicted on the ecosystem, and importantly; (v) pre- and post-restoration assessments should be completed. Under this framework, and by setting

explicit timeframes and developing conceptual models to show the ecological mechanisms for restoration (Jansson *et al.* 2005), researchers and managers can more succinctly understand the ecological processes being altered during restoration. While other valid strategies and approaches for measuring the success of restoration have been proposed and occasionally evaluated (see Woolsey *et al.* 2007; Roni *et al.* 2008; Beechie *et al.* 2010; Golet *et al.* 2013), the concepts outlined by Palmer and colleagues can be easily applied to most common types of restoration. In particular, given that degradation has mostly occurred over decades or centuries, setting restoration targets within such a historical context is important, and recognises that restoration will also take a long-term commitment (Murray-Darling Basin Commission 2004; Fryirs *et al.* 2008; Kondolf *et al.* 2008; Winter *et al.* 2009; Pittock and Finlayson 2011).

Importance of fish populations

Rivers often sustain subsistence, commercial, or recreational fisheries that can be of cultural or economic importance (Bernhardt *et al.* 2005). Because of human impacts and habitat degradation, many fish species have become threatened with extinction, or their populations have declined substantially (Collares-Pereira and Cowx 2004). Many types of restoration and threat abatement are being done globally in an attempt to halt and reverse these declines, including restoring fish passages, removing pests, re-stocking, revising fishing regulations, restoring habitat, and changing land-management practices.

Fish are frequently targeted as the principal beneficiaries of stream restoration works for two reasons: (1) as higher-order predators within most freshwater systems, they are useful indicators of ecological processes at lower trophic levels (Cabana and Rasmussen 1994); (2) many fish species are valued highly by society (Feather *et al.* 1999), and are often a major way in which humans interact with, and benefit from, waterways. However, the cryptic nature of many fishes means that there are inherent difficulties in measuring a response to restoration at a population scale given that some species are projected to recover over time frames that vastly exceed the period of typical restoration projects (e.g., several decades; Trexler 1995), and hence the success of many river restoration programs that have fish populations as a key indicator is often uncertain (see Collier 2017).

Indeed, the global track record in measuring the success of large-river restoration programs is still poor regardless of the taxon of interest (Palmer *et al.* 2005; Collier 2017). Long-term monitoring data of restoration projects are scarce (Bernhardt *et al.* 2005), and adequate funding is scant. Additionally, measuring the responses often includes only one metric (i.e., diversity of vegetation community), and ignores other aspects of population-level responses that might more meaningfully enable managers to determine cause-and-effect relationships (i.e., redistribution of individuals, changes in mortality rates, and changes in recruitment). In addition, natural systems are highly variable, and changes can arise in response to many different drivers; this means that the ability to disentangle responses due to management interventions — from either natural fluctuations or other causes — is necessarily challenging (Holling 1973; Wood 2010). Finally, natural systems can take many years to respond to change — particularly when the restoration occurs only at local (i.e., site) scales, while the life-history processes of the taxa of interest might be distributed over a much greater range. As such, monitoring the responses to restoration to determine their effectiveness for biological outcomes continues to be emphasised (Palmer *et al.* 2005; Lake *et al.* 2007; Höckendorff *et al.* 2017).

Increasing management effectiveness for fish restoration in lowland rivers

Given that managing and restoring damaged ecological communities is strongly linked to our knowledge of the biological effects of restoration (Lake 2001; Palmer *et al.* 2005), it seems clear that monitoring the ecological responses to planned restoration is essential for developing this knowledge (Palmer *et al.* 2005; Downs *et al.* 2011). In riverine ecosystems, monitoring fish populations is widely used to track river health (Cowx and Gerdeaux 2004; Woolsey *et al.* 2007), and such monitoring data are regularly used to measure how management interventions, such as stock enhancement, providing water for the environment, or improving habitat, influence the ecology of waterways. River restoration programmes around the world such as the AU\$500 million Living Murray program in Australia (mdba.gov.au/programs/tlm), or the US\$7.8 billion Kissimmee River Restoration Project in Florida, USA (Koebel 1995), use fish-monitoring data to assess ecological health. Increased emphasis on improving river catchments and fish populations over the past two decades (Lake *et al.* 2007; Whiteway *et al.* 2010) means that such large investments come with the requirement for extensive

monitoring. However, given the scale of the investment in environmental improvement, there is surprisingly little information with which to test the reliability and accuracy of fishery-assessment methods, or indeed, the outcomes of fishery-improvement measures themselves.

Thesis objectives and structure

The Murray-Darling Basin is important for Australia culturally and economically and water from the system is used extensively for agricultural irrigation. Restoration is necessary; and recovering fish populations provides a stimulus for restoration; however, improvement is impossible when interventions are poorly monitored and validated. My thesis provides evidence that restoration activities are succeeding, and provides a series of recommendations for managers that can be used by practitioners to improve the river restoration agenda.

I present here a thesis structured around two themes: *(i)* understanding which factors negatively impact fish populations, and *(ii)* examining how management interventions interact with the drivers of variation in fish population size. This approach recognises that while there is uncertainty in the predicted impacts of any intervention on target outputs, we can test assumptions that can be translated into clearly articulated hypotheses and become the subject of targeted investigation.

My over-arching aim with this thesis is to generate data that add to the literature of restoration of fish populations, but also provide recommendations that inform interventions such as the delivery of water for the environment, the re-introduction of fishes for conservation objectives, and restoring instream habitat heterogeneity to boost fish biomass. My studies ‘close the loop’ on several knowledge gaps related to the success of management interventions, allowing researchers and managers to deliver interventions greater certainty of desired outcomes. In particular, the research I present here aligns with recommendations under the Murray-Darling Basin Authority’s Native Fish Strategy (Murray-Darling Basin Commission 2004). This strategy is a collaborative approach to progress restoration for fish, and developed hypotheses (outlined below) align with the objectives of this strategy. Figure 2 provides a broad structure to demonstrate the alignment of my work with key drivers and processes of interest to river and fishery managers.

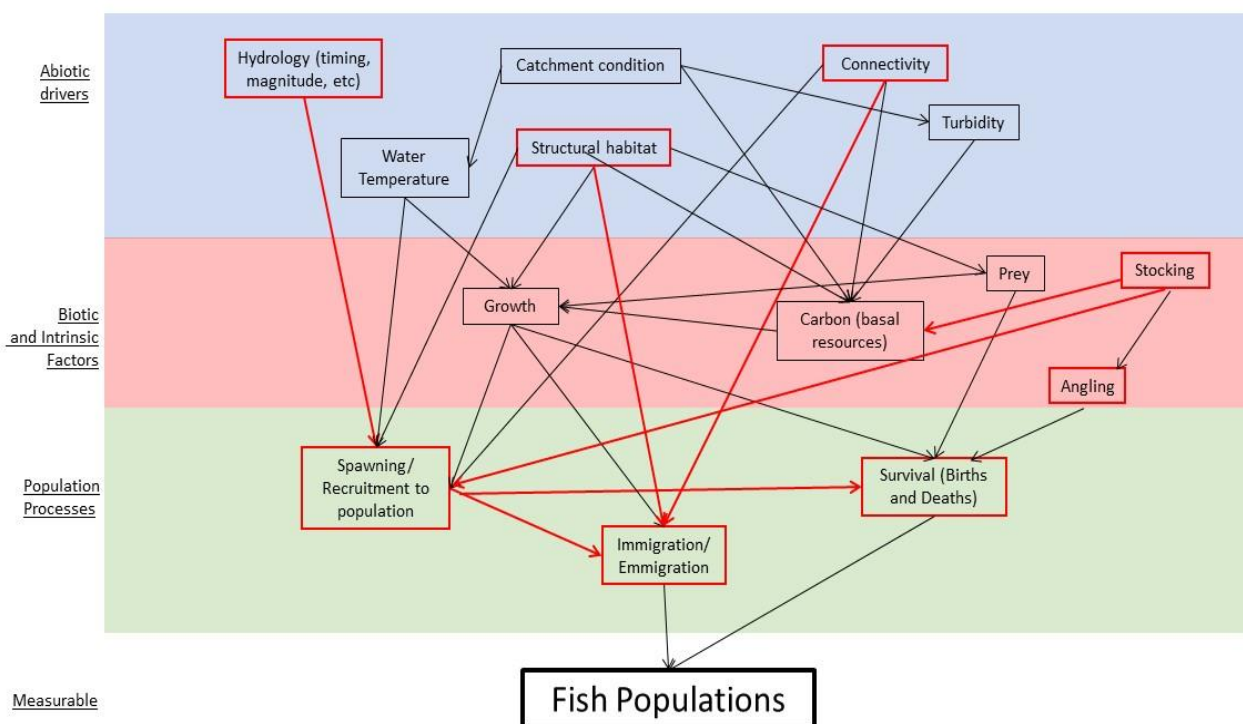


Figure 2. Model outlining the principal drivers and important processes considered in this thesis influencing fish populations for freshwater ecosystem management in the Murray-Darling Basin. Red shading indicates processes I examined here. ‘Abiotic drivers’ as listed (hydrology, water temperature, catchment condition, structural habitat, connectivity, turbidity) are elements of freshwater ecosystems that river managers can use to form a basis of an understanding of how restoration interventions can be used to alter fish populations, and ‘Biotic/Intrinsic factors’ (growth, carbon, prey, stocking and angling) describe elements important to fish population processes at the scale measured here. ‘Population processes’ are the demographic processes leading to a change in the target organism population size. Further information can be found in the chapter outline, below.

Data chapters (2 to 5) are either published or submitted for publication and are presented in the form of either the published paper (chapters 2-4) or the submitted format with tables and figures interspaced throughout the text (Chapter 5). All data chapters are co-authored, with acknowledgement made at the start of each chapter. All tables and figures are embedded within the text and the numbering of figures and tables begins at one for each chapter. However, all chapters are tied to the overarching aim of my PhD research, and I present them as a cohesive flow of work reflecting my research philosophies as they have developed in the General Discussion (Chapter 6).

The structure of my thesis is as follows:

Chapter 1: General Introduction:

Introduces the rationale for the thesis, and describes the outline.

Chapter 2: River floodplain interactions

Measured drivers and processes — hydrology, immigration and emigration, connectivity: In this Chapter, I examine the interactions between the main river channel and off-channel habitat areas in a regulated reach of the Murray River. River and floodplain regulation in the Murray Darling Basin has decreased connectivity between floodplain wetlands and main-stem rivers. While off-channel habitats are important for increasing survival, feeding, and reproduction opportunities of fish populations because of increased habitat diversity offered by floodplains, there is a paucity of information about the drivers of population fluctuations in these systems, and in particular how they interact with populations in main channel habitats. My aims were to investigate the cues that stimulated fish movement to and from off-channel habitats. I hypothesised that (1) river water levels influence the abundance and community composition of small-bodied native and non-native fish moving between the main river and off-channel habitats, and that (2) more fish would move at night rather than day to avoid predation.

Chapter 3: Recovery of a critically endangered species

Measured drivers and processes: survival, stocking: This case study unpacks the recovery program of the Critically Endangered trout cod *Maccullochella macquariensis* within the Ovens River, Victoria, with particular reference to the use of stocking as a management intervention. I demonstrate that a well-planned and implemented stocking program was necessary to re-establish an endangered fish population in a large, lowland river. In this chapter, I assessed the success of this stocking regime to test the following hypotheses: (1) that the duration of this stocking program (10 years) was important for its ultimate success (i.e., the establishment of a naturally reproducing population) by allowing for the likely annual mortality of some stocked cohorts; (2) the growth and reproductive output of

hatchery fish did not differ from those of wild-bred individuals (measured by chemical marking of hatchery fish before release); (3) that genetic diversity (as measured by the number of alleles) in a stocked population was less than in a natural population because of inbreeding and the founder effect.

Chapter 4: Sampling efficiency and parameter certainty

Measured drivers and processes: hydrology, immigration and emigration, connectivity: Deciphering trends in datasets depends on our understanding of how sampling methods modify results. In this chapter, I examined the relationships between environmental covariates and sampling efficiency for boat-mounted electrofishing. I hypothesised that capture probability would be influenced by factors including species, fish size, and environmental variables. The data supported this hypothesis, and demonstrated that all of these variables — and in particular species, water depth, and turbidity — had large impacts on capture probability.

Chapter 5: Population dynamics in response to intervention

Measured drivers and processes: hydrology, immigration and emigration, connectivity, survival, recruitment to population, angling: In this chapter I focused on the response of two target fish species to a management intervention (re-introduction of large woody habitat to a degraded river reach). In particular, I estimated movement, growth, capture and survival across different spatial and temporal scales, hypothesising that the restoration of structural woody habitat at a reach scale (> 100 km) in a large, lowland river results in a net increase in population size for two target species of native fishes, rather than merely attracting fishes already present in areas adjacent to restored habitat.

Chapter 6: General Discussion

The general discussion provides a summary of the findings of the four data chapters, and in particular details how these findings contribute to both the scientific pool of knowledge on this topic, but also how the findings are being used to inform management. The general discussion provides a summary of each data chapter, and outlines the importance of robust data to inform restoration of structural habitat, allow connectivity, and improve population vital rates of fish populations during restoration programs

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Chapter 2

The effect of water level on lateral movements of fish between river and off-channel habitats and implications for management

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Overall percentage (%)	90%			
Certification:	This paper reports on original research I conducted during the period of my Higher Degree by Research candidature and is not subject to any obligations or contractual agreements with a third party that would constrain its inclusion in this thesis. I am the primary author of this paper.			
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By signing the Statement of Authorship, each author certifies that:

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Contribution to the Paper	Collected data, entered some data, helped edit manuscript		
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The effect of water level on lateral movements of fish between river and off-channel habitats and implications for management

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Abstract. Off-channel habitats, such as wetlands and backwaters, are important for the productivity of river systems and for many species of native fish. This study aimed to investigate the fish community, timing and cues that stimulated movement to and from off-channel habitats in the highly regulated Lake Hume to Lake Mulwala reach of the Murray River, south-eastern Australia. In 2004–05, 193 712 fish were collected moving bi-directionally between a 50-km section of the Murray River and several off-channel habitats. Lateral fish movements approximated water level fluctuations. Generally as water levels rose, fish left the main river channel and moved into newly flooded off-channel habitats; there was bi-directional movement as water levels peaked; on falling levels fish moved back to the permanent riverine habitats. Fish previously classified as 'wetland specialists', such as carp gudgeons (*Hypseleotris* spp.), have a more flexible movement and life-history strategy including riverine habitation. The high degree of lateral movement indicates the importance of habitat connectivity for the small-bodied fish community. Wetlands adjacent to the Murray River are becoming increasingly regulated by small weirs and ensuring lateral fish movement will be important in maintaining riverine-wetland biodiversity.

Additional keywords: Australia, carp gudgeon, floodplain, Murray River.

Introduction

The regulation of rivers and their floodplains by dams and weirs has caused major changes in freshwater systems around the world (Walker *et al.* 1978; Nicola *et al.* 1996; Williams 1998). These impacts include altered flow regimes (including unseasonal flooding and drying cycles), barriers to fish migration, thermal pollution, proliferation of invasive species, loss of in-stream habitat, loss of flow variability and decreases in primary productivity (Ricciardi and Rasmussen 1998; Nicol *et al.* 2004; Sherman *et al.* 2007). Over the past 20 years in Australia, there has been a shift away from studying the effect of in-stream barriers towards management and on-ground restoration techniques that may help ameliorate the problems. With most of continental Australia, in particular the south-east region, still subjected to the longest drought on record (2001–2010), rivers and their biota are showing signs of increasing stress (Bond *et al.* 2008). Consequently, river restoration is firmly entrenched on the social and political agenda with several major environmental rehabilitation initiatives underway.

For fish, many of the restoration programs concentrate on the main river channel (e.g. new fishways, re-introduction of large woody debris; Nicol *et al.* 2004; Barrett and Mallen-Cooper

2006). Off-channel habitats are, however, also important for fish populations because of the increased habitat diversity offered by floodplains, with heightened survival, feeding and reproduction opportunities (Junk *et al.* 1989; Zeug and Winemiller 2008). Improving lateral connectivity is also important for fish populations as floodplains provide feeding and nursery zones (Copp 1997; Castello 2008), and fish community structure, functioning and subsequent fishery production can relate to river–floodplain connectivity (Junk *et al.* 1989).

To date, in temperate Australia, the movements of small-bodied (<100 mm long) fish species between the main river channel and off-channel habitats, such as shallow wetlands, has received relatively little attention. The terminology used in some of the management literature describes small-bodied fish as 'wetland specialists' or 'generalists', whereas some large-bodied fish are 'main channel specialists' based on their early life-history (McCarthy *et al.* 2006). However, it is likely that many small-bodied fish regularly move between off-channel habitats and the main river channel, and small-bodied fish can numerically dominate floodplain and riverine fish communities. The degree to which fish move between these separate habitats is of particular importance in managed river systems where water-saving

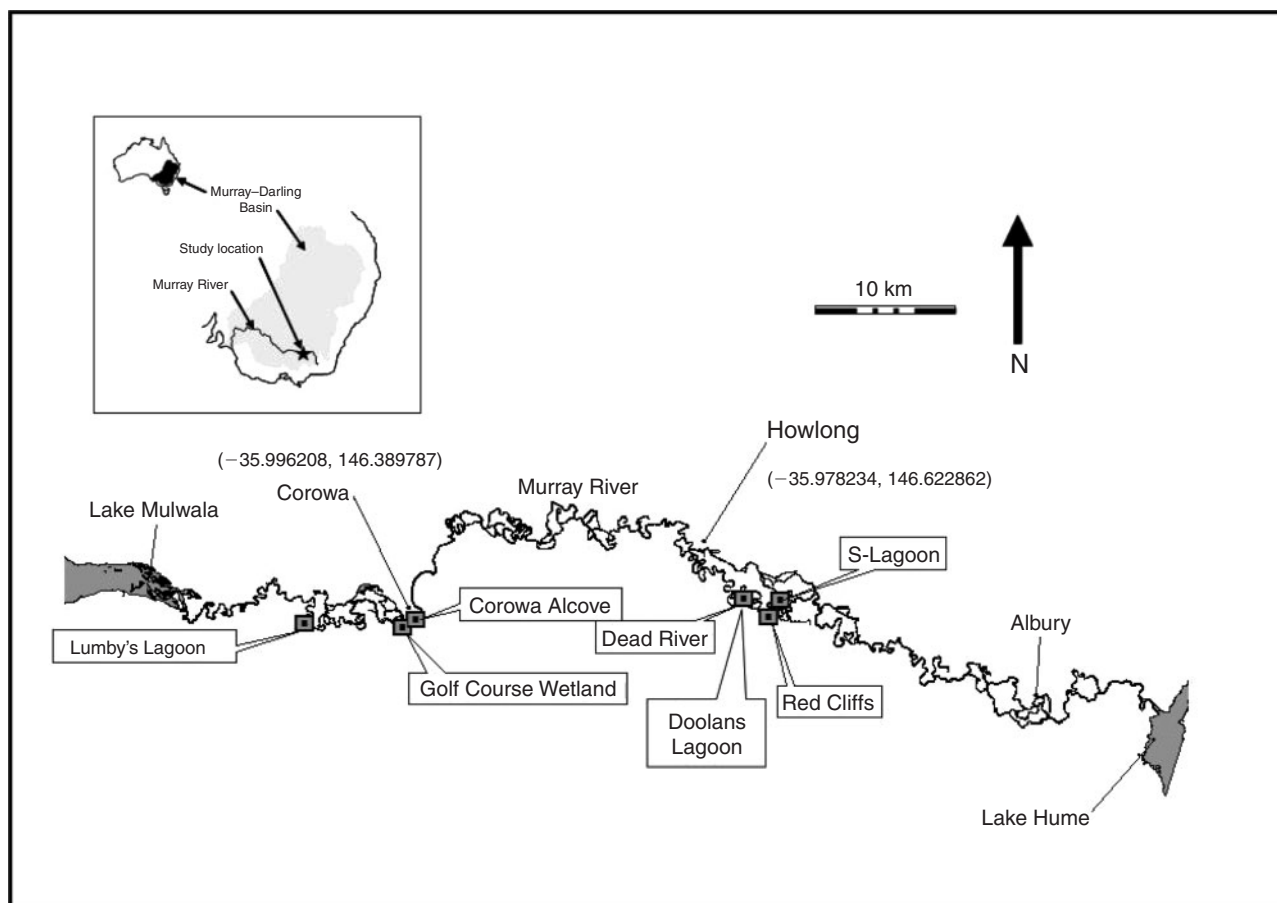


Fig. 1. Study area between Lake Hume and Lake Mulwala, in south-eastern Australia.

initiatives can involve construction of wetland regulators that may impede fish movements (Jungwirth 1998; Jones and Stuart 2008).

The aims of this study were to investigate the river water level cues that stimulated fish movement to and from off-channel habitats. We hypothesised that river water levels influence the abundance and community composition of small-bodied native and non-native fish moving between the main river and off-channel habitats. We also predicted more fish to move at night rather than day to avoid predation.

Materials and methods

Study area

The study area was in south-eastern Australia, on the upper Murray River between Lake Hume and Lake Mulwala (150 river-km). This reach is one of the most highly degraded sections of the entire 2200-km long Murray River due to the large amounts of irrigation water delivered between the two anthropogenic storage lakes. Hence, the Murray River between Lake Hume and Lake Mulwala essentially acts as a major irrigation conduit for water between August and April each year, and as such, has an inverted flow regime (high in summer, low in winter), which provides unseasonal connections between the river and its floodplain. With an annual irrigation release, the highly regulated reach

of Murray River examined in the present study provides annual opportunities for fish to access adjacent anabranches, billabongs and other floodplain habitats.

A total of seven sites were sampled with four of the study sites (Dead River, Doolans Lagoon, Red Cliffs and S-lagoon) in the vicinity of the township of Howlong (35°58'36.123 S, 146°37'26.836 E). The remaining three sites (Lumbys Lagoon, Golf Course Wetland and Corowa Alcove) were near the township of Corowa (35°59'40.847 S, 146°23'27.780 E) (Fig. 1) ~30 river-km downstream. All sites had a direct association either with the Murray River or a major anabranch via a connecting channel.

Each site was chosen to represent the off-channel habitats in the study area (usually backwaters or wetlands) and were predominately shallow (<1.0 m depth) or occasionally deep (up to 2.4 m depth), productive wetlands and differ from main river habitats with their relatively shallow well-vegetated margins and slightly warmer and more turbid waters. The substrate of the wetlands was dominated by clay and sand. The type of off-channel habitat (backwater or wetland) and their relative importance as fish habitat was not specifically compared. The wetland-river connections were usually narrow (1–2 m wide) channels that commenced to flow following an increase in river level.

The Murray River in the study area is ~100 m wide and up to 5 m deep with a highly regulated discharge regime from the

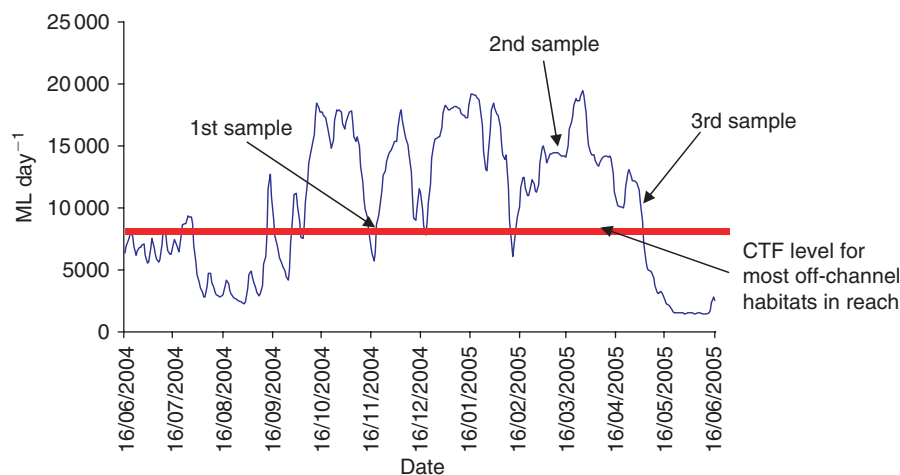


Fig. 2. River discharge (ML day^{-1}) for 2004–05 showing sampling occasions and the commence to flow (CTF) level.

deepwater outlets on Hume Dam (3.06 GL), ~ 60 km upstream (Fig. 1). The average daily flows in this river reach can fluctuate between 1400 and 27 000 ML day^{-1} depending largely on the needs of downstream irrigators. The irrigation season runs primarily between August and May, which leads to high summer discharges and depressed winter discharges. This variability in river discharge causes the adjacent wetlands to connect and disconnect multiple times within an average irrigation season. There is also considerable thermal pollution in this reach with the water temperature depressed by 1–5°C in spring and summer (September to March; Sherman *et al.* 2007).

Sampling

Sampling was undertaken between November 2004 and May 2005 to encompass a variety of water level conditions (Fig. 2). Each site was sampled during three different water levels to establish the use of each off-channel habitat by resident fishes and to determine any emigration/immigration. Due to the high variation (depending on irrigation requirements) in river flows in the study reach (between Lake Hume and Lake Mulwala), not all water level types were surveyed at all sites. The three surveyed water level types were: (i) rising water level (beginning of irrigation season and thereafter opportunistically); (ii) high water level (during irrigation season, water steady, i.e. neither rising or falling); and (iii) falling water level (end of irrigation season and opportunistically). These water levels were considered a surrogate for river discharge (ML day^{-1}) and other inherent change in river conditions (e.g. water velocity).

Our assumption during sampling was that fish collected during the three sampling periods (rising, high and falling) were representative of those instantaneous river conditions and not those immediately antecedent. For example, in this heavily regulated river reach, water levels could fall between ‘rising’ and ‘high’ sampling events but fish collected were still assumed to reflect the capture conditions of the day. Our observations of fish led us to believe that these assumptions were appropriate as fish abundance appeared to quickly respond to new flow conditions. In addition, we did not assume that fish collected moving into the wetland during a rising flow were the same ones that moved out

during a falling flow. River flows also provide artificial access for fish to floodplains, hence our observations might represent adaptations to local regulated conditions rather than natural seasonal patterns or movement behaviours in other parts of the Murray River.

Two sets of double-wing fyke nets were set within the river–wetland connection of each off-channel habitat, facing bi-directionally, to catch fish moving in and out of the off-channel habitats. Large-mesh fyke nets (20-mm stretched mesh) were placed on the outsides (both river and wetland sides), with fine-mesh fyke nets (0.5-mm stretched mesh) on the insides (Fig. 3). The large-mesh nets were set to catch large-bodied fish, while smaller species passed through these and were captured in the fine-mesh nets, thus the nets might collect the majority of fish sizes and species. Nets were checked as close as possible to dawn and dusk at each site to give an indication of diurnal patterns (Balcombe and Closs 2004; Baumgartner *et al.* 2008). Each site was sampled for 3–4 days (i.e. six to eight net checks) at each water level type.

All fish collected were individually weighed (nearest g) and measured (nearest mm) (fork length (FL) or total length (TL) depending on tail morphology), and were released well outside the net fleet in the direction they were originally going. In the case of large catches of small-bodied fish, a random sub-sample of 50 individuals of each species was weighed and measured individually, after which the remainder was weighed in bulk (by species). Some catches were so large that weighing the fish in bulk by species was not possible (i.e. more than 4000 fish) – in these cases a random sub-sample (100 fish) of the catch was taken to determine species composition (including weights and lengths of each individual in the sub-sample). The remainder of the sample was then weighed in bulk.

Statistical analyses

To test our two hypotheses, the effect of water level type (three levels – rising, high, falling), direction (two levels – moving into the off-channel habitats, moving out of the off-channel habitats) and time (two levels – day, night) on the number (count) of fish

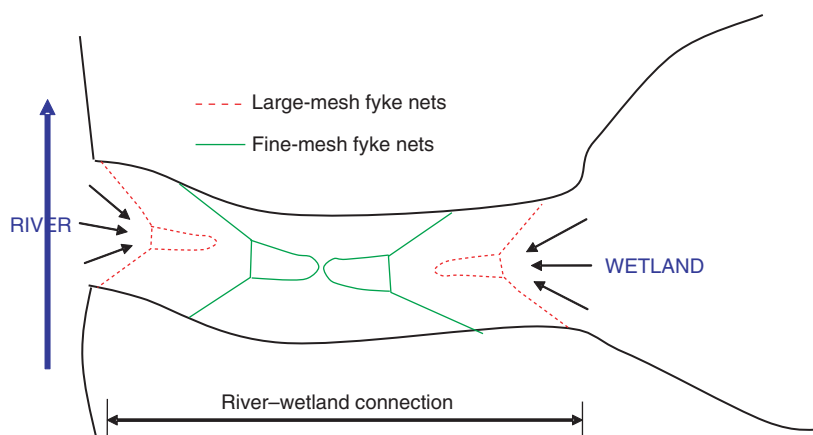


Fig. 3. Fyke net configuration as set in the channels between the Murray River and the off-channel habitat.

caught at a particular site were analysed using Poisson regression. The sampling effort at each site (amount of time each net was set) was fitted in the model as an offset, after taking natural logs. An offset is a term added to the model, with a known rather than an estimated coefficient. Including the sampling effort as an offset means that predictions from the model are equivalent to catch per unit effort (CPUE). An over-dispersion parameter was also included in the models to account for extra Poisson variation. We were not interested in differences in the mean responses among sites *per se*; rather, we were interested in inferences across all sites. Hence, site was fitted as a random effect in the model by fitting a random intercept for each site with the fixed effects being water level type, direction and time. All models were fitted in the software package R ver. 2.7.0 (R Development Core Team 2007) using the package lme4 (ver. 0.99875–9) (Bates 2007).

We fitted 10 models to the fish catch data with each model specifying a different combination of terms for the fixed effects. The most complex model included all main effects and interactions including the three-way interaction. The relative support for each of these models was assessed by calculating Akaike's Information Criterion (AIC), corrected for small sample size and over-dispersion (QAIC_c) (Burnham and Anderson 1998). QAIC_c values were rescaled as differences between the model and the model with the lowest QAIC_c value (Δ QAIC_c). For the model with the most support, credible intervals were calculated by sampling from the posterior distribution of the parameters of the fitted model using Markov Chain Monte Carlo (MCMC) sampling (Gelman and Hill 2006). The 95% credible intervals were calculated from the posterior distribution containing 10 000 samples, after discarding a burn-in of 1000 samples.

Results

A total of 193 712 fish from 13 species were captured during the sampling period. The dominant species were carp gudgeons (*Hypseleotris* spp. (90.7%)), with 175 654 individuals collected (Table 1). In general, more fish were captured moving in and out of shallow wetlands than were caught moving in and out of backwaters or the deep wetland surveyed. The greatest abundance of fish were collected from one of the shallow wetlands, Lumbys Lagoon, with 54 027 native fish and 1221 non-native fish captured (Table 1). Sites at Doolans Lagoon and Dead River

also revealed large numbers of fish with more than 35 000 native fish captured at each site, including eight large-bodied golden perch (*Macquaria ambigua*) at each. At Corowa Alcove, 29 258 native fish were captured over the sampling period, while at Red Cliffs only 1034 native fish were captured. However, Red Cliffs was only sampled on a rising water level.

Total catch model

To test the first hypothesis that river height influences the abundance index (CPUE) of small-bodied native and non-native fish moving between the main river and off-channel habitats, models were fitted to the total catch and also separately to catches of the three most abundant species, carp gudgeons, Australian smelt (*Retropinna semoni*) and Eastern Gambusia (*Gambusia holbrooki*). The other fish species had insufficient data for estimation. For the total catch, model selection indicated that the model including all possible interactions between water level type, direction and time had much higher support than any other model, with a difference in QAIC_c of 35.7 with the next best model (Table 2). Differences in QAIC_c of more than 10 indicate almost no support for the next best model (Burnham and Anderson 1998). Hence, this model indicated that the total CPUE differed depending on the direction (moving in or moving out of the off-channel habitats). However, the number of fish caught going in each direction was, in turn, dependent on river height (rising, steady, falling) and time (day or night) and our original hypothesis was supported.

Our second hypothesis that more fish move between the main river and off-channel habitats at night than at day, was not supported, because the highest CPUE occurred during the day compared with night. When the water level type was rising or steady, a higher CPUE was recorded for fish moving into the off-channel habitats compared with the CPUE for fish moving out. Conversely, when the water level type was falling, a higher CPUE was recorded for fish moving out of the off-channel habitats compared with fish moving in (Fig. 4).

Species models

For models fitted to the three fish species with sufficient data, model selection indicated that only the main effects of water level

Table 1. Fish species, numbers and catch per unit effort (CPUE) of fish moving in and out of off-channel habitats sampled alongside Murray River, south-eastern Australia, in 2004–05

Direction	Diurnal	Netting time (min)	Total CPUE (fish min ⁻¹)	River level	Native species										Non-native species					Total				
					Australian Smelt	Carp gudgeon	Unspecked hardyhead	Flat-headed gudgeon	Golden perch	Murray cod	Murray jollytail	River blackfish	Carp	Goldfish	Gambusia	Redfin perch	Oriental loach							
In	Day	384.00	17.69	Rising	52	6645	14	64	0	0	0	0	0	0	0	0	0	0	13	0	0	0	0	6794
In	Night	1038.75	21.39	Rising	1289	19615	742	154	4	1	2	0	0	0	0	0	0	0	12	277	17	0	0	22215
Out	Day	348.00	20.48	Rising	5683	1414	5	10	1	0	0	0	0	0	0	0	0	2	0	0	0	0	0	7127
Out	Night	1050.00	1.20	Rising	67	1012	3	31	0	0	2	0	0	0	0	0	0	0	0	48	6	0	0	1260
In	Day	392.86	56.14	Steady	137	20979	289	9	0	0	0	0	0	0	0	0	0	1	626	11	1	0	0	22053
In	Night	926.94	33.33	Steady	285	29829	470	75	14	0	0	2	0	0	0	0	0	16	138	58	1	0	0	30890
Out	Day	388.46	23.81	Steady	87	7738	26	2	0	0	0	0	0	0	0	0	0	0	1394	3	0	0	0	9250
Out	Night	839.12	33.90	Steady	337	27056	590	200	11	0	0	0	0	0	0	0	0	14	216	12	3	0	0	28444
In	Day	551.25	10.89	Falling	15	5542	0	3	0	0	0	0	0	0	0	0	0	1	437	3	0	0	0	6001
In	Night	1048.58	18.45	Falling	17	18933	0	104	0	0	0	0	0	0	0	0	0	34	260	0	0	0	0	19348
Out	Day	551.26	51.84	Falling	0	27820	0	41	0	0	0	0	0	0	0	0	0	22	696	0	0	0	0	28579
Out	Night	1048.58	11.21	Falling	1	9071	0	183	0	0	0	0	0	0	0	0	0	35	2442	6	1	0	0	11751
				Total	7970	175654	2139	876	30	1	4	2	2	2	218	125	6223	443	29	29	29	29	29	193714

Table 2. Results of the model selection procedure for 10 models fitted to the total catch of fish in off-channel habitats comparing movement direction, river level type and time and their interactions

Models including two- and three-way interactions also include all terms for the main effects. The 'constant' model contains a term for the overall grand mean only. QAIC_c, Akaike's Information Criterion corrected for small sample size and over-dispersion; Npar, number of parameters; Δ QAIC_c, difference in QAIC_c between the model with the lowest QAIC_c and all other models

Model ^A	QAIC _c	Npar	Δ QAIC _c
Three-way interaction	3303.7	14	0
Direction	3339.4	4	35.7
Constant	3412.4	3	108.7
Water level	3425.2	5	121.5
All two-way interactions	3598.4	12	294.7
Main effects + direction × water level	3606.2	9	302.4
Main effects + time × water level	3743.0	9	439.3
Direction + time + water level	3752.9	7	449.2
Main effects + direction × time	3834.0	8	530.3
Time	3853.7	4	549.9

^ATerms included in the model are as outlined in the section 'Statistical analysis'.

type, direction and time had the most support for both *R. semoni* and *G. holbrooki* (ΔQAIC_c of 25.1 and 47.6 with the next best model, respectively). For *Hypseleotris* spp., the model including all possible interactions between water level type, direction and time was the most supported (ΔQAIC_c of 31.9 with the next best model). For *R. semoni*, the CPUE was highest during the day and when the water level type was rising, whereas for *G. holbrooki*, the CPUE was also highest during the day but when the water level type was falling (Fig. 4). For *Hypseleotris* spp., the patterns of CPUE were the same as those for the total catch.

Discussion

Lateral fish movement

In the present study of the upper Murray River, large numbers of fish were captured moving bi-directionally between the main-river and off-channel habitats. The highly regulated river reach provides annual opportunities for fish to access adjacent anabranches, billabongs and other floodplain habitats due to the managed irrigation season. The ecological purposes of the lateral fish migrations were not clarified but are probably related to the increased habitat diversity offered by floodplains with heightened survival, feeding and reproduction opportunities (Balcombe and Humphries 2006).

River height and lateral fish movement

In the upper Murray River, lateral fish movement approximated water level fluctuations and generally as the Murray River rose, fish left the main river channel and moved into newly flooded off-channel habitats. However, there were also bi-directional fish movements as water levels peaked, and on falling water levels, movement back to the permanent riverine habitats occurred (Fig. 5). Hence, although water levels (as a surrogate measure of river flow) strongly influenced fish movement, the sampled populations still displayed a diversity of responses with some

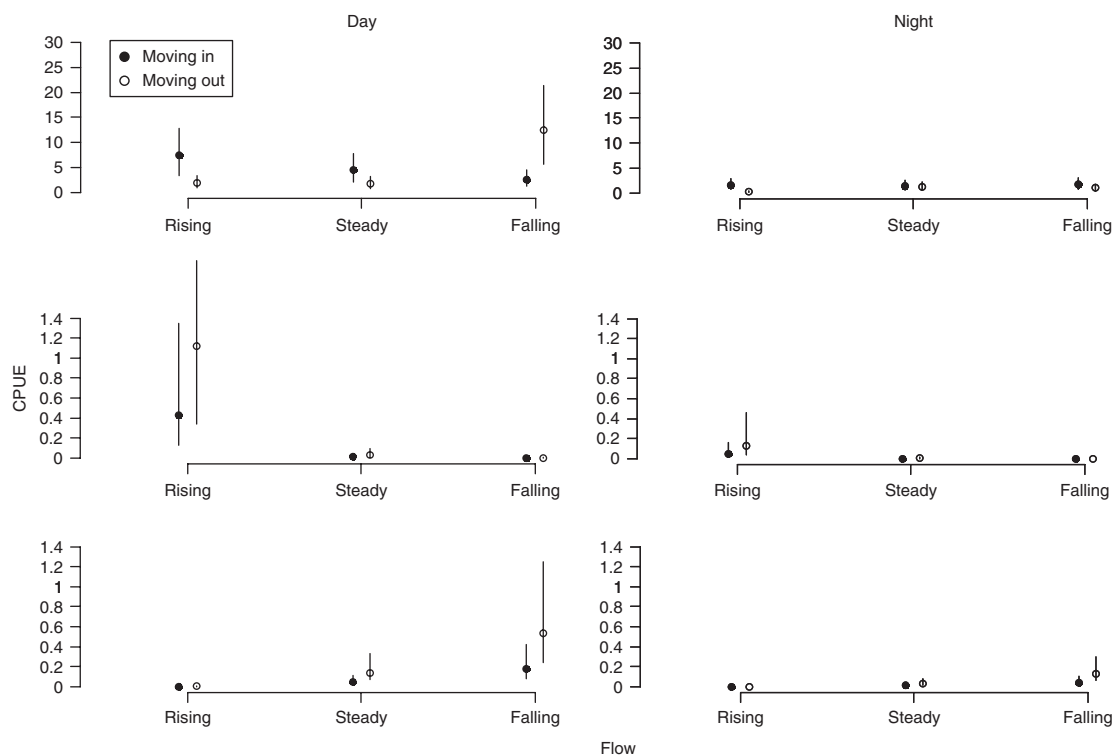


Fig. 4. The predicted catch per unit effort (CPUE) (fish min⁻¹) from the best-fitting models for all fish species combined (row 1), *Retropinna semoni* (row 2) and *Gambusia holbrooki* (row 3) showing the effects of flow (rising, steady, falling) and time (day, night). Closed circles are predictions for fish moving into the off-channel habitats and open circles are for fish moving out of the off-channel habitats. Error bars are 95% credible intervals.

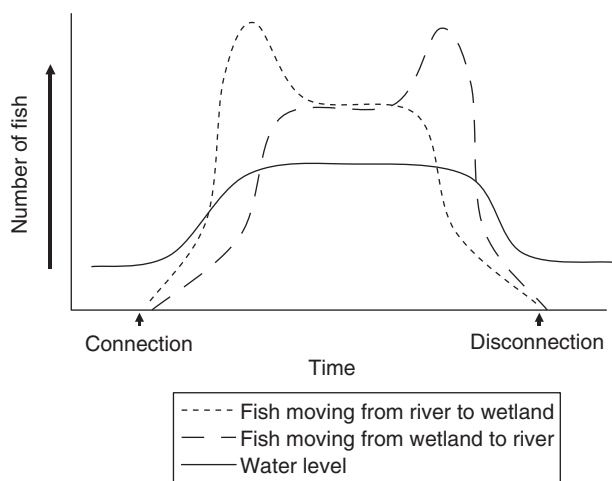


Fig. 5. Movement model of fish using the river-wetland connection.

fish moving back to the Murray River during high river levels. The Murray River appears to act as more than a refuge from off-stream stranding but also as a regular habitation area.

Lateral movement of fish, in the Murray River, is dependent on the connecting channels between riverine and off-channel habitats in which movements of fish have occasionally been shown or hypothesised (Jones and Stuart 2008). Nevertheless, in many studies of fish populations in wetlands of south-eastern

Australia, fish fauna are sampled either exclusively within the river or exclusively within the wetland. This historical sampling regime has inadvertently led to some of the management literature classifying fish as ‘wetland specialists’ (e.g. carp gudgeons and Australian smelt) or ‘generalist’ (e.g. Australian smelt and flat-headed gudgeons) species (McCarthy *et al.* 2006). Other management literature has highlighted the lack of a specialist riverine or wetland fish fauna and speculated that this probably reflects the naturally unpredictable nature of Australia’s flood-plain systems, dry climate and recent marine origins of the native fish fauna (Darlington 1957; Gehrke and Harris 2000). Our results, for the species sampled, also suggest little evidence for distinct river- or wetland-only habitat preferences but emphasise the importance of wetland and main-channel interactions.

Typically, the wetland- and river-dwelling fish collected in this study also showed strong associations in the river-wetland connection, indicating large exchanges of biomass with the main channel (shown diagrammatically in Fig. 5). This observation is supported by longitudinal movement of thousands of Australian smelt, carp gudgeons and unspotted hardyhead in new fishways on the Murray River (Stuart *et al.* 2008). These fish species, and others, have occasionally been managed as ‘wetland specialists’ but actually appear to have a more flexible movement and life-history strategy including riverine habitation.

Similar trends have been observed in rivers and streams on other continents. Roach *et al.* (2009), using stable isotope analysis, found that lateral movement of fishes between channel

and floodplain habitats in Venezuela was an important factor in the net transfer of organic carbon. Similarly, Lasne *et al.* (2007) conclude that there is a need for a high level of connectivity between the main channel and the floodplain in the Loire River to conserve native fish diversity. In particular, they indicated that the number of native species increased with increasing connectivity, while the number of exotic species present increased with increasing isolation from the main channel. In North America, Sullivan and Watzin (2009) describe that intact channel floodplain connections are critical for providing persistent floodplain and main channel for fish communities.

Many small-bodied fish appeared to return to the Murray River, particularly on a falling river, while others remained in the off-channel habitats where in the semi-permanent billabongs they might have high survival while exploiting the floodplain resources (Balcombe and Humphries 2006). Under natural flow conditions, opportunities to access off-channel habitats might have been less frequent but the time taken before disconnection would have been longer, allowing fish more time to escape stranding. For small-bodied fish, there is a trade-off between re-entering the permanent refuge of the main river channel and remaining in billabongs, which occasionally dry (Suarez *et al.* 2004). The current drought (8+ years) has resulted in the complete drying of many off-channel habitats and lateral re-population of billabongs from the Murray River is likely to be an important aspect of drought recovery. Hence, the exchange of fish between river and floodplain is likely important in maintaining biodiversity.

Some small-bodied native fish appear to recruit more strongly following flooding, (i.e. the flood pulse concept; Junk *et al.* 1989). In contrast to this was the high abundance of short-lived (<4 years), small-bodied fish collected in the Murray River during the present drought (Stuart *et al.* 2008). Hence, to maintain local populations, movement and recruitment must also necessarily occur during the frequent drought events (recently up to 8 years) or during the annual within-channel spring irrigation flows. For short-lived fishes, annual access to key low-lying wetlands is still likely to be important in maximising recruitment and population recovery following drought. For this reason, annual irrigation flows that are highly managed might still provide considerable benefits for small-bodied fish populations.

The narrow floodplain–river connecting channels were important for fish moving between these separate riverine and floodplain habitats. In the Murray–Darling Basin, flow through these channels has been historically controlled by large numbers of earthen levees to control flooding (Dexter *et al.* 1986). More recently, the drought has caused river managers to disconnect some wetlands from the main river to limit evaporative water loss. For some wetlands, new floodplain regulators are proposed and these would be used to cause a managed inundation event, primarily for riparian tree health. In these regulated systems, fish can be adversely impacted by floodplain regulation and maintaining lateral connectivity is likely to be important for river–floodplain fish assemblage biodiversity (Jones and Stuart 2008).

Diel and water-quality cues

Several fish species showed strong diel behaviour and this appears to be one of the underlying factors triggering

bi-directional movement to and from off-channel habitats. When the diel patterns of individual fish link with population level responses, there can be changes to whole fish communities over the daily cycle and this information might be important in the management of rivers and their wetlands (Mallen-Cooper 1999; Baumgartner *et al.* 2008). For example, drawdown of rivers and closing of floodplain regulators to dry off-channel habitats should be managed operationally within the appropriate diel context to minimise stranding of fish (Hohausova *et al.* 2003; Jones and Stuart 2008).

Movement of fish into the off-channel habitats continued as the floodplain and river levels were declining, and this suggests other movement cues. The occasional temperature depression in the main river, caused by a nearby large dam, might have cued fish to enter the warmer floodplain environments. Alternatively, the plume of nutrient- and food-rich floodplain waters entering the river might also have stimulated fish to move off-stream. Such lateral movements of small-bodied fish may be in response to a combination of abiotic water quality parameters and their specific life-history stage needs (feeding, spawning, refuge/dispersal) (Roach *et al.* 2009; Sullivan and Watzin 2009).

Several non-native fishes also moved from the Murray River into the off-channel habitats, which suggests that during seasonal low flows these species also utilise permanent refuges in the main river. On rising flows, *Gambusia* left the river channel and entered the floodplain where, in the warm shallow floodplains, they breed and can displace and impact upon native fishes (Wilson 2005). These observations are important for controlling pest fishes as the river–floodplain connecting channels are natural movement bottlenecks where there are predictable fish movements, opportunities to manipulate discharge and constricted sites for targeted control efforts (Jones and Stuart 2008).

Restoring connectivity for fish is also a significant aspect of drought recovery for uncommon or threatened species (e.g. olive perchlet, southern pygmy perch and Murray jollytail) that might occasionally disperse. Providing greater passage for small-bodied migratory fish also achieves a more holistic goal of restoring passage for all aquatic migratory biota (Northcote 1998) and increases available resources for larger-bodied species.

There are often restrictive longitudinal or lateral perceptions of fish demographics but our results again confirm that these gradients are intimately linked (Jungwirth *et al.* 2002). With floodplains becoming increasingly disconnected from their rivers, there remains a great challenge in maintaining riverine–wetland biodiversity. Meeting this goal might readily be achieved by restoring lateral river–floodplain connections and enhancing the natural exchange of fish. Managing valuable floodplain habitats as an integral and connected part of whole river systems will likely have great biodiversity benefits.

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Chapter 3

*Reintroduction success of threatened Australian trout cod (*Maccullochella macquariensis*) based on growth and reproduction*

Statement of Authorship

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Principal Author

Name of Principal Author (Candidate)	Jarod Lyon		
Contribution to the Paper	Co-ordinated sampling, led and co-ordinated data entry, undertook analysis, acted as lead and corresponding author		
Overall percentage (%)	85%		
Certification:	This paper reports on original research I conducted during the period of my Higher Degree by Research candidature and is not subject to any obligations or contractual agreements with a third party that would constrain its inclusion in this thesis. I am the primary author of this paper.		
Signature		Date	10/7/17

Co-Author Contributions

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

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

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Contribution to the Paper	Assisted with study design, edited manuscript		

Signature		Date	15/11/2017
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Contribution to the Paper	Analysis of gonad samples, assisted with editing		
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Signature		Date	18/12/2017

Reintroduction success of threatened Australian trout cod (*Maccullochella macquariensis*) based on growth and reproduction

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Abstract. Internationally, re-introductions of endangered species into their former ranges have largely failed. Here we assess a successful reintroduction program of the endangered trout cod (*Maccullochella macquariensis*) and examine factors contributing to this success. Stocking of marked fish (all stocked fish were marked) occurred between 1997 and 2006 in the Ovens River, south-eastern Australia, where trout cod were historically abundant but locally extinct by the 1980s. We found no natural recruits (i.e. from spawnings of stocked fish in the wild) over the age of six, indicating that natural recruitment started at most five years after stocking began. Of the 83 fish we examined for sexual maturity, 12 were immature, 20 were male, and 51 were female. The body length at which 50% of the population can be considered mature was 325 and 250 mm for females and males, respectively. The length at which 90% of the population was mature was 394 and 318 mm for females and males, respectively. The smallest mature female was 245 mm. Average relative fertility was 9 eggs g⁻¹ fish weight. The results we obtained provide valuable insights into the aspects contributing to the success of reintroduction programs for endangered freshwater species.

Additional keywords: fish, *Maccullochella macquariensis*, recruitment, reintroduction, stocking, threatened.

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Introduction

Reintroduction of native fishes into areas from which they have been extirpated is being embraced globally as a means to reduce the probability of species-wide extinctions. There are two main reasons why fish are reintroduced to the wild: (i) for fisheries management (i.e. restocking to replace fish removed) and (ii) conservation (i.e. to prevent extinction) (Brown and Day 2002). For native fish conservation, a basic premise needs to be considered when reintroducing individuals: the threats suspected or known to have caused extirpation need to be managed and attenuated before, during and after the reintroduction itself (Reading *et al.* 1991; Brown and Day 2002). However, in some cases, the resources enabling successful

management are not available even though the threats are known. As such, reintroductions of animals into their former range have largely failed (Reading *et al.* 1991).

Many fish species have a long history of captive breeding and subsequent release, both for fisheries and conservation objectives. The general life history of most fishes, which allows large numbers of offspring to be produced for a relatively small investment (compared to other taxa), makes this possible (Rakes *et al.* 1999; Brown and Day 2002). Reading *et al.* (1991) discussed a holistic model for reintroduction which takes into account not only biology, but also socioeconomic, organisational and authoritative aspects in considering why a species has become extinct in parts of its natural range. From a global

perspective, reintroductions of threatened fishes are only occasionally successful. In the Colorado River Basin, USA, stockings of the endangered razorback sucker *Xyrauchen texanus* have been occurring for more than thirty years, with limited success (Schooley and Marsh 2007), and while small-scale captive breeding of threatened fishes in the south-eastern USA has been done, the success of re-introductions could be considered mediocre (Rakes *et al.* 1999).

The Murray–Darling Basin in south-eastern Australia has experienced considerable land-use change since European settlement in 1788 (Bradshaw 2012). As such, fish populations there have declined because of habitat loss, altered flow and temperature patterns, in-stream sedimentation, introduced (alien) fishes and population fragmentation caused by in-stream barriers and over fishing – issues that have been consistent with reduction in freshwater fish numbers in many river systems globally (Barrett 2004; Kondolf *et al.* 2008; Honea *et al.* 2009; Winter *et al.* 2009). The Australian trout cod (*Maccullochella macquariensis* Cuvier) was once considered widespread in the southern tributaries of the Murray–Darling Basin (Berra 1974; Harris and Rowland 1996). However, over the past fifty years, its distribution and abundance have declined. Trout cod are a long-lived (>20 years), large-bodied species, with a maximum size of 16 kg and 850 mm total length (Harris and Rowland 1996). They occupy a range of habitats, but are strongly associated with large woody instream habitats (Nicol *et al.* 2007). Trout cod are now listed nationally as *Endangered* under the Australian Environment Protection and Biodiversity Conservation Act (*EPBC Act 1999*) and are listed as *Endangered* by the IUCN Red List (www.iucnredlist.org, accessed 10 November 2011).

In the Ovens River system located in the southern Murray–Darling Basin, trout cod were locally extinct by the 1980s (Cadwallader and Gooley 1984). In an attempt to re-establish viable populations, captive breeding programs were established in the 1980s to produce fingerlings for recovering populations (Ingram *et al.* 1990). Hatchery-reared juveniles bred at the Department of Primary Industry (DPI) Snobs Creek Hatchery were stocked into the Ovens River for 10 consecutive years starting in 1997. In this paper, we assess the success of this stocking regime to test the following hypotheses: (1) the duration of this stocking program (10 years) was an essential element for its ultimate success; (2) hatchery fish do not differ from wild-bred individuals (measured by chemical marking of hatchery fish before release) in terms of growth and reproduction; (3) the release of yearling fish improves the viability of such stockings; and (4) genetic diversity (as measured by the number of alleles) in a stocked population is less than in a natural population because of inbreeding and the founder effect (Frankel and Soulé 1981). The results have implications for other conservation programmes for endangered species that use re-introduction as a tool for recovery.

Methods

Fish were stocked in the region of the lower Ovens River system downstream from Wangaratta and upstream of the influence of Lake Mulwala (Fig. 1). The lower Ovens River in this area is a typical lowland river characterised by deep pools with shallower

connections, and a braided floodplain with numerous anabranches and backwaters. Long-term average discharge (1891–2000) for the river is 1640 gigalitres year⁻¹ (MDBA 2003).

Fish were stocked as both fingerlings (0+) and one-year olds (1+) to test the assumption that yearling fish had a higher probability of survival to adult size than fingerling fish (Table 1). We applied chemical marks to otoliths of hatchery-reared fish, by immersing fish for 24 h in a solution of oxytetracycline (a chemical which permanently marks the otolith). In 2007, twelve months after the cessation of the 10-year stocking program, we collected a sample of the population using electrofishing and angling: 47 trout cod in February and 84 fish in the August to November spawning period (when sexual maturity was more easily determined). We killed captured fish and returned them to the laboratory for further processing.

Otoliths

We examined otoliths to assess growth, age structure, and to determine whether or not sampled fish were hatchery-reared or wild-bred. From each of the 131 fish sampled, we removed sagittal otoliths, then washed and stored them dry before sectioning. We first examined sections using fluorescence microscopy for specifically marked growth rings to determine whether each sampled fish was originally stocked, and also used otoliths to determine the age and growth of each individual fish. Sections were viewed with transmitted light at 25× magnification. Ages were estimated by counting the completed zones (translucent – opaque sequence). A customized image analysis system (Morison *et al.* 1998) was used to mark and count increments along a transect between the primordium and the proximal edge of the section, adjacent to the dorsal side of the sulcus.

Gonads

From the sample of 131 fish, we examined the gonads of 84 trout cod to determine sex and sexual development. Our protocol ensured collection over the trout cod spawning period to provide information on spawning times and condition throughout the season. We weighed all gonads to the nearest gram. For females, we preserved gonads in a solution of 85% formalin and counted a 1-g subsample of oocytes from each gonad to estimate fertility, determining reproductive maturity of individuals using an adaptation of a macroscopic, eight-stage descriptor (FI–VIII) developed for Murray cod *Maccullochella peelii*, a closely related species (Gooley *et al.* 1995). We did histology on a portion of the fish sampled to confirm macroscopic estimates of development by embedding a transverse medial sub-sample of each individually preserved gonad into a paraffin wax block, sectioning the block (6 µm), and staining it with Harris' haematoxylin and eosin (Luna 1968). We then mounted the section on a slide under a coverslip, numbered it, and staged it as per Gooley *et al.* (1995).

To estimate size at sexual maturity (L_{m50}), we categorised female and male trout cod as mature when they were macroscopically within stages IV–VIII (see Gooley *et al.* 1995 for stage description). For each sex, we estimated size (total length) at maturity by determining the proportion of mature and

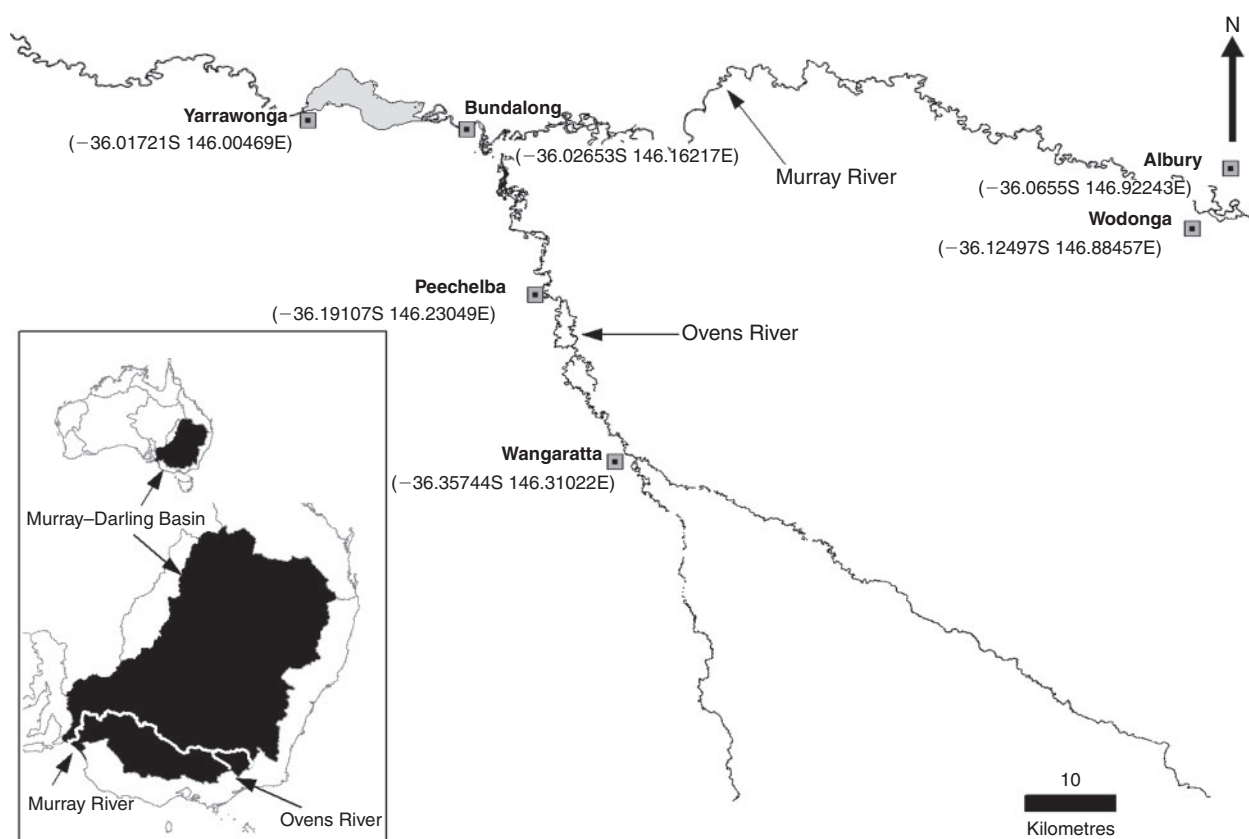


Fig. 1. Map of study area.

immature fish in each 10-mm length class, and then fitted a logistic function to the data using a non-linear, least-squares procedure weighted by sample size on each length class (see Brown *et al.* 2005).

Genetics

We extracted and purified DNA from finclip tissue collected from 50 trout cod caught from the Ovens River in the area where fish were originally released, and 50 fish from the Murray River between Yarrowonga Weir and Cobram (an area from which trout cod have not been stocked). The latter population was the source of broodstock used in the captive breeding program at DPI, Snobs Creek. We extracted total genomic DNA using the QIAGEN DNeasy tissue kit (QIAGEN Pty Ltd Doncaster, Melbourne). We genotyped individuals using nine microsatellite loci (Rourke *et al.* 2007), and analysed these data using GENEPOP version 3.3 (<http://wbiomed.curtin.edu.au/genepop>, accessed 2 July 2011) and ARLEQUIN 3.01 (Excoffier *et al.* 2005). We assessed whether the data conformed to Hardy–Weinberg equilibrium genotype frequency proportions (expected with random mating within populations), if F_{ST} deviated from zero (expected if there is genetic structure between Ovens and Murray populations), differences in number of alleles between populations and probability of assignment (showing how individuals can be best allocated to the alternative populations).

Table 1. Numbers of hatchery-reared trout cod released into the Ovens River between 1997 and 2006

Year	<i>n</i> fingerlings (~35 mm TL)	<i>n</i> yearlings (~180 mm TL)
1997	13 100	0
1998	24 000	653
1999	30 000	2430
2000	20 000	0
2001	51 700	0
2002	30 000	0
2003	44 260	0
2004	30 000	900
2005	24 000	0
2006	10 400	0
Total	277 460	3983

Growth model

To test whether growth in hatchery fish differed from wild-bred individuals, we constructed a standard nonlinear regression model of age against length using two common growth curves, 1. von Bertalanffy (1938) and 2. Gompertz (1825) respectively:

$$\text{Length} = L_a \times (1 - \exp(-k \times (\text{Age} - t_0))) \quad (1)$$

$$\text{Length} = L_a \times \exp(\exp(-k \times (\text{Age} - t_0))) \quad (2)$$

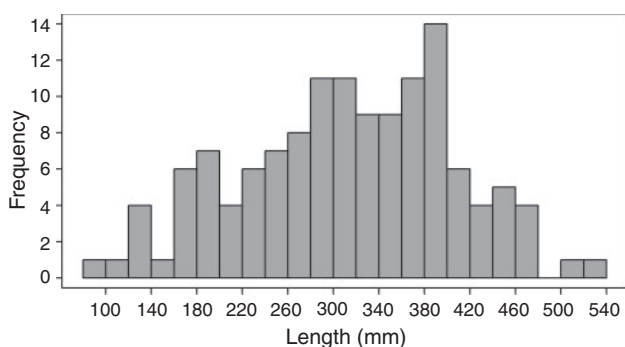


Fig. 2. Length–frequency of trout cod captured in the Ovens River, 2007 ($n = 131$).

where L_a is the asymptotic length, k the annual growth rate, and t_0 the theoretical age at zero length. We applied nonlinear least-squares estimation of the parameters for both growth models using the R package (R Development Core Team 2011) to examine differences between growth in wild and stocked fish.

Sexual maturity

To test whether maturity (as a function of length) differed between hatchery fish and wild-bred individuals, we fitted a multi-level logistic regression model treating the response variable stage (mature or immature) as exchangeable observations of a Bernoulli random variable, with the logit of the probability of being mature expressed as a linear function of effects according to sex, age, length and origin (hatchery-reared or wild-reared). The model included an interaction between age and length. We also modelled sex as exchangeable observations of a Bernoulli random variable with the logit of the probability of being male expressed as a linear function of effects according to length and origin.

We used Bayesian inference implemented through the program WinBUGS (Lunn *et al.* 2000) implemented in the R package (R Development Core Team 2011). Included in the data were fish that were of unknown sex and stage of maturation. In both cases we predicted missing values as part of model fitting; this technique allows for efficient use of all available data.

Results

We captured 131 trout cod in the lower Ovens River ranging in size from 88 to 522 mm total length (Fig. 2). Of the 131 tested fish 96 (72%) had a definite oxytetracycline mark (indicating that they were stocked), 35 had no mark. Wild-spawned and hatchery trout cod were present up to 9 years of age (Fig. 3).

Growth model

Age-length analysis indicated differences in growth between wild-spawned and hatchery-sourced trout cod (Table 2, Fig. 4). There were only marginal differences between both growth models explored (Table 2, Fig. 4).

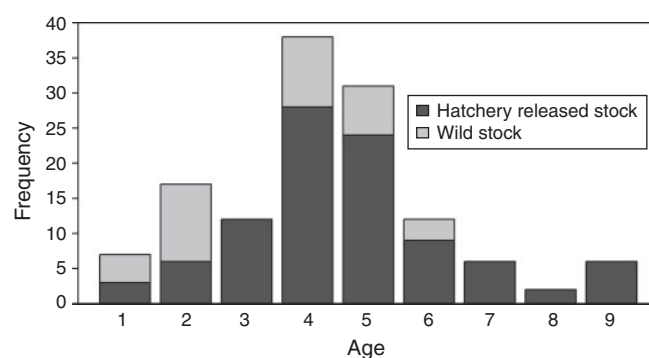


Fig. 3. Age (years) frequency distribution.

Sexual maturity

Of the 83 fish used to determine sexual maturity, there were 51 females, 20 males and 12 indeterminate-sex juveniles. We observed the earliest indication of spawning in a spent (F7) 385-mm female fish captured on 10 October 2007. By 12 November 2007 (our last sampling event), ~65% of mature fish had spawned. The smallest mature female (i.e. $\geq F4$) recorded on 30 Aug 2001 was 245 mm and four years old. The smallest female we confirmed to have spawned (i.e. F7) was caught on 12 November 2007 and was 283 mm and five years old. A six-year-old (373 mm and 688 g), unmarked fish (i.e. progeny of stocked fish) was confirmed as F7.

For females, Lm_{50} (i.e. length at which 50% of the population is mature) was 325 mm (95% credible interval: 289 to 381 mm), and Lm_{90} (i.e. length at which 90% of the population is mature) was 394 mm (347 to 486 mm) (Fig. 5). Eighty-three percent of the trout cod captured were females. For males, Lm_{50} was 250 mm (220 to 275 mm), and Lm_{90} was 318 mm (287 to 368 mm) (Fig. 6). For females, Am_{50} (i.e. age at which 50% of the population is mature) was 5.4 years (4.8 to 6.3 years), and Am_{90} was 6.6 years (5.8 to 8.1 years). For males, Am_{50} was 4.2 years (3.7 to 4.6 years), and Am_{90} was 5.3 years (4.8 to 6.1 years).

Gonads

Fertility ranged from 2027 oocytes in a 291 mm fish, to 14000 oocytes in a 450 mm fish, and average fertility increased with both length and weight. Average relative fertility was 9 eggs g^{-1} fish weight (range: 7 to 14 eggs g^{-1}).

Genetics

The proportions of homozygous and heterozygous genotypes in the Ovens River population differed from that expected under Hardy–Weinberg equilibrium. We detected no genetic structure between populations in the Murray and Ovens Rivers, and both populations appear to be homogeneous. The total number of alleles we detected in the Murray River population (49) was consistently lower than the number found in the Ovens River population (55).

Discussion

We have assessed the success of reintroduction of trout cod into the Ovens River by determining whether stocked trout cod

Table 2. Results from the age-length analysis of trout cod data

Model	All data		Hatchery-released		Wild-bred	
	$\hat{\beta}$ estimate	SE	$\hat{\beta}$	SE	$\hat{\beta}$	SE
<i>von Bertalanffy</i>						
L_a	582.53	44.66	552.16	40.24	2450.83	7014.30
k	0.19	0.03	0.22	0.04	0.03	0.09
x_0	-0.01	0.2	0.32	0.26	-0.88	0.70
		$r^2 = 86.2$		$r^2 = 82.9$		$r^2 = 91.3$
<i>Gompertz</i>						
L_a	505.70	21.16	491.83	20.65	697.05	242.80
k	2.19	0.14	2.48	0.28	2.16	0.21
t_0	-0.36	0.03	-0.41	0.05	-0.24	0.09
		$r^2 = 86.81$		$r^2 = 83.70$		$r^2 = 91.25$

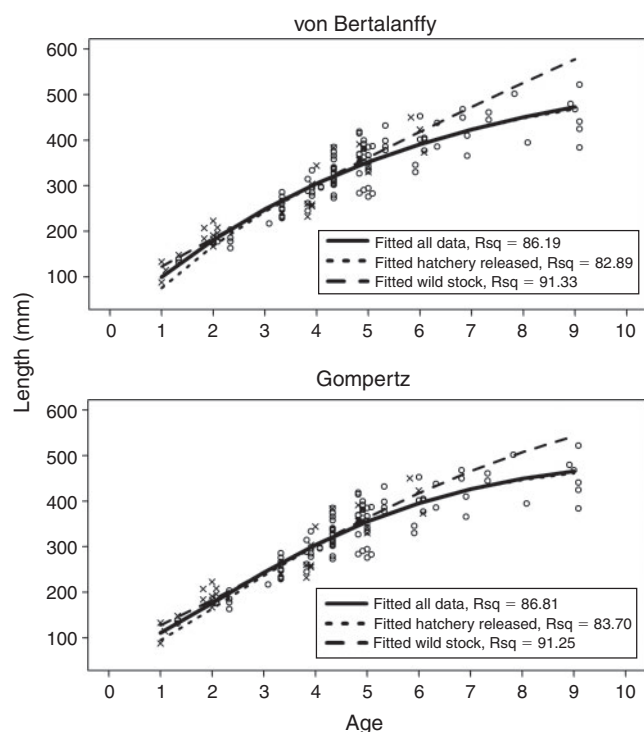


Fig. 4. Estimated age (years)–length relationship of trout cod for both von Bertalanffy and Gompertz growth curves: circles – hatchery-released, crosses – wild-bred.

survive in the Ovens River, whether they produced viable offspring, and their growth, fertility and genetic composition are comparable to wild-bred fish. According to these criteria, we can conclude the programme was successful. Since commencement of stocking, trout cod have been reintroduced into 32 sites in eight river catchments across the Murray–Darling Basin. Of these areas, natural recruitment has been confirmed in four rivers, and currently these stockings have resulted in what might be described as ‘self-sustaining populations’ at only three areas: the Goulburn, Ovens and Murrumbidgee Rivers (Ingram and Thurstan 2008). Other re-introduction sites, which were generally smaller, upland streams stocked over shorter time frames, have had limited success.

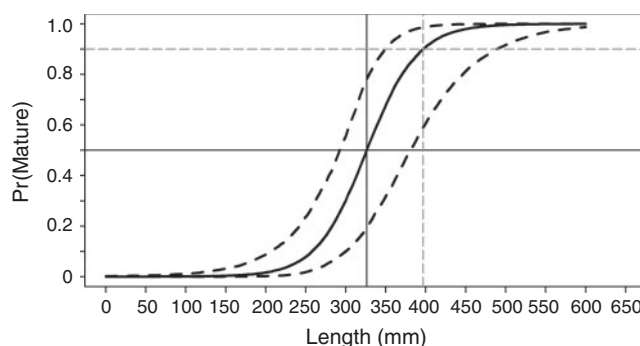


Fig. 5. Female trout cod maturity ogive. Solid line = median estimate; dashed lines represent 2.5 and 97.5% credible limits. Solid horizontal and vertical lines show $Lm_{50} = 325.12$ mm; dashed horizontal and vertical lines show $Lm_{90} = 394.18$ mm.

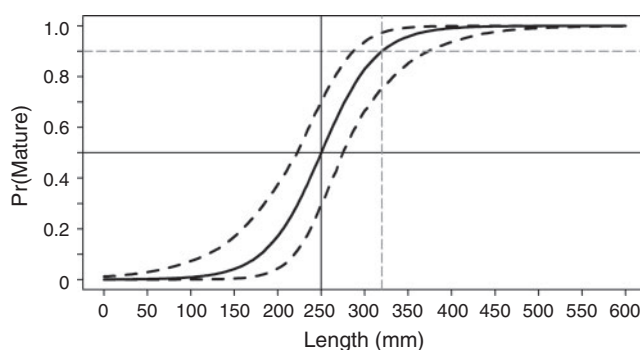


Fig. 6. Male trout cod maturity ogive. Solid line = median estimate; dashed lines represent 2.5 and 97.5% credible limits. Solid horizontal and vertical lines show $Lm_{50} = 249.54$ mm; dashed horizontal and vertical lines show $Lm_{90} = 318.30$ mm.

Length of re-introduction program

Previous population modelling for this species (Bearlin *et al.* 2002; Todd *et al.* 2004) indicates that there are a variety of re-introduction strategies that can be adopted to establish viable populations. The stocking strategy applied here was a long-term (over 10 years), moderate stocking regime (as described in Douglas *et al.* 1994) of between 10 400 and 51 700 fingerlings,

including three years where more yearlings were stocked (Table 1). This strategy is conservative (as defined by Bearlin *et al.* 2002), where such stocking rates are expected to achieve a high probability of success (establishment of a self-sustaining population, Bearlin *et al.* 2002). Additionally, Bearlin *et al.* (2002) and Todd *et al.* (2004) describe other stocking strategies where more fish are stocked over a shorter period, to achieve the same result.

We postulate that an important facet of a long-term stocking program for endangered species recovery is the increased chance of a stocked cohort encountering favourable environmental conditions that promote local survival, and in particular in the period immediately following release. In the current stocking program, fish stocked in 2003 and 2004 are more highly represented in our data than other stocked years and in particular subsequent years, indicating a higher rate of survival for the fish released in these years. If this were the case, it supports the conservative approach of releasing stock over a longer period of time by increasing the likelihood of encountering favourable conditions for survival. The proportion of fish stocked in 2003 and 2004 observed in our data could be because of sampling, spatial arrangement of fish within the river, and possibly dispersal. However, without information to the contrary, we conclude that the long-term stocking approach was important for establishing a wild breeding population where it appears that stockings from years other than 2003 and 2004 contributed relatively few fish to the population (and indeed, in some years, none).

Size, age and growth

As a general rule, large fish have a higher survival probability than smaller fish of the same species (Masuda and Tsukamoto 1998; Svasand *et al.* 2000). However, our results suggest that the stocking of yearling trout cod (in conjunction with fingerlings) had no discernable impact on the final population size or structure. Ebner *et al.* (2007) found that two year-old trout cod have high mortality rates (~100%) after release into the Murrumbidgee and Cotter Rivers in south-eastern Australia; a high proportion of these mortalities were probably caused by inappropriate conditioning (i.e. fish were reared in indoor tanks on an artificial diet, and had no previous contact with predators or prey). In contrast to yearlings, fingerlings released into the Ovens River were reared in outdoor earthen ponds, only live prey was available and fish were more likely to be exposed to predation (other fish, macro-invertebrates and birds).

The age structure of this population is approximately Gaussian (Fig. 4); however, few large (>500 mm) fish were captured and this is a cause for concern. Ongoing misidentification of trout cod by anglers might explain why large fish were poorly represented. Trout cod are voracious fish and therefore easily angled, so it is plausible that large trout cod (over the legal Murray cod length of 500 mm at the time of sampling, but now 600 mm) are being misidentified as Murray cod and removed.

Growth is different between released and wild fish; however, the difference is more likely associated with the sample size and/or the age/size distribution for wild-spawned (1–6: 88–450 mm) and hatchery (1–9: 132–522 mm) than those arising from physiological or metabolic differences between released and wild fish, or any effects of the marking procedure. We used two

standard growth models to estimate growth rates in both released and wild fish. The Gompertz model estimated lower parameter errors (Table 2); however, there were only marginal differences between the models explored (Table 2, Fig. 4). The rate of growth begins to slow between ages 4 and 5 most likely because of the onset of sexual maturity.

It is unlikely that the Ovens river population is receiving recruits from other populations (either stocked or natural) because of the absence of fish upstream before stocking, and the barrier formed by Lake Mulwala downstream. In addition, the fact that the species was considered functionally extinct in the Ovens river before the stocking event means that immigration into the area was absent or at least infrequent. As such, we are confident that the success was a result of the stocking program, rather than an artefact of immigration. It is noteworthy that the range of trout cod in the Ovens river has now expanded approximately 50 km both upstream and downstream from the original stocking sites (J. Lyon DSE, unpubl. data).

Genetics

Fish-stocking programs have received considerable criticism because of perceived impacts of hatchery-bred fish breeding with wild populations resulting in loss of genetic diversity or reduced viability (Allendorf 1991; Nock *et al.* 2011). Stocking Murray cod into the Murray–Darling Basin has resulted in a range of genetic effects from non-detectable change to substantial change in wild populations (Rourke *et al.* 2010, 2011). We showed that the stocked population in the Ovens River and the Murray River population, where parent fish for the captive breeding program were captured, are genetically homogeneous. The number of alleles detected in the Murray River (49 total) was consistently lower than the number of alleles found in the Ovens River population (55 total). These results might reflect the successful application of the breeding program protocol that aimed to maximise the genetic diversity of the fish produced. The breeding program followed genetic guidelines described by Douglas *et al.* (1994) which included regular replacement of captive broodstock with new broodstock caught from the Murray River population, maintaining a sex ratio of 1:1 in spawned broodstock, undertaking single-pair matings, avoiding repeat matings of the same pairs of fish, and mixing progeny from all matings together before re-stocking.

Wild-spawned fish and sexual maturity

Our data show that the first natural recruits into the system (i.e. spawned by hatchery-released fish) occurred three years after the beginning of the stocking program – a result that concurs with our data describing age at maturity where some Ovens River trout cod become sexually mature at 3 to 4 years. However, we only captured a few natural recruits until years 6 and 7 (when there was also a high survival of stocked fish) of the stocking program, again indicating the importance of sustained introductions to account for changes in yearly survival rates. Our smallest mature female fish, having spawned at 283 mm, 299 g and five years of age, is also smaller than expected, with the spawning weight range previously reported at 750–1500 g (Douglas *et al.* 1994; Koehn *et al.* 2008). Sarrazin and Barbault (1996) indicate that successful breeding of the first-born generation can be used as an indication of re-introduction success,

and here we recorded many stocked fish and one wild spawned female as having spawned (F7).

We found evidence for deviation from the expected 1 : 1 sex ratio; females dominated 2.5 : 1. Sex determination in many fish species can be influenced by physical conditions such as temperature (Devlin and Nagahama 2002; Penman and Piferrer 2008). A highly skewed sex ratio was observed in small population of hatchery-reared trout cod from the Snobs Creek Hatchery where there were 9 males to 1 female (B. Ingram DPI, unpubl. data). There might have been a sex ratio bias in the production of hatchery fingerlings, or that male survival in the wild after release is lower than that of females.

Lessons learnt

Our data clearly show the dynamics of a successful reintroduction of a threatened species, by applying a long-term stocking program to overcome environmental variability, which can result in failure of any particular stocked cohort. What is more difficult to explain is why the original extinction occurred, and why these threats did not prevent restocking success. The reasons for human-induced species decline are usually a synergistic combination of several processes (Brook *et al.* 2008), and here we assume that the processes that led to the decline included competitive exclusion and/or predation by introduced species such as carp (*Cyprinus carpio*) and redfin (*Perca fluviatilis*), barriers to migration, land-use change and overfishing (Cadwallader 1978; Ingram *et al.* 1990; Douglas *et al.* 1994). Although these threats likely have not totally abated in the Ovens River, the scale of their impact is greatly reduced. For example, the period of intensification of invasive species spread occurred between the 1950s and 1990s, after which their populations stabilised. There is also an increasing global emphasis on more sustainable recreational fishing practices (Granek *et al.* 2008; Douglas *et al.* 2010). As such, we suggest that species reintroductions can be done provided threat reduction occurs prior or in concert with restocking.

Ongoing threats to freshwater fish populations mean that re-introduction programs will need to continue if threatened populations are to be brought back from the brink of extinction, because river restoration alone is unlikely to provide enough impetus for fish to recolonise previous habitats on their own. The example presented here shows that large-bodied native fish reintroductions can be successful in lowland rivers. However, such re-introductions should be sustained and of sufficient magnitude to maximise establishment.

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Chapter 4

Efficiency of electrofishing in turbid lowland rivers: implications for measuring temporal change in fish populations

Statement of Authorship

Title of Paper	Efficiency of electrofishing in turbid lowland rivers: implications for measuring temporal change in fish populations
Publication Status	<input checked="" type="checkbox"/> Published <input type="checkbox"/> Accepted for Publication <input type="checkbox"/> Submitted for Publication <input type="checkbox"/> Unpublished and Unsubmitted work written in manuscript style
Publication Details	Lyon, J.P., Bird, T., Nicol, S., Kearns, J., O'Mahony, J., Todd, C.R., Cowx, I.G. and Bradshaw, C.J., 2014. Efficiency of electrofishing in turbid lowland rivers: implications for measuring temporal change in fish populations. <i>Canadian Journal of Fisheries and Aquatic Sciences</i> , 71(6), pp.878-886.

Principal Author

Name of Principal Author (Candidate)	Jarod Lyon			
Contribution to the Paper	Led sampling teams, undertook fish surgery, led data collection, compiled data, interpreted data, wrote manuscript, acted as corresponding author			
Overall percentage (%)	85%			
Certification:	This paper reports on original research I conducted during the period of my Higher Degree by Research candidature and is not subject to any obligations or contractual agreements with a third party that would constrain its inclusion in this thesis. I am the primary author of this paper.			
Signature	<table border="1" style="width: 100%;"> <tr> <td style="width: 60%;"></td> <td style="width: 20%;">Date</td> <td style="width: 20%;">12/07/2017</td> </tr> </table>		Date	12/07/2017
	Date	12/07/2017		

Co-Author Contributions

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

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

Name of Co-Author	Tom Bird			
Contribution to the Paper	Modelled data, contributed to writing			
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	Date	5/12/2017		

Name of Co-Author	Simon Nicol
Contribution to the Paper	Contributed to design, contributed to editing

Signature		Date	04/12/2017
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Name of Co-Author	Joanne Kearns		
Contribution to the Paper	Contributed to field data collection, contributed to data entry, edited manuscript		
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Efficiency of electrofishing in turbid lowland rivers: implications for measuring temporal change in fish populations

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Abstract: To quantify how electrofishing capture probability varies over time and across physiochemical and disturbance gradients in a turbid lowland river, we tagged between 68 and 95 fish·year⁻¹ with radio transmitters and up to 424 fish·year⁻¹ with external and passive integrated transponder (PIT) tags. We surveyed the site noninvasively using radiotelemetry to determine which of the radio-tagged fish were present (effectively closing the radio-tagged population to emigration) and then electrofished to estimate the proportion of available fish that were captured based on both this and standard mark–recapture methods. We replicated the electrofishing surveys three times over a minimum of 12 days each year, for 7 years. Electrofishing capture probability varied between 0.020 and 0.310 over the 7 years and between four different large-bodied species (Murray cod (*Maccullochella peelii*), trout cod (*Maccullochella macquariensis*), golden perch (*Macquaria ambigua ambigua*), and silver perch (*Bidyanus bidyanus*)). River turbidity associated with increased river discharge negatively influenced capture probability. Increasing fish length increased detection of fish up to 500 mm for Murray cod, after which capture probability decreased. Variation in capture probability in large lowland rivers results in additional uncertainty when estimating population size or relative abundance. Research and monitoring programs using fish as an indicator should incorporate strategies to lessen potential error that might result from changes in capture probabilities.

Résumé : Afin de quantifier les variations de la probabilité de prise à la pêche électrique dans le temps et le long de gradients physicochimiques et de perturbation dans une rivière turbide de basse terre, nous avons doté de 68 à 95 poissons·année⁻¹ de radioémetteurs et jusqu'à 424 poissons·année⁻¹ d'étiquettes externes et de transpondeurs passifs intégrés (PIT). Nous avons sondé le site de manière non intrusive par radiotélémetrie afin de déterminer lesquels des poissons radioétiquetés étaient présents (excluant du fait l'émigration pour la population radioétiquetée), puis effectué une pêche électrique pour estimer la proportion de poissons disponibles capturés selon cette méthode et des méthodes de marquage–recapture normales. Nous avons répété les levés par pêche électrique trois fois sur au moins 12 jours chaque année, pendant sept ans. La probabilité de capture par pêche électrique variait dans une fourchette de 0,020 à 0,310 sur les sept ans et pour quatre espèces de gros poissons (la morue de Murray (*Maccullochella peelii*), la perche Macquarie (*Maccullochella macquariensis*), la perche dorée (*Macquaria ambigua ambigua*) et la perche argentée (*Bidyanus bidyanus*)). La turbidité de la rivière associée à un débit accru avait une incidence négative sur la probabilité de capture. Plus la longueur des poissons était grande, plus la détection était élevée pour les poissons allant jusqu'à 500 mm en ce qui concerne la morue de Murray; au-delà de cette longueur, la probabilité diminuait. Les variations de la probabilité de capture dans les grandes rivières de basse terre introduisent une incertitude supplémentaire dans l'estimation de la taille ou de l'abondance relative des populations. Les programmes de recherche et de surveillance qui se servent des poissons comme indicateurs devraient comprendre des stratégies visant à limiter l'erreur qui pourrait résulter des variations de la probabilité de capture. [Traduit par la Rédaction]

Introduction

A cornerstone of biological sampling methods is the estimation of the presence or abundance of target organisms (Phillips et al. 2009; Magurran et al. 2010; Kepner et al. 2000). Most often, direct observation or capture of the entire population is not plausible, so

a census method needs to include a design that permits estimation of the number of unobserved animals (Seber 1973). Capture probability is often used as a coefficient that scales the relationship between the catch and true population size. It can be influenced by environmental (e.g., season, temperature), biological

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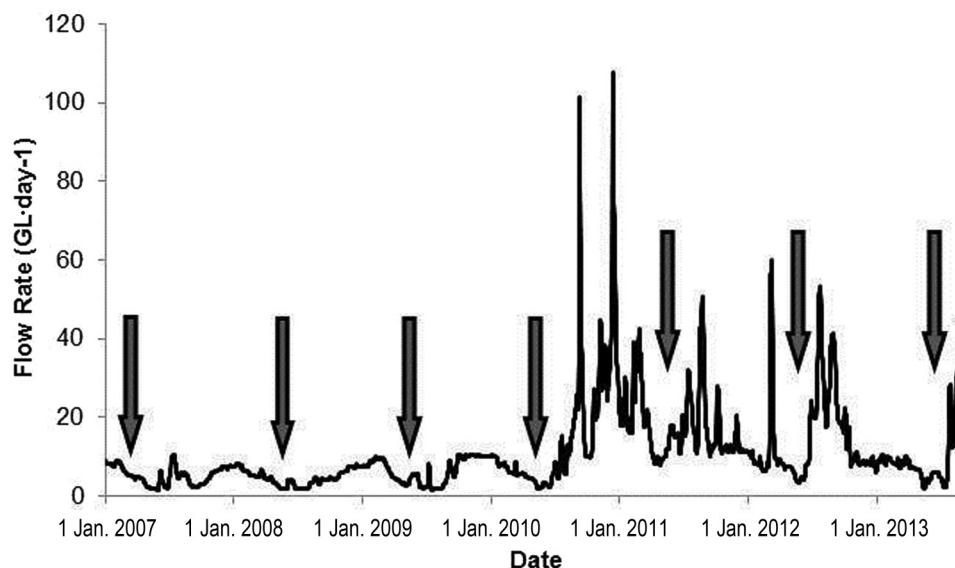
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Fig. 1. Murray River flows (10^6 L·day⁻¹) downstream of Yarrawonga from 2007 to 2013. Arrows indicate sampling occasions.



(species and size), and sampling equipment (selectivity) variability, so robust census methods should ideally include ways to estimate its associated variance. Capture probability can also vary temporally and spatially, so valid inferences about changes in population size need to take these into account.

In riverine ecosystems, monitoring fish populations is widely used to track river health, as fish are often viewed as a tangible “end product” of environmental improvement or fisheries management (Cox and Gerdeaux 2004; Woolsey et al. 2007) and are increasingly used to assess the actual and potential impacts of climate change (Bond et al. 2011; Parra et al. 2012). Such monitoring data are regularly used to measure how management interventions such as stock enhancement, the provision of environmental flows, or habitat improvement influence waterways. River restoration programs around the world, including the assessment of the ecological status of European Union surface waters (Schmutz et al. 2007), the AU\$500 million Living Murray program in Australia (<http://www.mdba.gov.au/what-we-do/managing-rivers/TLM-environmental-works-and-measures>), or the US\$7.8 billion Kissimmee River Restoration Project in the USA (Koebel 1995), use fish monitoring data to assess ecological health. The increased emphasis on improving river catchments and fish populations over the past two decades has been immense (Lake et al. 2007; Whiteway et al. 2010). With such a large investment comes the requirement for extensive monitoring; however, given the scale of the investment in environmental improvement, there is surprisingly little effort made to test the reliability and accuracy of fishery assessment methods or indeed the outcomes of fishery improvement measures.

Electrofishing is a widely adopted tool for assessing fish populations in rivers and small water bodies (Cox 1995; Rosenberger and Dunham 2005; Schmutz et al. 2007); it is relatively safe for fish (compared with other capture methods) and easily applicable to a wide range of waterways and habitats. However, electrofishing has limitations (Zalewski and Cowx 1990), and given the weight of the management decisions increasingly justified based on data collected via electrofishing, accurate data interpretation is essential.

Considerable literature exists describing the conditions that can affect capture probability using electrofishing (Zalewski and Cowx 1990; Pygott et al. 1990; Bayley and Austen 2002). These can include water depth, turbidity, conductivity, habitat structure, and operator experience. However, this literature typically describes patterns of capture probability in smaller streams with high water clarity, and little is known about larger lowland

streams with deep, turbid waters, where estimation is difficult (but see Harvey and Cowx 1996). Here we present the results of a 7-year electrofishing efficiency trial in a large, fifth-order stream in southeastern Australia. We investigated whether different species, fish size, and environmental variables influenced fish capture probability.

Materials and methods

Estimating absolute abundance for electrofishing in rivers is challenging because the true number of fishes available for sampling is usually unknown. Mark–recapture methods are commonly used to estimate population parameters in such a scenario, but are complicated in our case (and in many others) by the migration of fish out of the sampling area between sampling occasions. Previous attempts at fully accounting for the population (via poisoning or blocking the stream) have proven successful in some scenarios (Price and Peterson 2010), but are unlikely to be effective in a large river setting. Instead, we used a combination of radio transmitters and standard mark–recapture methods to estimate capture rates while accounting for temporary migration in and out of the study area.

Electrofishing capture probability trials were conducted during May and June (to coincide with low flow conditions) between 2007 and 2013 (i.e., 7 consecutive years; Fig. 1; Table 1). We chose a 2 km stretch (the maximum distance we could efficiently electrofish with two boats in 1 day) of the Murray River (a large lowland river in southeastern Australia) as the study site. This river length was further divided into 16 subunits (approximately 250 m long and 50 m wide), which equated to approximately the length of river the electrofishing boats could fish before the holding wells on the boat were full of collected fish. Within this 2 km reach, we radio-tagged between 68 and 95 fish, and PIT-tagged (passive integrated transponder) or externally tagged up to 424 fish, annually (see Table 2). We sampled the same site yearly to take advantage of radio transmitters that were still active from previous years, thus reducing costs and increasing our sample size.

At the start of the annual trials, we used two electrofishing boats (Smith Root Inc., Portland, Washington, USA — a commonly used gear type) to sample the 16 subunits. Each boat was randomly allocated eight subunits (i.e., boats did not operate together in any subunits). Both boats were fitted with Smith Root 7.5 GPP boat-mounted electrofishing units. Drivers and netters on both boats were highly competent, with a minimum 5 years of electrofishing

Table 1. Mean and standard deviation for discharge, turbidity, conductivity and stream gauge height (i.e., water level) during electrofishing capture efficiency investigations in the Murray River.

Year	Mean discharge (GL·day ⁻¹)	Mean turbidity (Secchi) (m)	Mean conductivity (S·m ⁻¹)	Mean gauge height (m)	Change in depth from 2007 (m)
2007	1.75±0.08	1.35±0.05	0.0028±0.00008	0.29±0.02	0
2008	2.36±1.14	1.30±0.01	0.0034±0.000113	0.43±0.26	+0.11
2009	3.19±0.27	1.44±0.09	0.0047±0.000112	0.65±0.05	+0.36
2010	2.34±0.54	0.97±0.07	0.0034±0.000458	0.45±0.13	+0.15
2011	15.59±2.46	0.63±0.03	0.0045±0.000295	2.35±0.29	+2.06
2012	3.92±0.41	0.85±0.10	0.0072±0.000147	0.79±0.07	+0.49
2013	4.28±0.55	0.87±0.13	0.0061±0.000134	0.85±0.09	+0.55

experience each. We operated the electrofishing gear with 1000 V, 60 Hz, a duty cycle of 40%, and between 5.5 and 7.5 amps (mean = 6 amps).

The fishing procedure involved one boat driver and one dip-net operator and ensured that, as far as practically possible, each subunit was sampled in its entirety (i.e., the whole 250 m × 50 m area was sampled). In some years when resources allowed, a chase boat (Daugherty and Sutton 2005) followed the electrofishing boat at a safe distance to collect any additional stunned fish that had not been collected by the dip-net operator. We placed all fish collected in an aerated live well on board the boat. At the completion of an electrofishing subunit, we identified collected fish to species, measured total length (nearest mm), and weighed (nearest g) and tagged each with both a uniquely coded subdermal PIT tag and an external floy tag, before fully resuscitating them. We retained up to 100 in total of the following species — Murray cod (*Maccullochella peelii*), trout cod (*Maccullochella macquariensis*), golden perch (*Macquaria ambigua ambigua*), and silver perch (*Bidyanus bidyanus*) — weighing ≥200 g for surgical implantation of a radio transmitter in any one year. In addition, we tagged previously unmarked fish with external or PIT tags and recorded the species, mass, total length, subunit of capture, and tag number if already tagged. All captured fish were then returned to the water unharmed. We radio-tagged a wide range of size classes of the target species to test the effect of fish size on electrofishing capture probability (Table 2).

The tags used were two-stage, 35 pulses per minute, 150 MHz radio transmitters with 300 mm antennae (model F1835, F1850, and F1815/F1505 Advanced Telemetry Systems, Isanti, Minnesota, USA) that weighed between 7 and 55 g in air and had a guaranteed life span of between 160 and 1200 days. We selected the tag model for each fish to ensure that the transmitter mass never exceeded 1.5% of body mass, thus minimizing disproportionate effects of tag size on behaviour. All tags had a “mortality switch” (a mercury motion sensor), which indicated when the animal had either died or shed its tag. Tags on all captured fish were checked to ensure that they were still transmitting (to ensure that nontransmitting fish were not recorded as telemetry recaptures). Tags were implanted following standard surgical procedures (O'Connor et al. 2009).

After a minimum of 3 days following their release, we tracked all fish with radio transmitters from a boat using a receiver and antenna (KoeHN 2006). We began tracking before 0800, and then after 0900, two independent electrofishing teams separately fished eight subunits using the same procedures used to capture fish for radio transmitter insertions. The dominant behaviour for Murray cod, trout cod, and golden perch during daylight hours is sedentary (KoeHN 2009; Crook 2004; Thiem et al. 2008), and we expected little movement of individuals away from the study reach during the day of electrofishing. However we expected some movement of fish at night between sampling occasions and possibly in response to the capture and tagging process. To account for such movement, the tracking team remained on site during electrofishing to confirm whether radio-tagged fish had moved away from the 2 km reach

between the morning recording and the time of sampling by the electrofishing boat. The tracking team applied discreet procedures to ensure that the electrofishing team did not know whether radio-tagged fish were present during electrofishing. The tracking of approximately 100 tagged fish to their exact location was not possible within the constraint of needing to have completed most tracking before electrofishing began. However, we were able to narrow the position of radio-tagged fish to within two subunit lengths (500 m). We were thus able to estimate the likelihood of fish emigrating from the sampling area, thereby removing this potential source of bias from estimates of capture probability (analysis described below).

We repeated tracking and electrofishing a total of three times annually, with a minimum 3-day interval between each occasion (i.e., over a minimum of 12 and maximum of 45 consecutive days annually). Stress-related hormones have been observed in fish for up to 24 h after electrofishing (Mesa and Schreck 1989), so we assumed that the interval between electrofishing sampling occasions was sufficient for the fish to recover from any residual effect from the previous electrofishing experience.

We collected environmental descriptors for each of the 16 subunits to estimate their influence on capture probabilities. The mean depth of each subunit using visual observation of the vessel's depth sounder while fishing was done in each year of sampling. The volume of structural woody habitat in each subunit was estimated using the methods outlined in Kitchingman et al. (2013). Depth and volume of structural habitat were correlated (Pearson's $R = 0.85$), and we only included structural woody habitat to minimize collinearity. The primary environmental variables hypothesized to affect sampling conditions between years were river discharge (for which we obtained values from the Murray Darling Basin Authority), mean river depth (m), turbidity (Secchi depth, m), and conductivity (S·m⁻¹). We used Secchi depth as a descriptor of flow-related sampling conditions given it was highly correlated with discharge (which in turn was correlated with annual mean river depth; $R = 0.88$) and less correlated with depth ($R = 0.65$). Secchi depth varied yearly (along with discharge that varied yearly during sampling between 1.64 and 19.97 GL·day⁻¹ in 2007 and 2011, respectively), but was stable within years (Fig. 1; Table 1). We assumed that turbidity conditions were consistent between subunits. Water conductivity also influences electrofishing success, and we also obtained daily values of this from the Murray Darling Basin Authority. We centred all continuous variables on the mean across all years and for fish length. We also centred lengths on each species' mean lengths. Where squared values were used in modelling, we squared the centred values.

Analysis

Movement of fish within and between sampling subunits was a potential source of bias, both in terms of estimating overall capture probabilities due to emigration of tagged fish and to spatial and temporal variability in the influence of predictor variables. We therefore used the combination of telemetry and capture-recapture data in a state-space model (King 2012) to infer the likely locations and capture probabilities of fish given their location. We assumed that (*i*) fish could move freely within and out of the

Table 2. Species data and mean (range in parentheses) total length (TL) used during electrofishing capture efficiency investigations in the Murray River.

	2007	2008	2009	2010	2011	2012	2013	Total
Murray cod (<i>Maccullochella peelii</i>)								
Mean no. of radio-tagged fish	51 (47–54)	46 (41–49)	39 (37–42)	35 (32–37)	24 (19–29)	22 (18–26)	20 (19–23)	237
% Recaptures radio-tagged fish	19 (15–23)	13 (4–21)	25 (24–26)	23 (22–24)	7 (4–10)	16 (5–33)	13 (11–17)	
No. of transmitter mortalities	2	1	0	0	0	0	0	3
Total no. of conventionally tagged fish	127	81	66	45	22	30	58	429
Total no. of recaptured conventionally tagged fish	32	30	23	14	7	8	15	129
TL mean (mm)	368 (213–1260)	395 (221–1320)	386 (160–1150)	414 (228–1180)	493 (238–1280)	545 (288–1150)	433 (215–1340)	
Trout cod (<i>Maccullochella macquariensis</i>)								
Mean no. of radio-tagged fish	12 (11–12)	14 (11–17)	17 (16–17)	15 (13–17)	29 (26–32)	39 (38–39)	24 (23–25)	150
% Recaptures radio-tagged fish	0	7 (6–9)	10 (6–13)	18 (12–23)	6 (0–12)	4 (3–5)	5 (0–12)	
No. of transmitter mortalities	0	1	0	0	0	0	0	1
Total no. of conventionally tagged fish	122	148	191	148	71	180	64	924
Total no. of recaptured conventionally tagged fish	17	23	21	17	9	31	7	125
TL mean (mm)	301 (201–556)	286 (182–530)	285 (154–538)	297 (178–538)	354 (165–536)	361 (154–498)	367 (223–500)	
Golden perch (<i>Macquaria ambigua</i>)								
Mean no. of radio-tagged fish	26 (23–28)	28 (20–36)	14 (11–18)	16 (13–18)	14 (12–18)	30 (28–32)	38 (26–54)	166
% Recaptures radio-tagged fish	10 (9–11)	6 (0–14)	14 (9–17)	4 (0–6)	7 (0–22)	5 (3–7)	7 (4–9)	
No. of transmitter mortalities	0	0	1	0	0	0	1	2
Total no. of conventionally tagged fish	54	62	36	42	51	119	109	473
Total no. of recaptured conventionally tagged fish	9	6	3	2	6	10	12	48
TL mean (mm)	432 (308–535)	420 (265–581)	422 (260–526)	426 (295–532)	429 (226–542)	420 (249–553)	414 (230–547)	
Silver perch (<i>Bidyanus bidyanus</i>)								
Mean no. of radio-tagged fish	0	0	1	2 (1–3)	2 (1–2)	0	0	5
% Recaptures radio-tagged fish	0	0	0	0	0	0	0	
No. of transmitter mortalities	0	0	0	0	0	0	0	0
Total no. of conventionally tagged fish	31	51	42	135	37	95	24	415
Total no. of recaptured conventionally tagged fish	1	3	1	1	1	2	0	9
TL mean (mm)	367 (282–445)	368 (260–438)	371 (237–474)	281 (152–423)	331 (240–417)	305 (200–394)	356 (283–442)	

Note: Mean number of radio-tagged fish denotes only those that are available for capture (i.e., tracked within the study reach and averaged over sampling events).

sampling area, (ii) fish could not be caught if they left the sampling reach, and (iii) capture probabilities and movement patterns varied with environmental and individual covariates. In the subsequent sections, we describe the movement and capture components of the model.

Movement model

We used a Gaussian random-walk model to estimate the locations of unobserved fish based on their last-known locations (distance in 250 m segments and side of the river). We assumed that the location (in metres along the river) of a fish at time t would be shifted from its location at time $t - 1$ by a normally distributed distance $D_{i,t}$. Thus, the model for location $L_{i,t}$ in metres was

$$L_{i,t} \sim \text{Normal}(L_{i,t-1} + D_{i,t}, \sigma_{\text{species}})$$

where the full model for $D_{i,t}$ was a linear combination of parameters including fish species, fish length, site-level structural woody habitat volume (m^3), Secchi disk depth (m), and whether or not the fish was captured in the previous occasion (0 or 1):

$$D_{i,t} = \beta 0_{\text{species}} + \beta 1 \text{length}_i + \beta 2 \text{wood}_{\text{site}} + \beta 3 \text{Secchi}_i + \beta 4 \text{capture}_{i,t-1}$$

where $\beta 0_{\text{species}}$ is a normally distributed random intercept for each species, and each β indicates a normally distributed parameter. We estimated the coefficients for factors relating to fish characteristics (length and previous capture) as normally distributed, taxon-specific random coefficients, whereas parameters that related to sampling conditions (wood, conductivity, and turbidity) were treated as fixed effects common across species. We recorded the capture location for each fish as the centroid of the 250 m subunit where it was first captured and tagged, along with the side of the river. Because sampling only occurred within the 2 km study reach, our data for estimating $D_{i,t}$ were restricted to observations within the 2 km study reach, which could potentially bias our estimates of $L_{i,t}$. We therefore additionally specified in the model that the $L_{i,t}$ were censored at 0 and 2 km.

We were also able to use the telemetry data to put finer bounds on the locations of radio-tagged fish. First, we were able to discern whether each radio-tagged fish was in the 2 km reach. If it was absent, we were able to assign its location as either in the upstream or downstream segments beyond the 2 km reach and therefore not catchable. For individuals within the sampling area, we were able to truncate the distribution for $L_{i,t}$ to a 500 m section, allowing for greater precision in the estimation of D .

To determine in which bank of the river a fish was given its last location, we assumed that whether or not the fish switched sides at time t was the outcome of an exchangeable random Bernoulli trial:

$$B_{i,t} \sim \text{Bernoulli}(\varphi_i)$$

where the parameter φ_i is the probability of switching for individual i . We tested logistic regression models for φ_i that included species, river discharge, site, and the logit of φ_i . Based on $L_{i,t}$ and $B_{i,t}$ we assigned the site ($S_{i,t}$) of each unobserved fish as being in one of the 16 subunits or outside of the sampling reach. We then used $S_{i,t}$ to determine the conditional capture probability for each fish.

Electrofishing observation model

We modelled the observed captures $Y_{i,t}$ of each fish as exchangeable Bernoulli trials:

$$Y_{i,t} | S_{i,t} \sim \text{Bernoulli}(\theta_{i,t,S_{i,t}})$$

where $Y_{i,j} = 1$ if a fish is captured at time j and 0 if it is not, and $\theta_{i,t,S_{i,t}}$ is the probability of capture conditional on individual, time-, and site-dependent factors. For fish that remained within the sampled reach, we modelled $\theta_{i,t,S_{i,t}}$ using a logistic regression:

$$\begin{aligned} \text{logit}(\theta_{i,t,S_{i,t}}) = & \alpha 0_{\text{species}} + \alpha 1_{\text{species}} \text{length} + \alpha 2_{\text{species}} \text{length}^2 \\ & + \alpha 3_{\text{species}} \text{radio} + \alpha 4 \text{wood} + \alpha 5_{\text{species}} \text{capture}_{t-1} \\ & + \alpha 6 \text{Secchi} + \alpha 7 \text{conductivity} + \alpha 8 \text{wood}_{\text{site}} \\ & \times \text{length}_i + \alpha 9 \text{conductivity} \times \text{length}_i \end{aligned}$$

where each α is a normally distributed parameter specific to each predictor, and $\alpha 0_{\text{species}}$ is a normally distributed random intercept for each species. Because of the differences in size, behaviour, and habitat choice in the four species used in this study, we included species-specific random coefficients for all fish characteristics (individual length, whether they had a radio tag implanted, whether they were captured in the previous occasion). For sampling-related parameters (for each subunit, structural woody habitat volume, water turbidity – Secchi disk depth for each day of sampling, and water conductivity), we tested models both with species-specific random effects and with effects assumed to be the same across species.

Model ranking

We took a multistep approach to model ranking. We first ran all possible combinations of models in which the movement parameters varied and capture probabilities were assumed to be equal across all individuals. We recorded the deviance information criterion (DIC; Spiegelhalter et al. 2002) scores. We then built a set of 180 candidate models that included different combinations of random and fixed parameters in the conditional capture model. Where variables were potentially correlated (such as habitat complexity and site depth), we excluded combinations of strongly correlated variables. We compiled all models for the JAGS programming language (Plummer 2003) and ran them using the R2jags package (Su and Yajima 2012) in R (R Development Core Team 2013). Using a 24-core desktop computer, we ran each model with three chains in parallel for 200 000 iterations, with a burn-in period of 50 000 iterations and keeping every 150th sample using the GIBBSIT (Raftery and Lewis 1996) procedure in R (library = mcgibbsit) (Warnes 2011) to confirm that chains were sufficiently long. We also calculated Bayesian p for each model to provide an indication of goodness of fit. For the top-ranked model, we reported the mean value of the posterior distribution of Markov chain Monte Carlo (MCMC samples) for each parameter, as well as 95% Bayesian credible intervals.

Results

River discharge, water height, turbidity, and conductivity were relatively stable within years but varied between sampling years (Table 1; Fig. 1). In particular, during the first 4 years of the study, water levels were low and had comparatively low turbidity (i.e., high Secchi depth readings). In contrast, year five of the study was dominated by higher discharge and turbid sampling conditions. Years six and seven had moderate discharge and turbidity readings (Table 1). Within each 250 m subunit, structural woody habitat loadings were measured once during 2013 (Table 3), varied between 0 and 188 m^3 , and were assumed to have been stable over time. During the 7-year electrofishing study, we captured and tagged 2241 fish and implanted 558 radio transmitters across all species (Table 2). Species-specific values are reported in Table 2.

The first step of model ranking revealed that a model including factors for taxon and a taxon-specific coefficient for fish length was the top-ranked by over 10 DIC points (DIC = 6630 versus 6640 for the next-highest ranked model). We therefore proceeded with model selection using these two factors in all subsequent models.

Table 3. Mean depth and structural woody habitat loadings within the 16 subunit sites.

Subunit	Mean depth 2007 (m)	Habitat loading (m ³)
1	1.1	46.2
2	1.2	117.5
3	1.1	74.03
4	1.1	14.62
5	0.6	14.62
6	0.5	119.34
7	1.5	102.34
8	1.5	99.58
9	1.7	58.48
10	0.9	99.58
11	0.7	102.34
12	2.1	188.16
13	2.2	16.48
14	1.8	14.62
15	1	0
16	0.9	74.03

The next step of model ranking revealed that the top-ranked model for conditional capture probability included a random intercept for taxon, a species-specific quadratic relationship with individual fish length, turbidity, conductivity, structural woody habitat loadings, presence of a radio tag and a species-specific interaction between conductivity and fish length. This model was also related to a similar model in which the conductivity \times length interaction was exchanged for a species-specific interaction between structural woody habitat loading and fish length (Table 4). Both of these top-ranked models had high Bayesian p (0.46, Table 4), indicating good model fit.

We estimated the species-specific probability of being captured during any single survey in each year using the length, turbidity, conductivity, and taxon parameter estimates (Table 5), along with the mean lengths of species within each year and annual turbidity and conductivity. In general, Murray cod had the highest annual capture probabilities (mean = 0.24, range: 0.16 to 0.31), followed by trout cod (mean = 0.083, range: 0.05 to 0.11), golden perch (mean = 0.08, range: 0.03 to 0.08), and silver perch (mean = 0.005, range: 0.001 to 0.01) (Fig. 2). For all species, capture probabilities were lowest in 2010–2011 and highest in 2009. On average, capture probabilities increased when Secchi disk readings were higher.

For all species, fish length was related to capture probabilities, with some species (Murray cod, trout cod, golden perch) having a quadratic relationship with fish length (Table 5), although the linear parameter for length in all species was imprecise, with 50% credible intervals that overlapped 0. We therefore included only the quadratic term when describing the relationship between length and capture probability, resulting in a peaked relationship for most species. For Murray cod and golden perch, fish \sim 400 mm had the highest capture probabilities, whereas the maximum was \sim 350 mm for trout cod (Fig. 3). There was a weak negative relationship between conductivity and capture probabilities, with the difference in conductivity encountered (0.0028 S·m⁻¹ in 2007 versus 0.0072 S·m⁻¹ in 2012) resulting in a 20% increase in relative capture probabilities, although the 95% credible intervals for the conductivity parameter overlapped 0 (Table 5). In addition, the model showed a positive length \times conductivity interaction for golden perch and a weakly supported interaction for trout cod and silver perch, indicating that larger fish were relatively more likely to be captured as conductivity increased. (We note here that the conductivity range tested during our experiment is small.) The amount of structural woody habitat at a subunit level influenced capture probability, with fish being almost twice as likely to be captured in sites with high structural woody habitat loads than in

Table 4. Model descriptions top-ranked models for capture probability according to the deviance information criterion (DIC).

Capture Model	pD	p	DIC	Δ DIC
Telemetry tag, Secchi, wood volume, length, length, conductivity, (wood volume \times length)	320	0.460	6491	0
Telemetry tag, Secchi, wood volume, length, length, conductivity, (conductivity \times length)	320	0.460	6491	0
Telemetry tag, Secchi, (wood volume + length)	321	0.425	6496	5
Telemetry tag, wood volume, length	314	0.427	6496	5
Telemetry tag, Secchi, wood volume, length, conductivity, (wood volume \times length), (conductivity \times length)	329	0.467	6498	7
Telemetry tag, wood volume, length, (wood volume \times length)	322	0.443	6499	8
Telemetry tag, wood volume, length, conductivity, (conductivity \times length)	322	0.443	6499	8
Telemetry tag, wood volume, length, conductivity, (wood volume \times length), (conductivity \times length)	327	0.444	6500	9

Note: All models included a random intercept for taxon and shared same movement model (taxon + length). Table headings: pD is a measure of the number of parameters used; p indicates Bayesian p and Δ DIC is the relative difference between each model and the top-ranked model. Where terms are subscripted by “species” in the text, the term is species-specific.

sites with low structural woody habitat loads. There was also a positive relationship between capture probability and wood volume \times fish length, indicating that larger fish were more likely to be captured as wood volume increased (Table 5). The top-ranked models did not include a term for whether or not a fish had been captured on a previous occasion (Table 4).

The movement model demonstrated that on average, fish did not move from their site, but that movements of up to two sites away in either direction (upstream or downstream) were possible. The mean distance moved was close to zero sites, with standard deviations of around one site for all species, and larger fish moved farther downstream between sampling occasions than did smaller fish (Table 5). Site and turbidity were not included in the top-ranked models; however, the top-ranked model did include a random effect for site in the probability of switching banks. On average, site-specific bank-switching probabilities ranged from 0.05 to 0.35 (mean = 0.15).

We did not find evidence for spatial autocorrelation between catch rate in adjacent subunits (Mantel’s I ; $p > 0.08$ for all species and years). In the movement model, fish mostly stayed within the subunit in which they were captured, and if they did move, it was most likely to an adjacent subunit. As a consequence, fish that were tagged in subunits closer to the margins of the 2 km reach were more likely to migrate out between sampling events, although some did return.

Discussion

Our experiment represents a method for estimating the capture probability of fish (electrofishing efficiency) — information necessary to construct protocols for the credible estimation of fish population parameters and trends. Without estimates of capture probability, the ability to track changes in fish population size as a function of environmental variation or in response to a particular condition is potentially compromised. Others have used alternative methods coupled with electrofishing, such as netting, trawling, piscicides, explosives, or draining of the water body, to estimate capture probability (e.g., Bayley and Austen 2002;

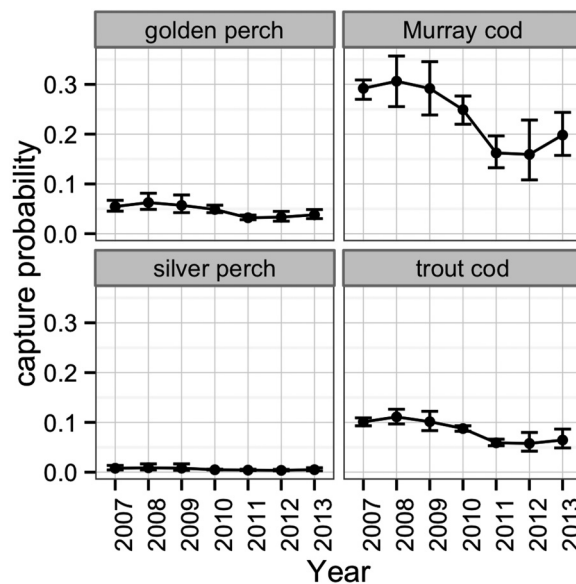
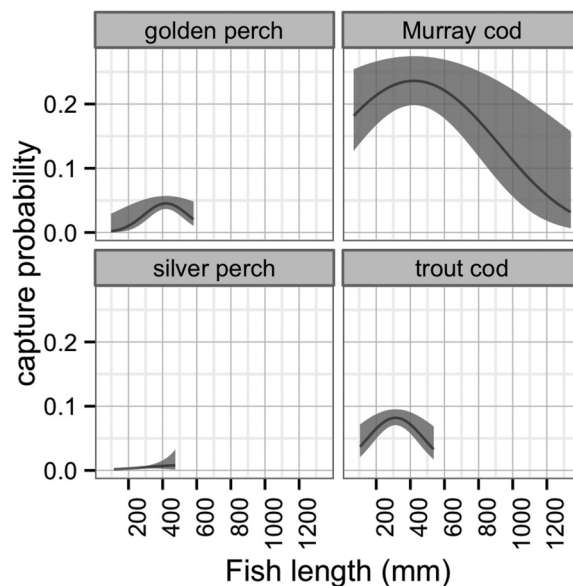
Table 5. Model-averaged parameter estimates for the two top-ranked models based on the deviance information criterion (DIC).

Parameters	Value
Intercept(mc)	-1.174 (-1.771, -0.479)
Intercept(sp)	-5.235 (-6.444, -4.273)
Intercept(tc)	-2.416 (-2.879, -1.938)
Intercept(gp)	-3.049 (-3.816, -2.351)
Conductivity	-0.008 (-0.021, 0.004)
Conductivity × length(mc)	0 (-0.003, 0.004)
Conductivity × length(sp)	0.012 (-0.004, 0.03)
Conductivity × length(tc)	0.004 (0, 0.008)
Conductivity × length(gp)	-0.008 (-0.021, 0.004)
Length ² (mc)	-0.027 (-0.08, 0.022)
Length ² (sp)	-0.085 (-1.072, 2.148)
Length ² (tc)	-0.194 (-0.526, 0.057)
Length ² (gp)	-0.314 (-1.199, 0.189)
Secchi	0.864 (-0.043, 1.687)
Telemetry(mc)	0.498 (-0.103, 1.146)
Telemetry(sp)	0.424 (-1.454, 2.148)
Telemetry(tc)	-0.044 (-0.702, 0.52)
Telemetry(gp)	0.744 (0, 1.551)
Wood volume	0.01 (0.008, 0.014)
Wood volume × length(mc)	0 (-0.003, 0.004)
Wood volume × length(sp)	0.012 (-0.004, 0.03)
Wood volume × length(tc)	0.004 (0, 0.008)
Wood volume × length(gp)	0.007 (-0.001, 0.017)
Movement parameters	
Length(mc)	-0.11 (-0.2, -0.01)
Length(sp)	-0.26 (-1.01, 0.29)
Length(tc)	-0.09 (-0.26, 0.11)
Length(gp)	-0.32 (-0.85, 0.03)
Intercept(mc)	-0.18 (-0.33, -0.06)
Intercept(sp)	-0.16 (-0.66, 0.24)
Intercept(tc)	-0.07 (-0.24, 0.12)
Intercept(gp)	-0.13 (-0.34, 0.1)
Standard deviation(mc)	1.08 (0.998, 1.098)
Standard deviation(sp)	1.09 (1.07, 1.12)
Standard deviation(tc)	1.09 (1.08, 1.11)
Standard deviation(gp)	1.11 (1.10, 1.12)

Note: All fish-specific parameters have taxon-specific estimates (mc, Murray cod; sp, silver perch; tc, trout cod; gp, golden perch). Data in parentheses indicate 95% Bayesian credible intervals around parameter estimates. Interaction terms are denoted with "×". Length parameters are based on length measured in millimetres.

Achleitner et al. 2012; Hedger et al. 2013), but our nonlethal approach is a more acceptable method, especially for native and threatened species.

Capture probability varies across several important environmental, biological, and methodological gradients in large lowland river systems (Bayley and Austen 2002; Speas et al. 2004) and is specifically related to habitat use by the target species (Mouton et al. 2012). It is therefore important to estimate the degree to which capture probability varies under specific sampling and environmental conditions so that the statistical robustness of population estimates can be assessed and, where possible, corrected accordingly as a function of the calibrated gear methodology (Bayley and Austen 2002). Specifically, we determined that peak electrofishing detection in this system varied according to species, but was generally at its maximum for all species in the range of 300–450 mm total length (Fig. 3). Larger fish are generally the most susceptible to electrofishing because of their greater electric potential differences (Zalewski and Cowx 1990) and nerve dimensions stimulated by the electrical field (Lamarque 1990; Reynolds 1996). However, in larger lowland rivers (>50 m wide), this trend could be counteracted by the tendency for larger fish to occupy deeper habitats that are more impacted by turbidity and where capture probability is generally lower (e.g., Bayley and Austen 2002; Mouton et al. 2012). Our results support this hypothesis, and

Fig. 2. Mean probability that a tagged fish of average size will be captured by an electrofishing survey given that it is present in a sampling site and given the mean sampling conditions (across all days of sampling and all sites sampled) in each year. Data for each year are calculated based on the model-averaged parameters in the top two capture models. 95% credible intervals are also indicated.**Fig. 3.** The relationship between mean probability of being captured in a single survey and mean length for each of the four species studied: Murray cod, trout cod, silver perch, and golden perch. Grey areas indicate 90% credible intervals. Each curve is based on the model-averaged taxon-specific intercept and length squared parameters estimated in the two top capture probability models.

electrofishing might result in an under-representation of large adult fish in samples taken from lowland rivers.

We demonstrate that in the same site, using the same gear and settings, and with experienced electrofishing crews, capture probability can vary markedly both within and among years (Fig. 2). Our estimates of capture probability are consistent with other estimates for single- and multipass electrofishing in large rivers

(Bayley and Austen 2002), indicating that this capture method detects fish with a probability typically <0.5 (and in our case, well below that). Species-specific detection varied considerably over time; for example, Murray cod detection varied from 0.16 to 0.310 over the 7-year trial. By contrast, trout cod capture probabilities were relatively stable (0.07 to 0.12). Although morphologically similar (apart from differences in adult size), these two species occupy different habitats in riverine systems (Koehn 2009); therefore, differential habitat use is more likely to be the principal determinant of capture probability rather than differences in species morphology (see Mouton et al. 2012).

Mesa and Schreck (1989) found that cutthroat trout (*Onchorhynchus clarkii*) hid in more complex habitats after electrofishing. Lowland, warm-water species are often more cryptic than salmonids, and Australian freshwater cods and perch are strongly associated with complex habitats (Koehn 2006). Electrofishing teams can exploit this during sampling, and the increases in capture probabilities associated with wood volume likely reflects an increase in the efficiency of the electrofisher operators (who know where to “look” for fish when habitat is present). As such, we suggest that accounting for habitat volume and other interactions between the behaviour of fish and fishers in detection models will be important for estimates of population size.

Had our marked fish avoided the electrofishing teams, we would have expected a reduction in capture probability over time. Instead, we found no evidence that a fish captured in the previous sampling period was more or less likely to be captured again in the following period. As such, the high variance we observed likely represents random variation associated with this monitoring method and probably reflects normal fluctuation in fish behaviour. Indeed, Bohlin and Cowx (1990) found that a small proportion of any population appears to be invulnerable to capture by electrofishing and that this proportion varies between species and habitat complexity. Mesa and Schreck (1989) suggested that wild cutthroat trout require at least 24 h to recover from electrofishing, tentatively indicating this should be the minimum time elapsed between passes. Our minimum recovery time of 3 days between sampling events (noting that this was not a depletion trial — we returned all captured fish for potential resampling) was thus sufficient to avoid capture probability biases.

Sampling conditions also played an important role in determining capture probabilities. In deep and turbid waters, electrofishing capture efficiency is typically low (Bayley and Austen 2002), although in some shallower and moderately turbid waters, capture efficiency can be higher (e.g., for salmonids; Speas et al. 2004). Deep, turbid waters are characteristic of most lowland rivers, but we still observed a decreasing capture efficiency as turbidity and daily river discharge increased. In particular, our ability to detect Murray cod in 2011, where sampling was done during river discharge of around $15 \text{ GL}\cdot\text{day}^{-1}$, was approximately half of when sampling was done at flows of $1.8\text{--}2.5 \text{ GL}\cdot\text{day}^{-1}$. One explanation is that increased turbidity and river discharge hamper electrofishing crews from seeing stunned fish in the water (Pygott et al. 1990; Flotemersch et al. 2011). Further research is required to obtain an understanding of the individual effects of both depth and turbidity, and by recording maximum depth at the site of capture for each fish, a “proportion of the water visible” estimate can be calculated and included in models. Variation in water conductivity can also affect capture probability. In our case, water conductivity fluctuated little across time (between 0.0028 and $0.0072 \text{ S}\cdot\text{m}^{-1}$ over all sampling events). Even so, conductivity appeared consistently in our top-ranked models; and while this was true across all size classes, larger fish were more likely to be captured as conductivity increased. Because of the link between conductivity and turbidity, this interaction suggests that the relationship between conductivity and capture probability is driven more by electrochemical

phenomena for larger fish, whereas for smaller fish, the relationship is mainly driven by water turbidity.

In summary, our results show that the effectiveness of electrofishing can vary considerably in large lowland systems. Unless the data can be corrected for such variation in capture probability, any population estimates arising should be viewed with caution (Cowx 1995; Flotemersch et al. 2011). We have shown how a model that can correct for variation in sampling conditions can account for some of this variation in capture probabilities. Unfortunately, estimating stream-specific capture probability is both difficult and expensive. To that end, Bayley and Austen (2002) recommended that “calibration” projects be implemented to estimate capture probability across a range of environmental conditions, fish species, and fish sizes. A benefit of such an approach is that it requires only a single investment, rather than trying to gather detection data for every project where electrofishing is used. In this case, care must be taken to account for variability between survey teams and other external conditions.

As such, we recommend that calibration should be a regular part of any sampling design where funding permits. As a general recommendation, sampling should include some level of replication to allow for assessment of the variation in capture that is due to sampling alone. Where possible, analysis of sampling efficiency can be augmented when sampling known populations, as we demonstrate here. We note that for many studies, this might be infeasible because of logistic constraints (Flotemersch et al. 2011). In some cases, it might be suitable to analyse relative change in fish population structure, or fish body condition, rather than total population size or comparisons of catch per unit effort. However, this approach should be used with caution, given that prevailing environmental conditions as well as the characteristics of individual fish can influence capture probabilities; thus, certain cohorts might go undetected in some conditions unless sufficient replication is applied. Furthermore, any calibration made on groups of fish that have different likelihood of detection — such as those that can emigrate undetected from the study area — should take into consideration the confounding effect of permanent or temporary migration. Failing to do so could introduce substantial bias into estimated parameters.

Sampling for cryptic taxa within inherently variable systems will always introduce some uncertainty. Given this, electrofishing is and will continue to be one of the safest, most cost-effective, and most easily replicated methods with which to survey large-bodied fish in freshwater environments. However, we promote active and ongoing research to increase our understanding of its limitations, which in turn will improve study design and increase the confidence of population parameter estimates.

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Chapter 5

Increased population size of fish in a lowland river following restoration of structural habitat

Statement of Authorship

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Publication Details	Lyon, J.P., Bird, T., Kearns, J., Nicol, S., Tonkin, Z., Todd, C., O'Mahony, J., Hackett, G., Kitchingman, A., Bradshaw, C.J.A. (in review). A large-scale, multi-year field trial demonstrates increased carrying capacity of fish in a lowland river following a structural habitat restoration program. Submitted to Ecology and Evolution, December 2017. 35 pp.

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Name of Principal Author (Candidate)	Jarod Lyon		
Contribution to the Paper	Developed methodology, led sampling teams, undertook fish surgery and tagging, led data collection, compiled data, interpreted data, wrote manuscript, acted as corresponding author		
Overall percentage (%)	80%		
Certification:	This paper reports on original research I conducted during the period of my Higher Degree by Research candidature and is not subject to any obligations or contractual agreements with a third party that would constrain its inclusion in this thesis. I am the primary author of this paper.		
Signature		Date	18/12/17

Co-Author Contributions

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

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

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Increased population size of fish in a lowland river following restoration of structural habitat

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Summary

Most assessments of the effectiveness of river restoration are done at small spatial scales (<10 km) over short timeframes (< 3 y), potentially failing to capture large-scale mechanisms and time-lags of ecosystem response. To test the hypothesis that populations of two species of large-bodied, predatory native fishes would increase in response to a large-scale structural habitat restoration program, (re-introduction of 4450 structural woody habitats into a 110-km reach of the Murray River, south-eastern Australia), we collected annual catch, effort, length, and tagging data over eight years for Murray cod (*Maccullochella peelii*) and golden perch (*Macquaria ambigua*) in a restored ‘intervention’ reach and three neighbouring ‘control’ reaches. We supplemented mark-recapture data with telemetry and angler phone-in data to assess the potentially confounding influences of migration among sampled populations, heterogeneous detection rates, and population vital rates. A Bayesian hierarchical model was used to estimate changes in population parameters including immigration, emigration, and mortality rates. For *M. peelii*, we observed a three-fold increase in abundance in the population within the intervention reach, while populations declined or fluctuated within the control reaches. *M. ambigua* densities also increased 2-fold, in the intervention reach. Our results indicate that restoring habitat heterogeneity, by adding structural woody habitats, can increase the abundance of target fish populations and raise the carrying capacity of fish in a large, lowland river. Successful restoration of poor-quality ‘sink’ habitats for target species relies on connectivity with high-quality ‘source’ habitats. We recommend analysis of restoration success across appropriately large spatial and temporal scales can help identify mechanisms and success rates of other restoration strategies such as restoring fish passage or delivering environmental water.

Keywords: Structural woody habitat, stream restoration, Murray cod, golden perch,

resnagging, meta-population, scale, citizen science

Introduction

Demonstrating tangible outcomes of catchment restoration, particularly at broad spatial scales (> 100s of km) has been challenging (Bernhardt *et al.* 2005; Palmer *et al.* 2005), and most assessment of ecological outcomes have focussed on restoration of smaller restoration efforts (Lake 2001; Palmer *et al.* 2005). The long timeframes of ecological responses seldom align with the shorter timeframes of funding programs (Bernhardt *et al.* 2005; Lindenmayer *et al.* 2012; Cooke *et al.* 2017), and it can be difficult to disentangle the effects of management interventions from those arising from other environmental drivers (e.g., climate variation) without appropriate spatial replication and/or extensive time-series data (Likens 1989; Frainer *et al.* 2017). One strategy increasingly applied is to shift effort from monitoring many smaller interventions to assessing fewer, longer-term restoration projects and investing more resources into well-designed monitoring programs (Callahan 1984; Lindenmayer *et al.* 2012; Lohner & Dixon 2013). This approach assumes that learning from a few well-monitored interventions will provide more robust evidence for effective application of the interventions elsewhere (Swirepik *et al.* 2015). However, examples of broad-scale river restoration successes backed by rigorously designed monitoring programs, especially of large enough spatial and temporal scales, remain scarce.

Predatory fish are useful indicators of ecological processes, such as carbon uptake occurring at lower trophic scales (e.g. Tonkin *et al.* 2017), are highly valued by society for commercial and recreational purposes (Feather, Hellerstein & Hansen 1999) and often need ecological restoration following anthropogenic disturbances to waterways that exclude them from optimal habitats (Collares-Pereira & Cowx 2004; Dudgeon *et al.* 2006). Globally, restoration and threat abatement efforts to halt and reverse these declines include restoring

fish passage, removing pests, providing environmental flows, re-stocking, revising fishing regulations, changing land practices, and restoring habitats (Dudgeon *et al.* 2006). One restoration method is reintroduction of structural woody habitat. Structural woody habitat plays many roles within stream networks (Zalewski, Lapinska & Bayley 2003), and for riverine fishes it provides habitat and protection for feeding, shelter and spawning (Crook & Robertson 1999; Tonkin *et al.* 2016). Given the ecological importance of SWH, it is logical to test the response of target fish populations to restoring habitats, both to demonstrate ecological outcomes and justify future investment.

Our study examines the response of the fish in a reach of the Murray River in south-eastern Australia where structural woody habitat was restored (an ‘intervention’ reach), with three neighbouring populations of fish in ‘control’ reaches. Using the *a priori* predictions of the conceptual model (that our intervention would increase carrying capacity of native fish within intervention reach), we modelled the changes in population size of two large native predatory fish species — Murray cod (*Maccullochella peelii*) and golden perch (*Macquaria ambigua*) over eight years following restoration within the intervention and control reaches. While studies by Nicol *et al.* (2001) and Nicol *et al.* (2004) provided data that showed that large-bodied fish used restored habitats, our aim was to test the hypothesis that restoration of structural woody habitat at a reach scale (> 100 km) in a restored reach of large, lowland river results in a net increase population size for two target species of native fishes rather than merely redistributing fishes already present.

Methods

System overview

The Murray River is Australia’s longest river and forms a major component of the Murray-Darling Basin with a catchment area of 1.07 million km² (Walker 1992). Flow is highly

regulated for irrigation with large impoundments on the Murray River and its tributaries (Walker 1992). The natural flow regime was highly variable, characterised by peak flows in winter and spring, with low flows in summer and autumn. Flow regulation has reversed the seasonal pattern such that flows peak in summer and are lowest in winter, although some variability remains (minimum flow is 25% of mean, maximum is over 200% of mean), (Rutherford 1991).

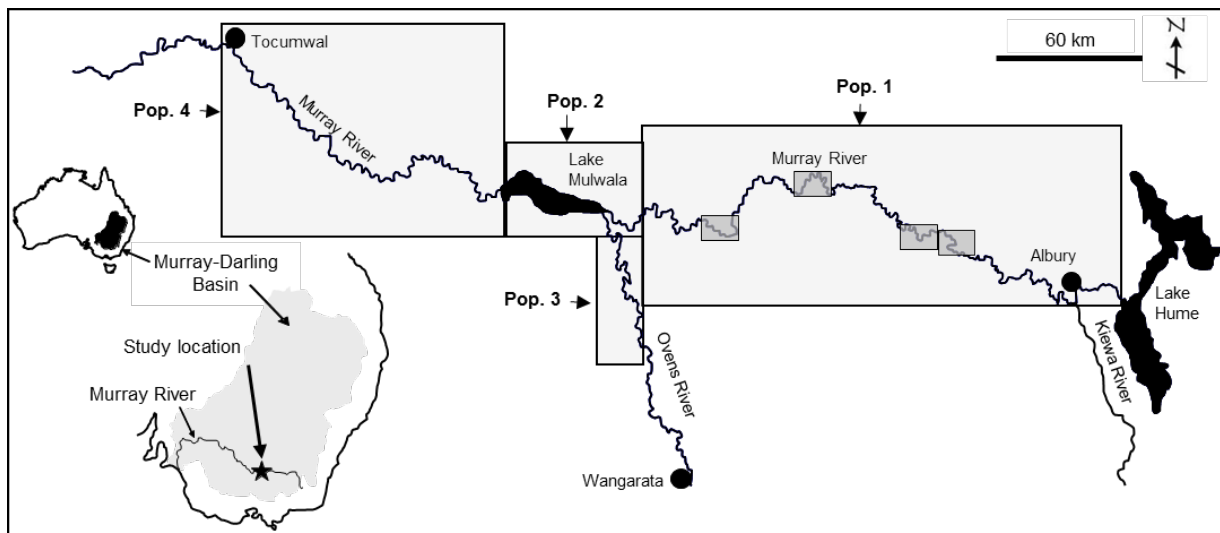
The two species in this study are medium- to large-bodied (Murray cod > 50 kg and 1400 mm maximum size, with females reproductively mature at 500 mm length with up to 100,000 eggs produced in large females; golden perch > 10 kg and 600 mm maximum size, with females reproductively mature at 300 mm length with up to 500,000 eggs produced in large females) native freshwater fish with a strong association with instream habitat that they use for refuge, cover for ambushing prey, and spawning sites (Koehn & Nicol 2014). These species are also long-lived; Murray cod can live up to 48 years (Anderson, Morison & Ray 1992), and golden perch up to 26 years (Mallen-Cooper & Stuart 2003).

Study description

Our study populations can be described as an ‘intervention reach (where structural woody habitat restoration works were done) and three ‘reference’ populations. These populations had varying connectivity (Fig. 1). The most upstream population (*population 1*) in the ‘intervention reach’ where we restored wood is in a section of the Murray River approximately 120 km long from Lake Hume to the junction of Lake Mulwala. The intervention was done between the years of 2007 and 2010 and involved reintroduction of 4450 large (mostly > 1 tonne) pieces of structural woody habitat sourced from natural trees recovered from a nearby, large road project, within four 5000-m priority zones interspersed at varying distances along the reach (Fig. 1). Data collection in this reach commenced in 2007,

prior to structural woody habitat restoration works, and forms the basis for a ‘before’ intervention baseline dataset. *Population 2* is located immediately below the intervention reach in Lake Mulwala and its tailwaters into the Murray and Ovens Rivers; this reach is formed by a 7-m weir used to divert water for irrigation and covers an area of 4450 ha when full. The Ovens River flows into the intervention reach approximately 5 km above its confluence with Lake Mulwala (Fig. 1). *Population 3* occupies the 80-km reach of the Ovens River between this confluence and the township of Wangaratta. *Population 4* is located immediately below Lake Mulwala downstream to the township of Tocumwal, a reach approximately 100 km long.

Figure 1: The study location in south-eastern Australia. *Pop* = Population. Priority resnagging zones are indicated by grey shaded boxes within *population 1*. Yearly number of sites sampled in each population can be found in Table S2.



Before restoration, Murray cod and golden perch abundances in *populations 2, 3 and 4* were considered ‘high’, whereas abundance of these two species in *population 1* was ‘low’ because of altered hydrology and lack of structural habitat (Nicol *et al.* 2004). Fish passage between *populations 1, 2 and 3* is unrestricted in all directions (Koehn *et al.* 2009), and

populations 2 and 3 are potential source populations each other and for *population 1*. While fish can pass downstream to *population 4* over weir gates or upstream from *population 4* via a fish lift which, movement is still restricted compared to background levels (Stuart *et al.* 2010).

Habitat types in the reach inhabited by *population 1* range from shallow, fast-flowing sections nearer Lake Hume to slow-flowing deeper pools (> 4 m) closer to Lake Mulwala (Fig. 1). This reach is degraded, with poor riparian and instream habitats with altered flow regimes. Over 25000 large pieces of structural woody habitat were removed from this reach from 1950 to 1980 to improve water conveyance. Depth (maximum depth = 14 m), flow, and turbidity characteristics of the reaches inhabited by *populations 2 and 3* differ from the other study reaches, and hydrology in the lower section of *population 3* is influenced by water levels in Lake Mulwala. A lake drawdown affected this hydrology during the sampling period of 2011, and may have impacted abundance estimates in *populations 2 and 3* for that year. The *in situ* structural woody habitat loads for *populations 2, 3 and 4* are high compared to that available to *population 1* (Kitchingman *et al.* 2016). Some removal of structural woody habitat occurred historically in the reach of *population 4*; however, the instream habitat is comparatively undisturbed, with large volumes of naturally occurring woodfall in the reach (Nicol *et al.* 2004). The depth characteristics of *population 4* resemble those in *population 1*. When irrigation offtakes exceed Ovens River inflow, the presence of Lake Mulwala leads to lower flow volumes in *population 4* than in *population 1*; however, the hydrograph remains essentially the same (Fig. S1).

The short distances between each of the populations (< 50 km) mean that they experienced similar climatic variation over the study period. Despite the Ovens River (*population 3*) being unregulated, river discharges and temperatures were consistent across all reaches over the study period (Fig. S1). River discharges and water temperatures had high

inter-annual variation, primarily driven by reduced inflows from 2006 to 2010 associated with the ‘Millennium drought’, severe flooding in 2010-2011, and the return of long-term average conditions during the final two years of the study (Dijk *et al.* 2013).

Given this spatial arrangement, we expected little difference in population dynamics across our study reaches arising from among-site climatic variation. We hypothesized that survival estimates among populations would be similar. Higher rates of movements were predicted from *population 2* and *3* into *population 1*, and lower movement rates from *population 4* into *populations 1* to *3* due to the obstruction imposed by the weir.

Monitoring design

We designed our monitoring approach to estimate annual changes over eight years in population size of both native fish species within the four study populations (Table S1, Note S1). We used a capture-mark-recapture approach to estimate population parameters for each species. Capture-mark-recapture techniques are potentially biased where individuals have systematic differences in their probability of detection (Huggins 1989), and where they can migrate in and out of the study area. For example, fish of varying sizes might occupy different habitats within a reach, which could affect sampling efficiency and lead to potentially large differences in capture probabilities (Bird *et al.* 2014; Lyon *et al.* 2014). To account for these potential sources of bias, we modified our sampling program by using (1) multiple sources of capture information, (2) focussed experiments to characterise capture rates, and (3) radio-tagging technology to estimate movement rates between reaches and estimate natural mortality. We complemented these data with measures of species-specific age and length structure; biomass, derived using region-specific length-weight relationships; movement and survival data derived from 1159 radio-tagged fish (fitted with mortality switches to identify when an animal had died); and fishery-dependent data collected through

an angler tag-return program.

Our survey sites were randomly located along the intervention reach (and not just the four priority resnagging priority zones; Fig. 1), to account for the possibility that the fish populations were governed by variability in available resources (i.e., the movement of fish into the intervention reach would mean a reduction of fish in adjacent reaches). Annual boat electrofishing surveys were done in discrete sites (150-250 m long, or about 1 ha) from 2006 to 2013 across the four populations (Table S2) between April and June each year. Reduced river discharge and flow variability at this time of year (i.e., end of the irrigation season) maximised electrofishing sampling efficiency (see Lyon *et al.* 2014). Nevertheless, there was still some variation in catch rate among years (Fig. S2).

Capture-mark-recapture

Using Smith-Root generator-powered pulsator boat-mounted electrofishing units, we collected fish with a single-pass, three-stage process that sampled all available habitats (described in more detail in Nicol *et al.* 2004; Nicol 2005). We weighed each captured fish to the nearest gram and measured its total length and/or fork length to the nearest millimetre. A uniquely coded external t-bar or dart tag was inserted adjacent to the dorsal fin on the left side of each fish > 200 mm in total length, and a Passive Integrated Transponder (PIT) tag was inserted into the stomach cavity. The external tags clearly displayed details for anglers to report relevant capture data (species, date, place of capture and fish length). Yearly detection studies informed our estimates of detectability across each species, sizes and environmental gradients. Briefly, we found that river discharge, species, and size class were important elements influencing rates of detection (see Lyon *et al.* 2014).

Citizen science

While electrofishing provided a replicable and robust basis for our capture-mark-recapture program, recapture rates in some reaches were low. Given potentially high rates of angling pressure in our study populations (J. Lyon, unpublished data), we sought help from recreational anglers to produce additional data to reduce uncertainty in parameter estimates. We used an angler phone-in program to collect tag return, location, size and mortality data from the public (via the details provided on our externally tagged fish). Combining tag-reporting by citizen scientists with capture-mark-recapture studies has been previously shown to improve parameter estimation (Barker 1997; Barker, Burnham & White 2004).

Radio tagging

Capture-mark-recapture models assume a ‘closed’ population where all animals are available for capture within a survey site between one sampling time and the next (Pradel 1996). In addition, angler and electrofishing data can only be collected from live fish, meaning that mortality must be inferred when using standard techniques. Because our study species are mobile, capture-mark-recapture estimates of populations can be biased, so we implanted a subsample (1159 individual fish —Table S3) with radio transmitters (150 MHz frequency; Advanced Telemetry Systems, Isanti, Minnesota, USA) to measure rates of immigration and emigration (see methods outlined in O’Connor *et al.* 2009). The appropriate size of implanted radio-transmitters depended on the weight of the fish, with the proportion of transmitter weight to body weight < 1.5% in air, to avoid compromising fish buoyancy. This ratio of transmitter weight to body weight has minimal effect on survival rates (Saddler, O’Mahony & Ramsey 2008). Battery life depended on the size of the transmitter, ranging from 45 to 1200 days. A proportion of the transmitters were coded with an 11 month off/one month on cycle to save battery life (and hence enable smaller transmitter size), so that mortality of

smaller fish could be tracked for greater periods (i.e. these fish were tracked for mortality signals during the one month 'on' period). We also marked radio-tagged fish with external t-bar/dart tags to account for mortality from removal by anglers.

To improve estimates of survival and movement rates derived through the capture-mark-recapture study, radio-tagged fish were recorded via an array of fixed radio towers to monitor movement between populations, and annual tracking surveys done to estimate mortality rates (via the mortality switch in the transmitters). Annual censuses of radio tags revealed fish location and mortality across all four study reaches. Given that fish often moved between reaches during foraging or spawning movements, condensed data to what we describe as 'permanent' migrations to inform our model. We assume that 'permanent' change occurred when an individual changed populations from where it was initially tagged for a period of at least 4 months prior to the end of the battery life of a transmitter.

Bayesian state-space model

We used a Bayesian implementation of a state-space model (King 2012) to estimate the probability of detecting individual fish within each study reach in each year, while accounting for the effects of individual variation in capture probabilities that arose due to inter-reach migration, mortality, sampling conditions, and effort. After accounting for such heterogeneity, we used modified estimates of size, population and year-specific estimates of individual capture probabilities to adjust the observed numbers of fish in each size class to expected numbers in the meta-population.

Our model was based on a Cormack-Jolly-Seber structure, which aims to estimate the rate of permanent departure from a population while accounting for capture probabilities < 1 . We used this model to estimate unbiased capture probabilities while accounting for unobserved mortality and transitions between reaches. The model had an annual time step,

with the assumption that fish could only ever leave the four study populations permanently — i.e., there was no temporary migration out of the study area. To accommodate other data sources, we used a state-space model parameterisation (King 2012). This model structure allowed us to account for likely sources of individual heterogeneity, arising from yearly individual variation in four additional types of state including each fish’s location (*population 1-4*), age, or survival and telemetry tag status that likely affected capture probability of the fish each year.

To build the state-space model, we first recorded for each fish ever captured a history y_i ($i = 1, \dots, N$, with $N =$ the total number of fish ever caught during the study) describing whether or not it was captured at time t ($t = 1, \dots, Y$) for each of the Y years of electrofishing, with y_{it} taking a value of 1 if i was captured, and 0 if not. Similarly, we recorded observation histories for each of the angler (R_{it}), telemetry (T_{it}), and logger tower (L_{it}) datasets. We then built histories for different states that could influence detection. By default in the Cormack-Jolly-Seber model, we first included a state for whether each individual was alive or dead (A_{it}), as in the standard Cormack-Jolly-Seber model. We then modelled transitions between alive ($A_{it} = 1$) and dead ($A_{it} = 0$) states as a random Bernoulli process:

$$A_{it+1} \sim \text{Bernoulli}(\psi A_{it}),$$

where ψ is the probability of individual i surviving from time t to time $t+1$. Because each population has different sampling conditions, we next included a state for the population (S_{it}) and allowed fish to migrate between populations each year (but only for fish with $A_{ij} = 1$). Collectively, we modelled the meta-population as a multinomial random variable:

$$S_{it+1} \sim \text{multinomial}(\omega S_{it}),$$

where ω is a 4×4 transition matrix describing the probabilities of moving between each of the four populations (or staying within a population) at each time step.

To account for individual changes in size (and therefore, capture probabilities —Bird *et*

al. 2014; Lyon *et al.* 2014), we modelled changes in individual age over time using sequential observations of how individuals grew in length (L_{it}) to estimate the parameters of a von Bertalanffy growth curve (separately for each reach where data were sufficient). We modelled growth based on the three-parameter von Bertalanffy growth function for asymptotic growth, where the length of individual i at time t is given by:

$$L_{it} = L_{\infty} - (L_{\infty} - L_0)(1 - e^{-k_{si}}),$$

where L_{∞} is the asymptotic size, L_0 is the size at which individuals enter the population (defined as 0 here), and k is the unitless growth parameter. Based on this growth equation, we modelled the observed change in length between two capture occasions using the von Bertalanffy growth curve:

$$g_{i(t_2-t_1)} \sim \text{Normal}((L_{\infty} - L_{i_{t_1}})(1 - e^{-k_{si}}), \sigma^2),$$

where $g_{i(t_2-t_1)}$ is the expected growth of individual i between times t_2 and t_1 , and k_{si} is the growth rate for population S_i .

Based on these parameters, we could model the expected size of each unobserved fish, and therefore, the influence of this size on the probability of detection. Finally, we included a state for whether each fish carried an active telemetry tag, which we modelled as a random Bernoulli variable:

$$D_{it+1} \sim \text{Bernoulli}(\gamma D_{it}),$$

where D_{it} records whether individual i carried an active telemetry tag at time t , and γ is the probability of that tag remaining active.

We also modelled all observation data as random Bernoulli variables with probability p of observing an individual fish with a sampling type depending on the states for each individual. For electrofishing, angler return, and radio-tower observations, we set $p = 0$ if the fish was dead. However, because telemetry tags were detectable in both live and dead fish, we allowed p to be non-zero for tracking observations. We also modelled capture

probabilities using a logistic regression by allowing p_{yt} to vary as a linear function of size as well as varying among populations and years.

Because we accounted for major sources of variation in capture probabilities (i.e., migration, variation in size, and mortality), we estimated population size N_y for each year of the study by modelling the observed number of captures n_y within each age class as a binomial random variable with probability of capture defined by p_y and a vague Gamma (0.01, 0.01) prior distribution for the true population size N_y . We used Markov chain Monte Carlo sampling software JAGS in the R package *R2jags* (Plummer 2003; Su *et al.* 2011; R Development Core Team 2013) to generate samples from the joint posterior distribution for each model, running three chains of 150000 iterations each, and a burn-in period of 100000, keeping every 50th iteration for a total of 3000 iterations. We assessed convergence using the Gelman-Rubin diagnostic.

Results

Mark-recapture

We captured 8843 Murray cod and 4431 golden perch between 2006 and 2013. Of these fish, we tagged 4166 Murray cod and 3562 golden perch with PIT and external tags (Table S4), and 689 Murray cod and 466 golden perch with radio tags (to strengthen prior information on migration, mortality and detection). Over the study, anglers reported capturing 1338 tagged Murray cod and 275 tagged golden perch from our study reaches. Multiple size classes were represented in the Murray cod population structure; however, there was a clear effect of angling at larger cohorts (> 500 mm are subjected to angling pressure; Fig. S2) while golden

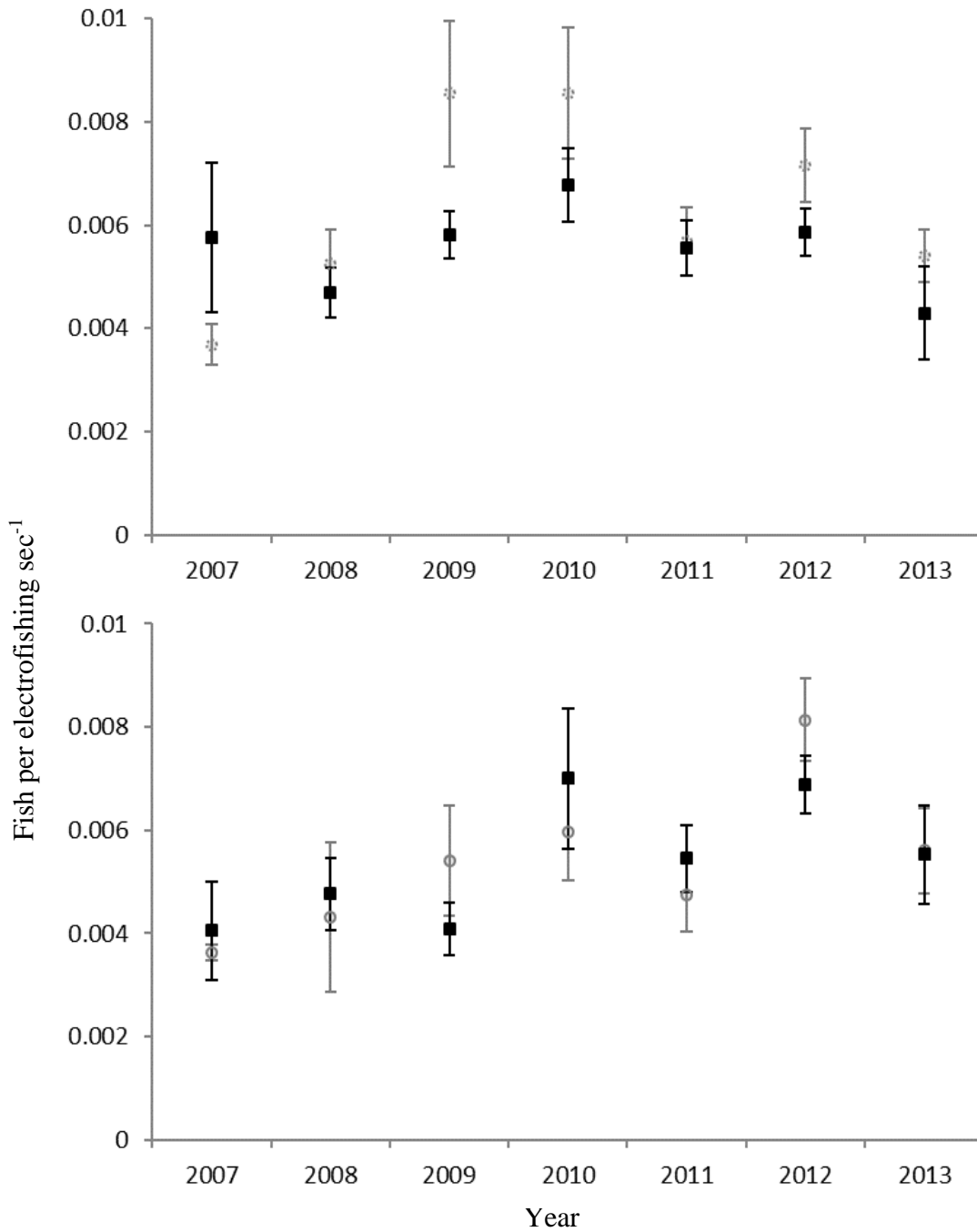
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perch were represented primarily by larger cohorts (Fig. S3). Total numbers of those Murray cod and golden perch captured, tagged, and recaptured (by researchers) are in Table S4.

Within our intervention reach, we observed no large shifts in catch per unit effort among sites within resnagged priority zones and sites that were in areas outside the priority resnagged zones (Fig. 2). As such, increases observed in the intervention reach were unlikely to be due to fish moving from within the intervention reach into the resnagging priority zones or, if this did occur, the previously vacated habitats were then occupied by different fish.

A total of 1288 (251 of these were kept) tagged Murray cod and 265 (135 of these were kept) tagged golden perch were recorded through our angler dial-in program.

Figure 2. Mean (\pm standard error) number of Murray cod (top) and golden perch (bottom) recorded per second during annual electrofishing surveys within the *population 1* for sites within the priority resnagged zones (filled boxes) and sites outside the priority resnagged zones (shaded boxes) from 2007 – 2013. Electrofishing surveys were undertaken following methods outlined in Nicol et al. 2004



Immigration and emigration

Both target species proved to be mobile, and there was exchange of individuals among populations. We measured a total of 558 ‘long-term’ location changes. We classified a movement as long-term when it had been in a different location to where it was tagged for at least 4 months prior to battery failure (when logging ceased). In addition to these, we also recorded many ‘short-term’ movements, where fish returned to their place of tagging; however, we did not include these in the model. Table 1 gives combined long- and short-term movements by year over the life of the study. Average annual probability of transition (both long- and short-term) for each species within each population was variable, and is provided in Table 2. Of our subsample of radio-tagged animals, 36 more fish immigrated into than emigrated out of the intervention reach (*population 1*). Conversely, there was a net decrease in ‘long-term’ immigration to *populations 2* and *3* combined (49 fish), while there was a net increase in ‘long-term’ immigration to *population 4* (13 fish). Fish moved among all four reaches, with most moving upstream from *populations 2* and *3* into *population 1*. Another seven individuals migrated upstream out of *population 4* using the fish lift, and into *population 1*. When scaled up to the population level (% of each population transitioning over the study period), *populations 2* and *3* were net exporters of adult recruits to surrounding populations (Fig. 3, Table S5). Mulwala weir formed an almost total barrier to upstream movement; however, downstream movement was higher with a large number of golden perch moving during the 2011 flood (Fig. 3)

Table 1: Total number of individual transitions between logger locations for Murray cod (MC) and golden perch (GP) between 2007 and 2013, for each study population.

	<u>2007</u>	<u>2008</u>	<u>2009</u>	<u>2010</u>	<u>2011</u>	<u>2012</u>	<u>2013</u>
<u>MC Pop. 1</u>	826	2932	8295	10973	15151	12199	13919
<u>GP Pop. 1</u>	654	3935	7673	9474	12063	6417	8965
<u>MC Pop. 2</u>	85	1212	1108	1766	4262	3488	4739
<u>GP Pop. 2</u>	0	338	433	1909	1275	598	952
<u>MC Pop. 3</u>	549	1455	1292	1018	2490	1769	3906
<u>GP Pop. 3</u>	303	2031	1920	2536	4628	4144	4994
<u>MC Pop. 4</u>	0	11	802	530	1299	1495	621
<u>GP Pop. 4</u>	7	243	684	3493	3345	1811	3217

Table 2: Average annual probability of transition between loggers (i.e., likelihood of moving) for Murray cod (MC) and golden perch (GP), by year and delineated by study population.

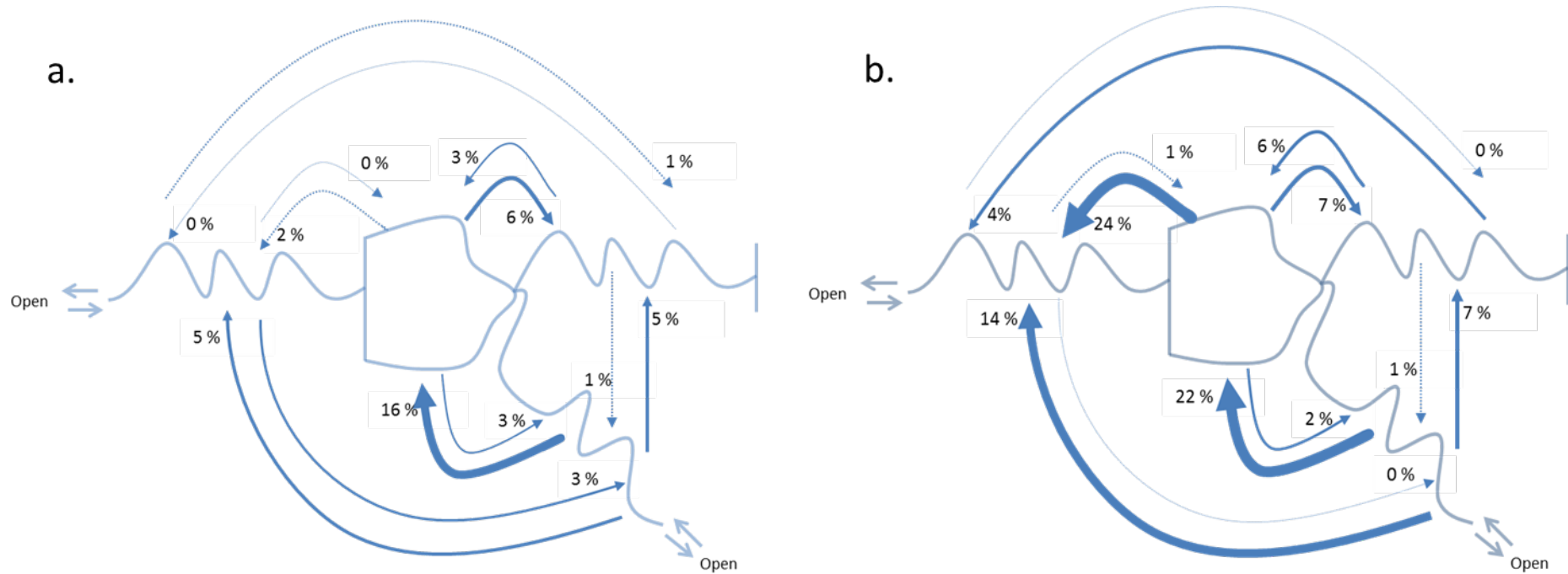
<u>Species</u>	<u>2007</u>	<u>2008</u>	<u>2009</u>	<u>2010</u>	<u>2011</u>	<u>2012</u>	<u>2013</u>
<u>MC Pop. 1</u>	0.560	0.528	0.497	0.548	0.597	0.465	0.719
<u>GP Pop. 1</u>	0.230	0.312	0.439	0.706	0.698	0.950	0.959
<u>MC Pop. 2</u>	0.596	0.626	0.510	0.660	0.606	0.726	0.986
<u>GP Pop. 2</u>	1.000	0.500	0.500	0.280	0.489	0.777	0.500
<u>MC Pop. 3</u>	0.810	0.697	0.529	0.510	0.505	0.600	0.779
<u>GP Pop. 3</u>	0.750	0.898	0.878	0.461	0.935	0.741	0.668
<u>MC Pop. 4</u>	1.000	0.996	0.553	0.563	0.800	0.751	1.000
<u>GP Pop. 4</u>	0.500	0.917	0.877	0.410	0.480	0.712	0.995

Survival

For both species, the model predicted that survival within *population 1* remained approximately constant across years (Fig. 4). In *population 4*, survival probabilities were generally stable, increasing slightly over time. *Populations 2* and *3* had variable survival probabilities and associated errors due to fewer tagged fish and fewer recaptures.

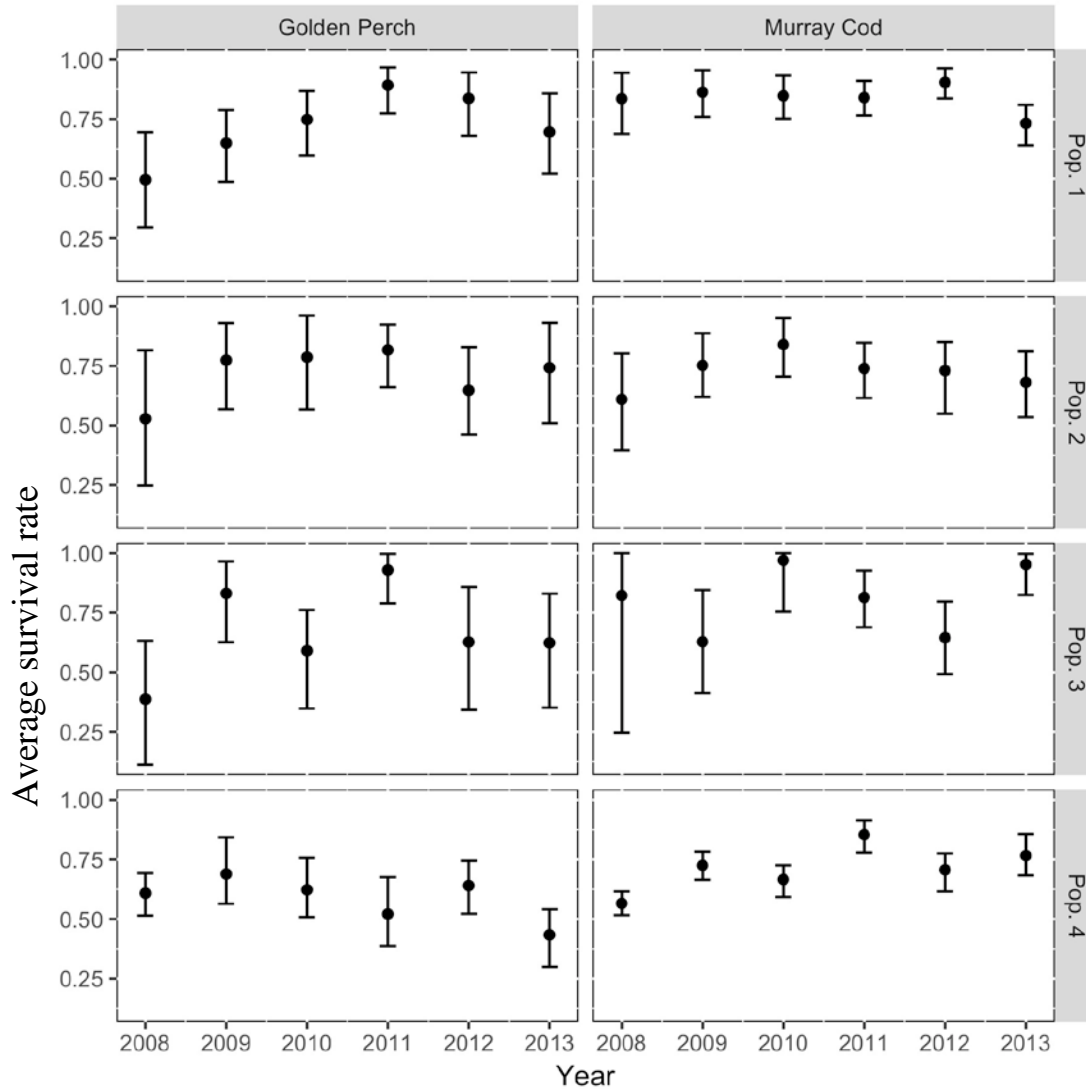
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- 1 **Figure 3.** Conceptualisation of study populations and their transition probabilities ('permanent' migrations within the study period measured in % of total radio-tagged
2 population) for Murray cod (a) and golden perch (b). Thickness of line is approximately proportional to scale transition.



3
4

Figure 4. Estimated survival probabilities of Murray cod and golden perch in that were >200 mm. Error bars represents the 95% credible intervals around the annual estimates. Note: estimates begin in 2008 due to few recaptures in the first two years.

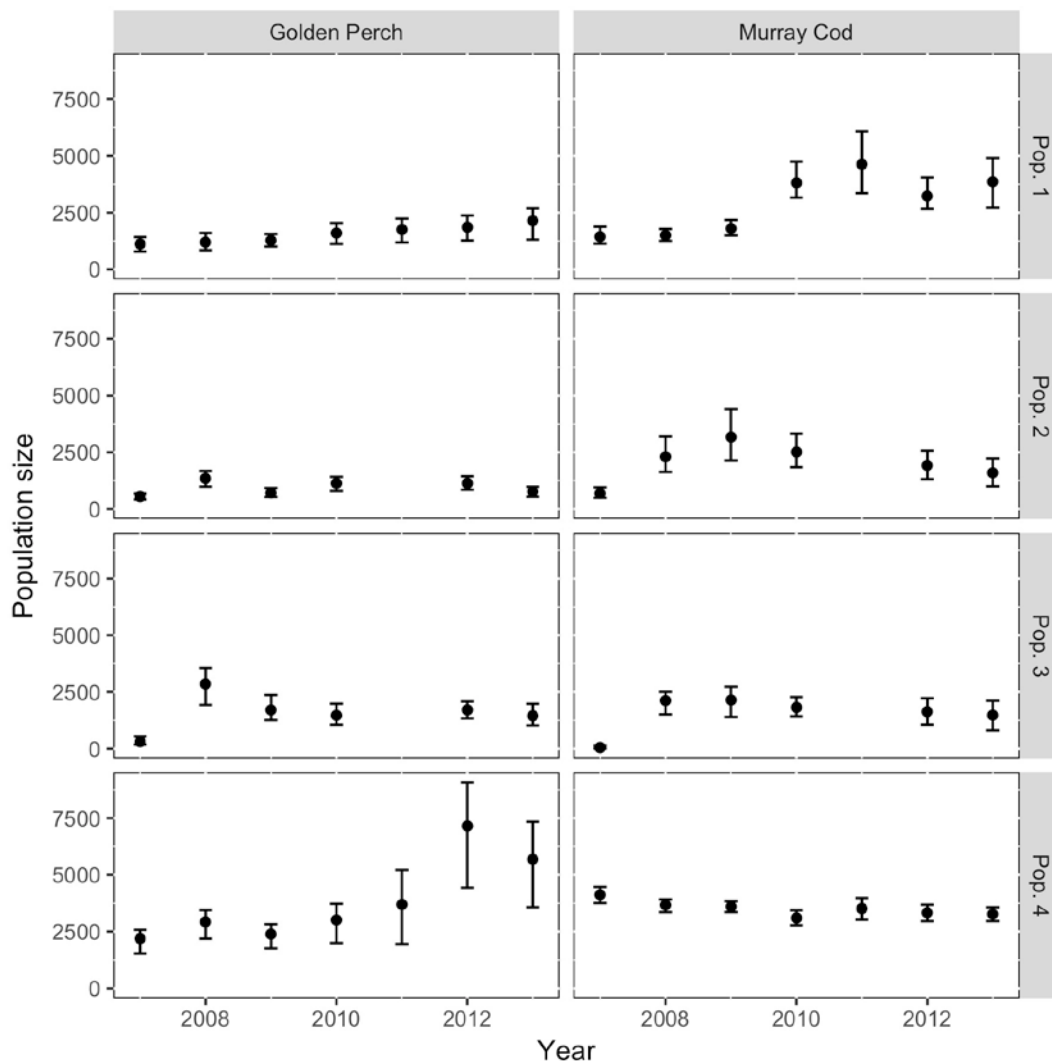


Population trends

The model estimated that the population size of Murray cod (> 200 mm within our sample sites) increased three-fold after resnagging (between 2006 and 2013) in *population 1* (the intervention reach), with a 30% decrease over the same period in *population 4* (which experienced the most similar geomorphic and hydrologic features, but was isolated from *population 1* by a weir) (Fig. 5). While variable, there was also an increasing trend in abundance for both *populations 2* and *3* over the same period, with a spike observed in 2011

coinciding with the lake drawdown (and hence potentially increased detection). Regardless, the peak in *population 1* does not coincide with a decline in either *populations 2* or *3*, suggesting a likely growth in Murray cod metapopulation size. Between 2006 and 2011, our sites in the intervention reach (*population 1*) held around 1000 golden perch > 200 mm, and increased slowly up to around 2000 animals over the course of the study, although the error in these estimates is large. Golden perch abundance in *population 4* roughly tripled following the 2010-2011 floods, mainly through adult fish immigrating during the flood year (see yearly catch ‘*n*’ in Fig. S3).

Figure 5. Estimated population size of Murray cod and golden perch (estimated total number of fish > 200 mm in sampling sites). Error bars are 95% credible intervals.



Discussion

We found that population size of target species in our the ‘intervention’ (*population 1*) reach increased following a habitat-restoration intervention in a large, lowland river. Migration of both Murray cod and golden perch among populations led to increased occupancy of the river reach where habitat was restored. The connectivity between our study reaches was (Tables 1 and 2, Fig 3) an important predictor, with most immigrants arriving from the closest adjacent populations where no barriers to migration were present.

Native fish populations in large, temperate Australian rivers have been, and continue to be, altered by anthropogenic activities (Koehn *et al.* 2008). Programs such as the Murray-Darling Basin Plan (Murray-Darling Basin Authority 2010) are investing in water recovery and other strategies to aid recovery of native fish populations. Demonstrating outcomes from investment and ensuring adaptive-management principles lead to continual improvement of environmental condition are essential for ensuring continued support for river restoration programs.

Role of connectivity and scale

In our study, transfer from source populations into the restored reach was above background rates; the intervention reach effectively sustained a larger number of adult fish as the population grew in response to the habitat restoration. Palmer *et al.* (1997) first posed the ‘field of dreams’ hypothesis (‘if you build it, they will come’) and connectivity to a source population is an important factor explaining the success of restoration projects across multiple spatial and temporal scales (Jansson, Nilsson & Malmqvist 2007). Hanski (1998) also provided a framework predicting how suitable source populations can fulfil the ‘replacement condition’ — that one population of animals occupies high-quality habitat to provide an overflow of recruits to ‘top up’ another population experiencing a recruitment or

survival bottleneck. These two frameworks clearly applied to both species in our study and are useful conceptual models. While it is unlikely that fish are moving in response to the restored habitat, we contend that during foraging or ‘ranging’ behaviour, fish might come across unoccupied areas of newly installed habitat (or newly vacated habitat if another fish has vacated an already present habitat to occupy a new one, creating an occupancy in the process) and then occupy it – adding to the population as described here. At large spatial scales, fish populations can act as metapopulations, where connected populations interact and influence one another (Levins 1969). Because the population dynamics of the species studied here are complex, with complicating phenomena such as variable migration, it could be useful to consider what we describe as ‘permanent’ movements in the context of metapopulation dynamics.

Quantitatively demonstrating the ecological processes that lead to successful restoration has become increasingly important for the restoration of degraded rivers around the world (Konrad *et al.* 2011; Davies & Gray 2015; Roberts, Anderson & Angermeier 2016; Turunen *et al.* 2017). Our results provide support for the dynamic-landscape model of life history of stream fish described by Schlosser (1991). An important consideration for successful restoration is the capacity to match restoration outcomes to target organisms (Bond & Lake 2005) — and the spatial scale of restoration and the temporal scale of the monitoring need to match the life history of the target organism (Palmer, Menninger & Bernhardt 2010). Here, the target species had a home range of > 100 km, the investment and scale of the restoration was large, our objective was to increase the population size of native predatory species, and we had a monitoring program designed to measure such changes at the relevant scales.

Habitat heterogeneity

Due to the connectivity with source populations, the reintroduction of structural woody habitats into our intervention reach meant that immigration of Murray cod and golden perch from their source populations occurred to newly available restored habitats, increasing the overall carrying capacity of the river system. Environmental heterogeneity in disturbed landscapes is one of the most important elements in maintaining fish populations in riverine habitats (Schlosser 1991), because variability in habitats across reach scales means that large-bodied predatory species can complete their life-cycle processes. Habitat heterogeneity also ensures that resident individuals can react to physical habitat changes by moving among populations (Schlosser & Angermeier 1995).

A continuing quandary for fisheries managers tasked with both biodiversity conservation and biomass harvest management in rivers is that the systems most in need of restoration are most often the largest. As such, unequivocal measurements of the success of intervention is challenging because of the broad spatial scales over which monitoring data must be collected. This elicits tension between scientific considerations and management practicality, and inevitability different definitions of restoration ‘success’ (Cooke *et al.* 2017). In our case, the altered flow regime and history of habitat degradation within the intervention reach mean that there was unlikely to be sufficient heterogeneity to support a spawning stock enough to offset mortality. However, the population is part of a larger meta-population that can provide ‘overflow’ recruits via immigration to counter this lack of localized recruitment, while still fulfilling its replacement condition. This leads to an increase in carrying capacity across the meta-population (see Lipcius *et al.* 2008).

Conclusion

We have demonstrated that a large-scale management intervention promoted a strong response from our target species by increasing the available structural habitat, effectively increasing the population size for target fish in the intervention river. However, success also relied on connectivity between population (i.e., Tables 1 and 2; Figure 3) that enabled transition of recruits into the restored reach. The implication for managers of large rivers for fishery and/or conservation outcomes is that instream habitat restoration is a viable technique to increase population size of large-bodied fishes in degraded rivers. In an era when delivery of environmental flows is increasingly being used to restore fish populations, restoration which complements flow should have broad appeal and application potential, particularly in areas where flows are limited by human needs, availability of water and/or infrastructural constraints.

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Author Contributions

SN, CT and JL conceived the study; JL, JO, GH, ZT, JK and CT collected the data; TB, JL and AK analysed the data; JL led the writing of the manuscript with assistance from CB. All authors contributed critically to the drafts and gave final approval for publication.

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Table S1. Summary of data collected to estimate population growth (collected in the intervention and two reference reaches).

N_t	annual electrofishing surveys, mark-recapture data, research angler data
individual age	annual counts of young-of-the-year juveniles, back-calculated age-structure data from otolith collections, stocking data
deaths	mortality from radio tags, capture-mark-recapture data, angler data for fishery-dependent surveys
migration	capture-mark-recapture data (fishery-dependent and -independent), radio tracking movement data

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Table S2. Site summary information in order of sampling. We amalgamated *populations 2* and *3* due to the smaller number of samples.

	Number of sites sampled							
Reach description	2006	2007	2008	2009	2010	2011	2012	2013
<i>Population 1</i>	110	171	225	169	178	170	170	209
<i>Populations 2 and 3</i>	21	30	67	49	39	65	28	39
<i>Population 4</i>	122	134	132	132	128	123	121	122
TOTAL	253	335	424	350	345	358	319	370

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Table S3: Summaries of target species surgically implanted with radio-tags

Species	Min weight (g)	Max weight (g)	Average weight (g)	Total number
Murray cod	13	43000	3783	689
Golden perch	252	4074	1466	466

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Table S4. Summaries for target species captured and tagged in 2004 and 2013 (including radio tagged). Numbers of individuals tagged and recaptured are given in parentheses.

Populations 2 and 3 have been combined due to the smaller samples.

	<i>Population 1</i>		<i>Populations 2 and 3</i>		<i>Population 4</i>	
	Murray cod	Golden perch	Murray cod	Golden perch	Murray cod	Golden perch
2004	26 (22, 1)	44 (42, 0)	8 (5, 0)	10 (10, 0)	1787 (690, 159)	207 (164, 26)
2005	42 (33, 0)	7 (6, 0)	9 (3, 0)	4 (0, 0)	1411 (705, 138)	195 (165, 22)
2006	63 (59, 1)	17 (16, 0)	21 (19, 0)	23 (18, 1)	1359 (705, 215)	223 (193, 25)
2007	64 (60, 3)	51 (51, 0)	21 (19, 0)	28 (28, 0)	870 (456, 238)	237 (187, 44)
2008	176 (124, 6)	100 (95, 2)	129 (113, 1)	123 (122, 1)	822 (450, 295)	369 (313, 49)
2009	97 (68, 6)	32 (30, 1)	128 (119, 1)	42 (40, 2)	675 (690, 312)	274 (164, 60)
2010	127 (103, 8)	57 (48, 6)	187 (107, 1)	64 (55, 2)	1028 (258, 201)	333 (287, 35)
2011	70 (52, 9)	44 (40, 1)	256 (216, 4)	141 (130, 3)	389 (115, 69)	258 (238, 24)
2012	116 (97, 8)	114 (104, 5)	73 (58, 6)	61 (60, 1)	623 (229, 123)	725 (674, 61)
2013	70 (53, 5)	95 (94, 1)	138 (67, 3)	60 (58, 1)	1 253 (256, 124)	546 (498, 57)
TOTAL	851 (671, 47)	561 (526, 16)	970 (696, 16)	556 (521, 11)	10 217 (4 554, 1 874)	3 367 (2 883, 403)

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Table S5. Summary of the model estimates outlining probabilities of transition and 95% confidence intervals. *Lower* and *Upper* refer to the lower and upper 95% Bayesian credible intervals. *Trans* [1,1] refers to the probability of a fish that was in *population 1* in a particular year remaining in *population 1* the following year. *Trans* [1,2] similarly refers to the probability of a fish moving from *population 1* to *population 2*. MC = Murray cod, GP = golden perch.

Transition	95% Credible Interval		
	Estimate	Lower	Upper
MC	mean	2.50%	97.50%
Trans[1,1] Pop.1->Pop.1	0.968	0.94	0.986
Trans[2,1] Pop.2->Pop.1	0.004	0.001	0.015
Trans[3,1] Pop.3->Pop.1	0.03	0.022	0.043
Trans[1,2] Pop.1->Pop.2	0.002	0	0.011
Trans[2,2] Pop.2->Pop.2	0.965	0.931	0.987
Trans[3,2] Pop.3->Pop.2	0.01	0.004	0.021
Trans[1,3] Pop.1->Pop.3	0.011	0.006	0.019
Trans[2,3] Pop.2->Pop.3	0.007	0.003	0.021
Trans[3,3] Pop.3->Pop.3	0.93	0.89	0.957
Trans[1,4] Pop.1->Pop.4	0.019	0.002	0.048
Trans[2,4] Pop.2->Pop.4	0.024	0.002	0.062
Trans[3,4] Pop.3->Pop.4	0.03	0.001	0.073
GP			
Trans[1,1] Pop.1->Pop.1	0.93	0.896	0.964
Trans[2,1] Pop.2->Pop.1	0.005	0.001	0.014
Trans[3,1] Pop.3->Pop.1	0.047	0.031	0.072
Trans[1,2] Pop.1->Pop.2	0.006	0.002	0.013
Trans[2,2] Pop.2->Pop.2	0.895	0.851	0.945
Trans[3,2] Pop.3->Pop.2	0.051	0.036	0.07
Trans[1,3] Pop.1->Pop.3	0.03	0.02	0.043
Trans[2,3] Pop.2->Pop.3	0.041	0.026	0.063
Trans[3,3] Pop.3->Pop.3	0.859	0.811	0.919
Trans[1,4] Pop.1->Pop.4	0.034	0.004	0.067
Trans[2,4] Pop.2->Pop.4	0.059	0.002	0.109
Trans[3,4] Pop.3->Pop.4	0.043	0.001	0.086

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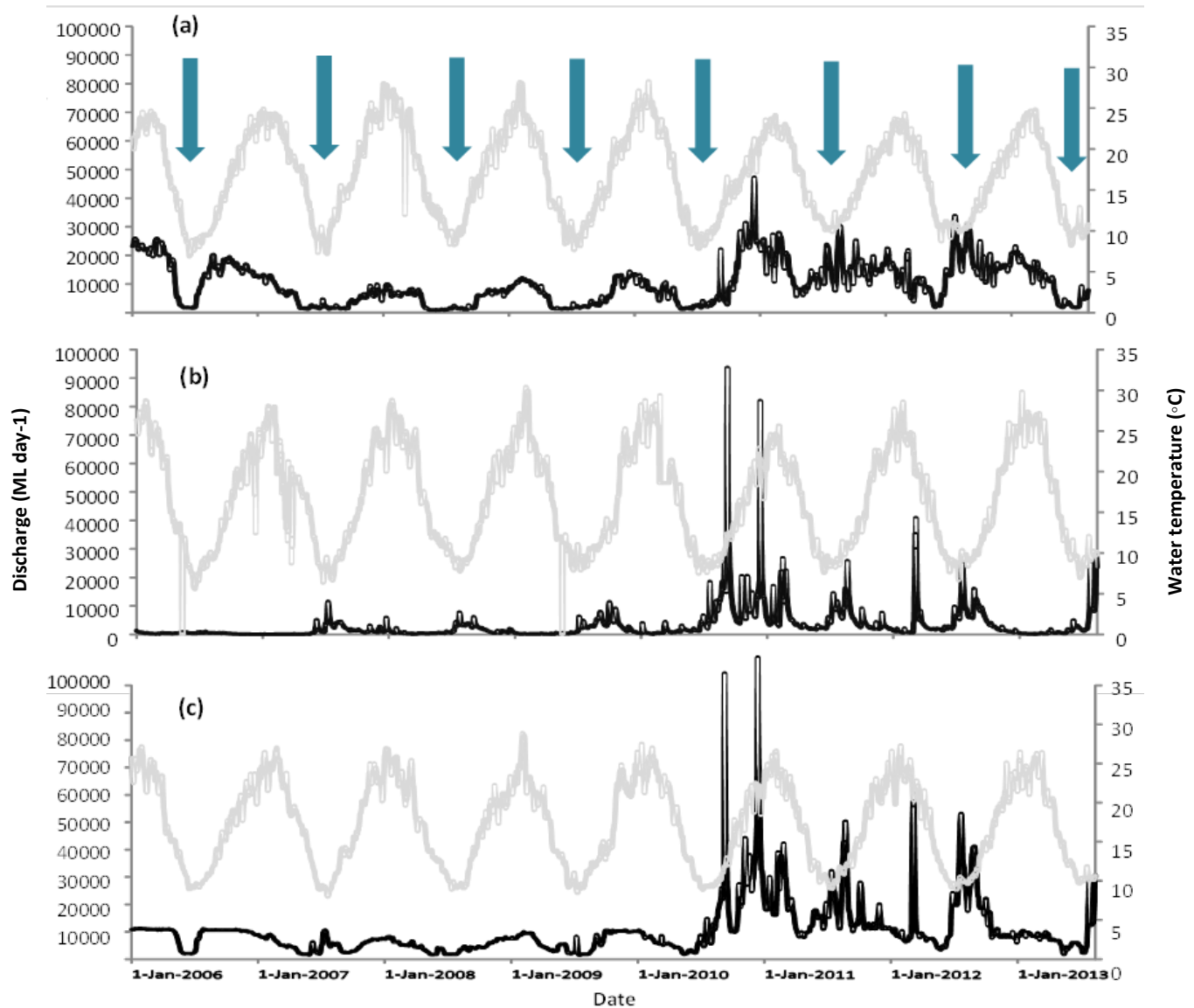


Figure S1. Discharge (ML/day) and temperature (degrees Celsius) within (a) *population 1*, (b) *population 3*, and (c) *population 4* between 2006 and 2013. Grey lines indicate water temperature, black lines indicate flow and arrows indicate sampling. Lake levels for *population 2* are not shown.

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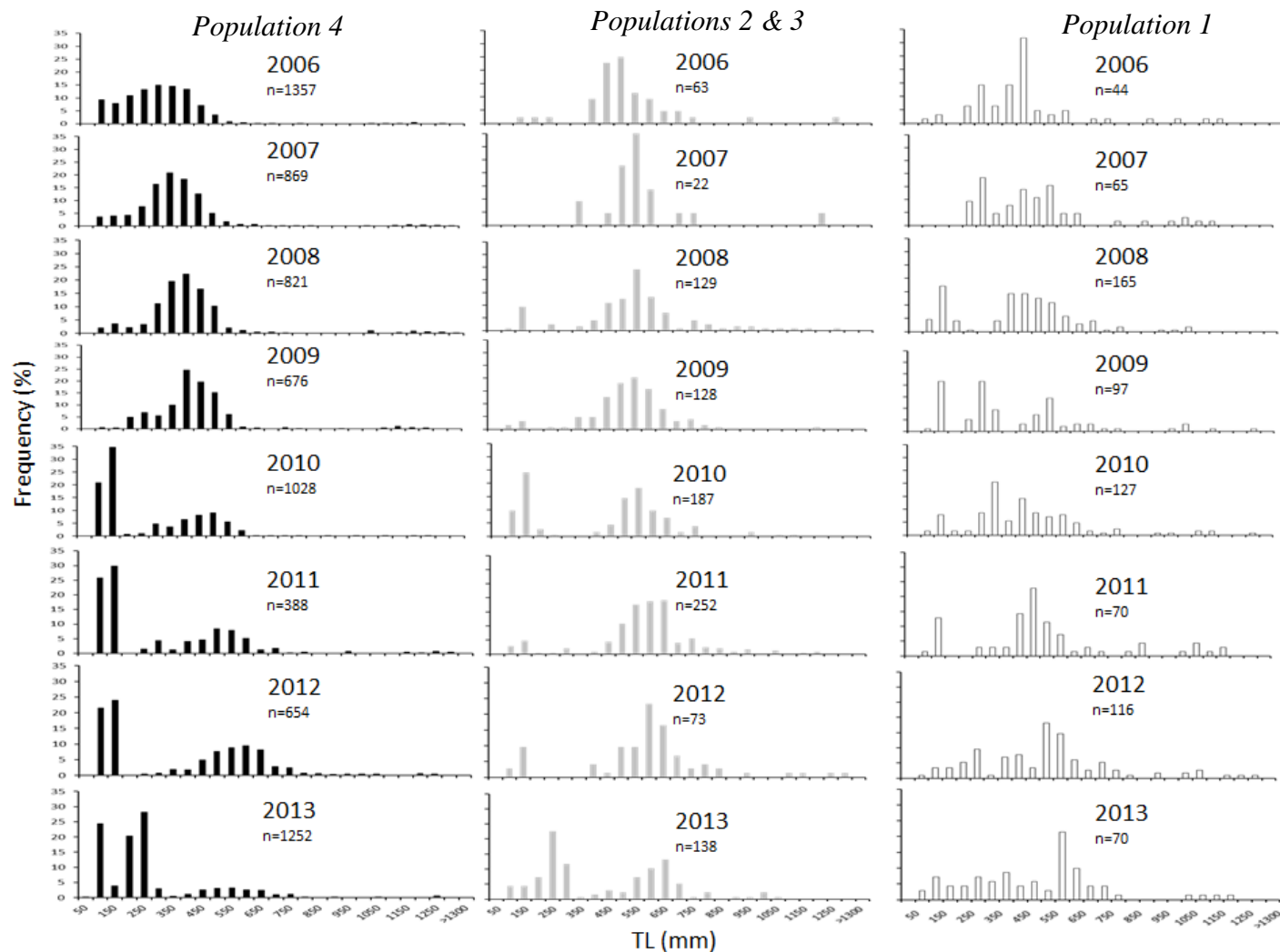


Figure S2. Length-frequency distribution of Murray cod collected during electrofishing surveys of each of the study reaches from 2006 – 2013. Numbers (n) of fish collected in each year are also presented. Note *populations 2 & 3* have been combined due to the low numbers captured

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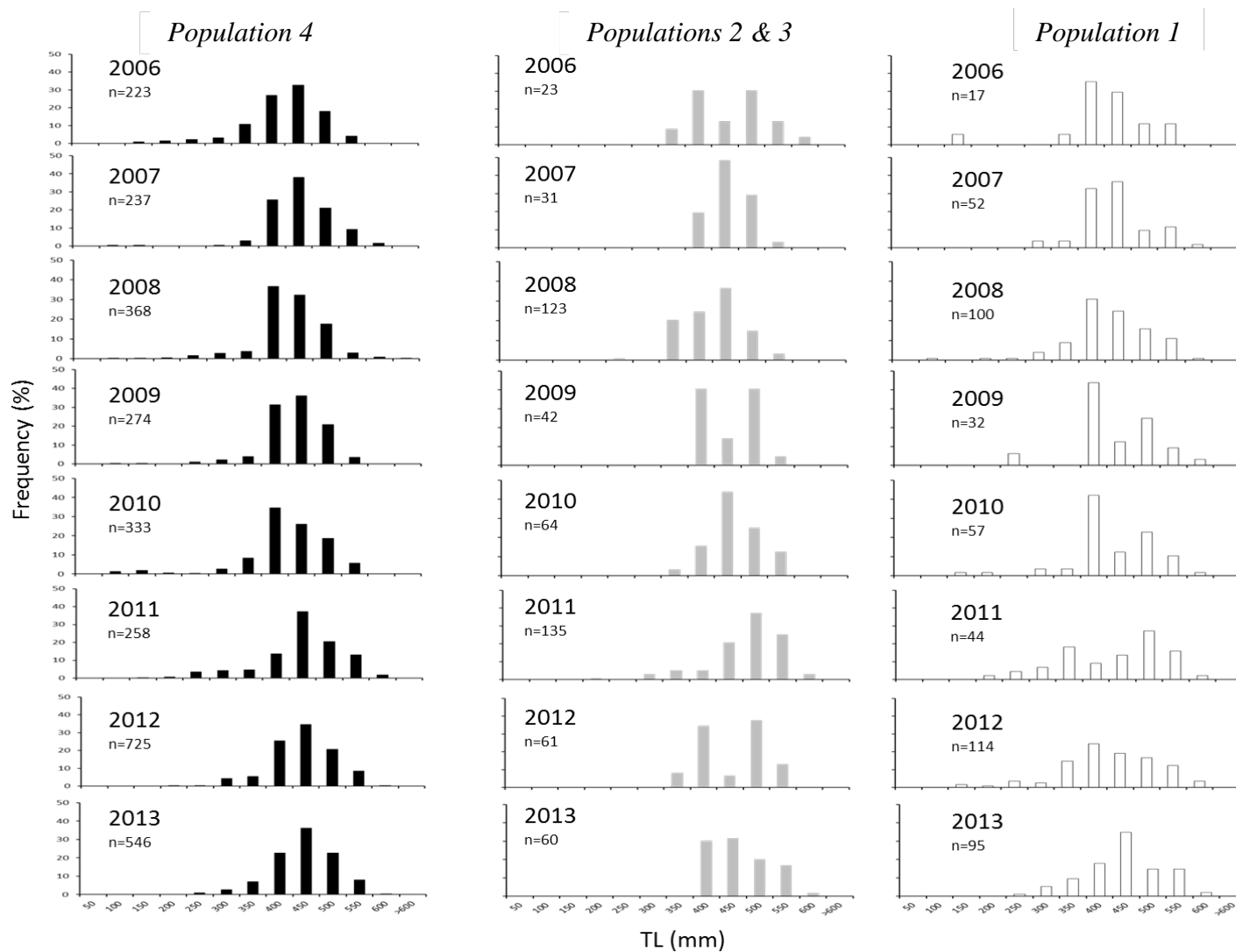


Figure S3. Length-frequency distribution of golden perch collected during electrofishing surveys of each of the study reaches from 2006 – 2013. Numbers (n) of fish collected in each year are also presented. Note *populations 2 & 3* have been combined due to the low numbers captured

Note S1

Monitoring design consultation

We developed our monitoring design through a consultative process with stakeholders and agency decision-makers to ensure it provided information that could be directly used by practitioners. This involved a review of currently known information on interactions between submerged wood and fish, and assessing the limitations of this information for use in management. Through stakeholder workshops, we determined which new knowledge was required, and identified the metrics that would assist decision makers to (1) determine the successes and failures of this restoration type, and (2) provide information that they could use to guide restoration and native fish management in other locations. We concluded that while there is evidence that native fish used restored woody habitats, it was unclear if this use was the result of a simple redistribution of existing individuals or a true increase in population size. We also determined that understanding the processes of survival, recruitment, immigration and emigration that can lead to changes in population size is an essential precursor to answering management questions regarding the importance of nearby source populations, hatchery stocking to supplement recruitment, and fishing mortality.

Chapter 6

General Discussion

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My research has provided reach-scale examples of fish-population responses to three restoration strategies (re-introductions of an extirpated endangered fish, increasing habitat heterogeneity, and ensuring lateral connectivity) in large river systems. I used a range of field, laboratory, and analytical methods to measure these responses, considering temporal and spatial variation and accounting for sampling efficiency. My thesis highlights the importance of using different sampling designs for measuring restoration success in lowland river systems in Australia. My approach also provides a platform for understanding the importance of connectivity and source-sink dynamics in aquatic systems, and of the role of source populations for driving recovery of fish populations into restored habitats. These areas of research have typically lagged analogous research in terrestrial ecosystems.

I focussed on investigating native Australian freshwater fishes, and my research adds to the growing body of work being produced by applied fish researchers in Australia, where large investments, such as through the Murray-Darling Basin Plan, are leading to an increased emphasis on science that informs and demonstrates that management interventions are being applied efficiently. The objectives of the Murray-Darling Basin Authority's Native Fish Strategy (Barrett 2004) describe an expectation that the cumulative impact of restoration actions (including those I tested), will increase native fish population abundance (for all native fish species combined) from current estimates of 10% pre-European levels to 60% of pre-European numbers (Barrett 2004). I found that three major restoration methods — (1) re-introduction of extirpated species, (2) restoring lateral connectivity and (3) increasing habitat heterogeneity, are valid restoration actions in the context of lowland river management. I found that the re-introduction of a threatened species (trout cod *Maccullochella macquarieensis*) was successful because the re-introduction program was scaled to match the low annual survival rates of stocked fish. I determined that managing connectivity between wetlands and their main channel habitat can enhance migration rates, and that increasing habitat heterogeneity at a reach scale can increase population size when there is a suitable source population for immigration. While the scope of the interventions I studied is broad, conceptually they align with the framework driving native fish restoration in the Murray Darling Basin (see Barrett 2004; Figure 1 in General Introduction). Below I summarise how the thesis chapters fit together under three main

Chapter 6

concepts: (1) the role of structural habitat, (2) connectivity within the environment, and (3) drivers of population vital rates. In addition to these detailed sections, I provide in Table 1 a summary of the results from the hypotheses I tested in each data chapter.

Table 1: Summary of tested hypotheses and key outcomes from each data chapter.

Chapter	Tested Hypothesis	Key Outcomes
2	<p>(1) Fluctuating water levels increase the abundance and community composition of small-bodied native and non-native fish moving between the main river and off-channel habitats</p> <p>(2) More fish move at night rather than day to avoid predation</p>	<p>(1) <i>Accepted.</i> Lateral fish movement approximated fluctuations in water level. Generally, as the Murray River rose, fish left the main river channel and moved into newly flooded off-channel habitats. However, there were also bi-directional movements as water levels peaked, and on falling water levels, fish moved back to the permanent riverine habitats. Highly regulated river reaches provide annual opportunities for fish to access adjacent anabranches, billabongs, and other floodplain habitats.</p> <p>(2) <i>Rejected.</i> The highest catch per unit effort occurred during the day, indicating that changes in water regime were more important than diel influences</p>
3	<p>(1) Survival of stocked fish is temporally variable</p> <p>(2) Growth and reproductive output of hatchery fish did not differ from those of wild-bred individuals</p> <p>(3) Genetic diversity (measured by the number of alleles) in a stocked population was less than that in a natural population because of inbreeding and founder effects.</p>	<p>(1) <i>Accepted.</i> Stockings from years other than 2003 and 2004 contributed few fish to the final population.</p> <p>(2) <i>Accepted.</i> There were no differences in growth or reproductive output between hatchery and wild-bred fish.</p> <p>(3) <i>Accepted.</i> We found no genetic structure between populations in the Murray and Ovens Rivers, and both populations appear to be homogeneous. The total number of alleles we detected in the Murray River population (49) was consistently lower than the number found in the Ovens River population (55).</p>
4	Increasing river turbidity and stream depth decreases probability of capture using boat electrofishing	<i>Accepted.</i> River turbidity (associated with increased river discharge) negatively influenced capture probability. Increasing fish length increased detection of fish up to 500 mm for Murray cod, after which capture probability decreased, and capture probabilities varied between species. Variation in capture probability results in additional uncertainty when estimating population size or relative abundance.
5	The restoration of structural woody habitat at a reach scale (> 100 km) in a large, lowland	<i>Accepted.</i> Restoring habitat heterogeneity by adding structural woody habitats increased the abundance of target fish populations and raised the carrying capacity of fish.

	river results in a net increase in population size for two target species of native fishes, rather than merely attracting fishes already present in areas adjacent to restored habitat	Successful restoration of poor-quality ‘sink’ habitats for target species relied on connectivity with high-quality ‘source’ habitats.
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Structural habitat

While restoring structural habitat (i.e. large instream structure such as ‘snags’) is an oft utilised restoration activity, debate continues about its effectiveness as a tool to restore fish populations (Collier 2017). My results demonstrate that interventions to restore structural habitat can increase fish population sizes — not by re-aggregating fish, but also by re-introducing essential habitat. Structural woody habitat plays an important role in a range of ecological, structural, and chemical functions considered essential in maintaining river health. This includes the provision of habitat, shelter, feeding, and breeding locations for fish (Zalewski *et al.* 2003); adding it into river systems essentially increases carrying capacity. Additionally, increased structural woody habitats can also indirectly enhance fish abundances by enhancing primary production via increased in-channel surface area for biofilm colonisation (Gawne *et al.* 2007). Investigations into the status of native fish in the Murray-Darling Basin have identified structural woody habitat removal as a factor in the decline of native fish populations (Murray-Darling Basin Commission 2004). While its removal has been identified as one major reason for the decline in native fish, other contributing factors include flow regulation, barriers to movement, alien species, reduced water quality, disease, and over-exploitation (Lintermans 2007; Lake 2012). Consequently, over half of the 46 native freshwater fish species within the Murray-Darling Basin are threatened or of conservation interest (Lintermans 2007). These include several large-bodied, long-lived species including trout cod (*Maccullochella macquariensis*) and Murray cod (*Maccullochella peelii*), where the positive association between both species abundance and structural woody habitat is well-established (Nicol *et al.* 2007).

Over the last two decades there has been a gradual shift in river-management practices following the recognition of the importance of structural woody habitat; river restoration is now being done to mitigate past practices (Erskine and Webb 2003). Structural woody habitat restoration (also

known as ‘resnagging’) in Australia has been historically limited, with scientific trials only beginning in the late 1990s (e.g., Brooks *et al.* 2004; Bond and Lake 2005; Scealy *et al.* 2007). Early trials in the Murray River (Nicol *et al.* 2001; Nicol *et al.* 2004) were designed as a ‘proof of concept’ in the Murray-Darling Basin, and provided a guide for submerged woody-habitat restoration in large lowland rivers to enhance fish populations. Since then there have been a few small-scale (2nd and 3rd order streams) studies of fish responses to the restoration of structural woody habitat (Howell *et al.* 2012; Howson *et al.* 2012). Against this background, my research has taken these proof-of-concept studies and built them into a robust program that demonstrates the role of resnagging in re-structuring fish populations in large rivers, most importantly by showing that resnagging can increase meta-population size regionally, rather than just re-distribute the fish already present in the environment.

Connectivity

In my thesis, I focussed primarily on connectivity of fish populations and their rates of movement between off-channel habitats and the main river channel, and how connectivity at scales relevant to management (i.e. reach scales) is important in driving success of habitat restoration programs (Chapters 2 and 4). Indeed, this work has led to others investigating how managers can use such connectivity to their advantage (Beesley *et al.* 2014). The importance of connectivity for managing fish resources is well-known, and researchers in Australia have focussed on longitudinal connectivity, particularly as it relates to barriers to fish passage (Bunn and Arthington 2002; Barrett and Mallen-Cooper 2006), in addition to lateral connectivity (Jones and Stuart 2008; Hermoso *et al.* 2012)

The connectivity within or among populations drives processes that govern the long-term persistence probability of species (Levin 1992). For fishes within freshwater riverine systems, interactions among patches of suitable habitat occur most frequently within defined areas (i.e., the channel), and fish use these dispersal corridors to fulfil their life-history requirements (i.e., spawning, foraging, refuge, permanent migration to new habitats) (Schlosser 1991; Crook 2004; Walther *et al.* 2011). As such, quantifying the dynamics of dispersal within and among populations of fishes that I have presented is essential information informing how population fluctuations across space and time

align with measures of restoration success, and this is especially important where rates of connectivity are altered and may be low or poor, such as can occur under regulated conditions.

Poor connectivity within the dispersal network means that small changes to aquatic systems can induce large changes in ecosystem functioning (Cowx and Welcomme 1998). While physical fragmentation on land generally disrupts connectivity, in aquatic systems, changes to the function of water itself can isolate populations — for example, through altered flow regimes that can lead to loss of cues or access to spawning sites, or with cold-water releases from below the thermocline of stratified dams which can be a behavioural barrier to connectivity (Lugg and Copeland 2014). Such impacts on the strata (such as temperature) that support aquatic life is in some ways akin to a permanent and lasting alteration of an entire terrestrial landscape, or even the terrestrial climate in which animals have evolved. This implies a rapidity in ecosystem shift that happens relatively more quickly and severely than is typically observed following disturbances in terrestrial systems (Kingsford 2000; Dudgeon *et al.* 2006). These phenomena imply that developing and implementing restoration frameworks in aquatic systems requires models derived from *in situ* data collected at the appropriate spatial and temporal scales.

Consequently, determining the environmental and biological conditions that influence dispersal (or colonisation) is a necessary step in predicting fish population dynamics and in managing restoration actions (Franzén and Nilsson 2013). While there are good data describing the movements of adult life stages of riverine fishes (Baras and Lucas 2001; O'Connor *et al.* 2005), the population-level scale of these movements (i.e., what proportion of the population moves) and how these affect population structure have received comparatively less research attention (e.g., Pompeu *et al.* 2012). For example, the factors that influence migration of golden perch, silver perch, Murray cod and trout cod include rising seasonal water temperatures, varying day length, and fluctuation in the magnitude, duration and timing of flows, particularly (but not exclusively) for adult fish (O'Connor *et al.* 2005). For example, juvenile silver perch tend to disperse upstream during even small increases in river flow (e.g. 0.2 m rise) (Mallen-Cooper 1999). Nevertheless, how these specific movements contribute to source or sink population dynamics is still poorly understood.

The role of movement in the life history of some species can be complex. For example, in trout cod in Australia with mobile larvae that drift downstream (Brown *et al.* 1998; Koehn and Harrington 2006), adults have strong site fidelity (e.g. < 300 m home range; Koehn *et al.* 2008; Thiem *et al.* 2008), even though some can move up to 70 km over a matter of days when migrating to spawning sties (Ebner and Thiem 2009). Increased movements of adults can also occur with high flows (Koehn *et al.* 2008). However, sub-adult trout cod (< 300 mm long) are mobile as mature fish and have been measured to move > 25 km from downstream of Yarrawonga Weir into Lake Mulwala (Stuart *et al.* 2010). Colonisation rates for restored habitats are expected to decline with distance from source populations (Franzén and Nilsson 2013); some trout cod settle into sub-optimal habitats, whereas others suffer increased mortality during migration (e.g., to irrigation offtakes; King and O'Connor 2007), or fail to colonise (e.g., cannot pass Yarrawonga Weir; Stuart *et al.* 2010). My work has shown that dispersal from source habitats (Dingle 2014) is the main function linking different sub-populations. In unmodified systems, it is such ranging behaviour that allows expansion into new habitats, after which time ranging behaviour becomes less probable when suitable resources are found (Dingle 1996). For managers tasked with restoring large rivers, ranging is a useful concept which provides a clear link between ecological theory and management practice.

The importance of connectivity in structuring fish populations at reach scales in riverine systems, and specifically in Australian rivers, has previously received only theoretical support (Bond and Lake 2005). While I acknowledge that in large rivers, many factors interact to complicate our ability to measure the ecological returns on management investment, and I conclude that the success of fish-restoration programs requires investments that allow collection of suitable data at the appropriate spatial and temporal scales – which broadly are dependent on the scale of the restoration being done. Measuring small systems where manipulations might be easier (Bond and Lake 2005) does not necessary scale up to large systems where restoration becomes meaningful for population persistence.

Population ecology

My approach to data collection included measuring population indicators such as recruitment, immigration, emigration, survival, and fish distribution. Rather than only measuring relative abundance of animals over time, it is also important to estimate population dynamics and vital rates, such as immigration, emigration, births and deaths (survival) (Lipcius *et al.* 2008). Studies designed to measure demographic rates such as survival and movement are commonly used to overcome the difficulty in accurately assessing populations where a complete census is not practical (Pine *et al.* 2003). In my research on the determinants of the successful re-introduction of trout cod, otolith analysis and gonad histology successfully elucidated such rates for this species (Lyon *et al.* 2012). Furthermore, gathering data on vital rates and population demography (Chapter 5) allowed me to estimate the rate of change of native fish populations in resnagged relative to non-resnagged areas. Standard monitoring often fails to measure the complexities of such programs because fish movements in riverine landscapes are dynamic, thus changing capture probability and potentially invalidating estimates of abundance and survival (see Lyon *et al.* 2014). Native fish also vary considerably in size (between 50 and 1400 mm) and can grow quickly, thus changing capture probability as well (Chapter 5). Finally, low capture probability means that small variation resulting from environmental stochasticity can potentially bias estimates of vital rates.

Conclusions

Climate change and increasing water demand has placed the Murray River and its constituent ecosystems under increasing stress, a common scenario worldwide (Battin *et al.* 2007). The upper Murray River system is highly regulated and the main river has been highly degraded, as well as being disconnected from its floodplain (Lyon *et al.* 2010). For aquatic biota, restoration such as in-stream habitat enhancement, stocking, or use of floodplain regulators has been a major component in restoring functioning ecosystems (Lintermans *et al.* 2008). In my thesis, I examined the role of migration and connectivity across various taxa and various scales to improve restoration programs. However, I did not assess the drivers of migration (e.g., river discharge and temperature), so this presents an opportunity for further research.

With river managers now already using my results, I encourage funders of restoration programs to ensure restoration investment is carefully planned to link ecosystems that can then lead to catchment-scale benefits. While large-scale habitat restoration, restocking of threatened species, and maintaining connectivity between main river channel and off-channel habitats are important for restoration success, it is also important that researchers use a strong conceptual framework to underpin their monitoring designs. Investment in river restoration continues to grow — in one Australian example, the construction of 12 new fishways along the main stem of the Murray River has cost AU\$80 million and restored large-scale ecosystem connectivity for migratory fish along 2000 km of main river habitat (Barrett and Mallen-Cooper 2006; Baumgartner *et al.* 2014). The public is increasingly aware of these investments, and as such governments have a growing interest in ensuring that they achieve the desired outcomes. The onus is on both managers and researchers not only to be bold in the design of studies that examine restoration success, but also to invest appropriate amounts into science programs which allow meaningful and useful results to be achieved.

To make such investments pay off, I propose the following when planning future fish-restoration programs:

1. **Measuring the distance to, connectivity of, and dynamics within source populations.** The probability of restoration success will increase if managers understand the role of scale and source sink dynamics of the target species.
2. **Ensure monitoring programs are scaled, both temporally and spatially, to match the scale of the restoration, and measure absolute abundance where possible.** Where not possible, measuring the processes that drive restoration success (such as changes in survival of immigration/emigration) is essential.
3. **Invest adequately in monitoring.** A population-monitoring approach is not always possible; however, several types of monitoring data can attest to the success of an intervention relative to single measures alone.

4. **In endangered-species recovery where stocking is applied, frameworks taking a long-term view are more likely to succeed.** There is great variation in the survival of hatchery-produced fish, which can greatly alter the probability of success.

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