Submission to the Murray-Darling Basin Royal Commission

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Contents

1. Sections of the Terms of Reference this submission addresses

This submission addresses sections 3, 5 and 12 of the Terms of Reference, as below:

> 3. Whether the Basin Plan in its current form, its implementation, and any proposed amendments to the Plan, are likely to achieve the objects and purposes of the Act and Plan as variously outlined in ss.3, 20, 23 and 28 of the Act, and the 'enhanced environmental outcomes' and additional 450 GL provided for in s. 86AA(2) and (3) of the Act, respectively.
>
> 5. If the Basin Plan is unlikely to achieve any of the objects and purposes of the Act and Basin Plan and/or the 'enhanced environmental outcomes' and the additional 450 GL referred to above, what amendments should be made to the Basin Plan or Act to achieve those objects and purposes, the 'enhanced environmental outcomes' and the additional 450 GL?
>
> 12. Whether the Basin Plan in its current form, its implementation, and any proposed amendments to the Plan, are adequate to achieve the objects and purposes of the Act and Basin Plan, the 'enhanced environmental outcomes' and the additional 450 GL referred to above, taking into account likely, future climate change.

2. Personal Background and CV

I am an aquatic scientist that has worked in the Murray-Darling Basin for over 30 years. I completed my PhD on fish ecology on the Murray River in 1996. I was a government scientist (NSW Fisheries) for 10 years and have been an independent consulting scientist advising on fish ecology, fish migration, river and floodplain rehabilitation for over 20 years. I have worked on over 100 projects across the Basin in that time, including projects at every weir and most floodplains along the Murray River from Yarrawonga to the sea.

Much of my present work is advising the governments of the Mekong River, especially Laos PDR and Cambodia, and the Mekong River Commission on fish ecology, fish migration and balancing the development of hydropower with food security, livelihoods and biodiversity. I include a CV in Appendix 1 and can provide further details if required.

Of specific relevance to this Royal Commission is a scientific paper I have in press with a colleague (Appendix 2) which provides much of the background for the following submission. Please note that this submission uses the science from the paper but is my own opinion and does not necessarily reflect the opinions of the co-author of the paper.

The major points from the paper are:

- The Murray drying to a series of pools in droughts is an exaggerated myth; it's natural state is a *flowing river*.
- A quantitative water balance model of the Lower Lakes shows they were fresh over 94% of the time and often for multiple years at a time.
- There was a spring pulse in flow every year in the Murray, even in extreme droughts.
- Weirs create pools like extreme droughts, which has severely impacted aquatic biota. Removing weirs can recreate the original *flowing river* and brings back native fish – with no extra water.

- Broad-scale connected flows are required for large migratory fish species in long-term decadal water plans.

3. Is the Basin Plan likely to achieve the objects and purposes of the Act and Plan?

3.1 Ecological Background

There is a fundamental division in river ecology between *flowing water* (lotic) and *stillwater* (lentic), which is river hydraulics. *Flowing water* is typified by "riffles" but includes any flow that is visibly moving (e.g. runs or glides), while *stillwater* includes pools and lakes. It is well known that there are different animals in these two habitats, including biofilms, aquatic insects, mussels, crayfish, and fish (see references in Appendix 2). That is, there is a *flowing water* ecology. The other ecological dimension to this specific ecology is that many species of fish have drifting larvae that require flowing water over wide spatial scales; some require 10s km, while other require 100s km (e.g. golden perch or callop).

The significance of this ecology becomes apparent when we consider the Basin Plan and SDL projects which are based on hydrology and inundated floodplain. A good example of the impacts of hydraulics is the Lower Murray River, where the lower 700km (Lock 1 to Mildura) are continuous weirpools (stillwater habitat). It is often stated that the Murray naturally "dried to a series of pools" in droughts (see references in Appendix 2), including in the scientific literature, and hence the weirpools have been seen as having a relatively benign impact. The paper in Appendix 2 used historical data and computer modelling to show that the Murray had permanent *flowing water habitats* and that multiple small-scale irrigation diversions upstream contributed to the well-known historical occurrences where the Murray River stopped flowing.

The river may have stopped flowing naturally and become a series of pools, but it is more likely a 1:1000-year occurrence. The weirpools of the lower Murray now create these 1:1000-year extreme, pool-like, conditions every year and often all year in a drought. Various species of fish (trout cod), crayfish (Murray crayfish), snails (river snail) are extinct in the lower river, while mussels and other fish (Murray cod) have severely declined in the lower Murray. Where there are flowing-water habitats present upstream (Figure 1) Murray crayfish and Murray cod thrive and trout cod persist. Surprisingly, this occurs in reaches that have highly impacted hydrology [discharge]) but much less impacted hydraulics; that is, they retain permanent flowing habitats over moderate (>100 km) and large (500km) spatial scales (Figure 1).

These data very strongly suggest that the hydraulic impacts of the lower Murray have had a far greater impact than previously realised and very likely, a greater impact than changes in hydrology. The corollary is that <u>water from the Basin Plan is extremely unlikely to recover these lost species in the lower Murray River unless the hydraulics of the river are addressed as well</u>. Similar principles apply across the Basin. This does not diminish the impacts of reduced flow on floodplains and the estuary but hopefully it might change the emphasis of flow management.

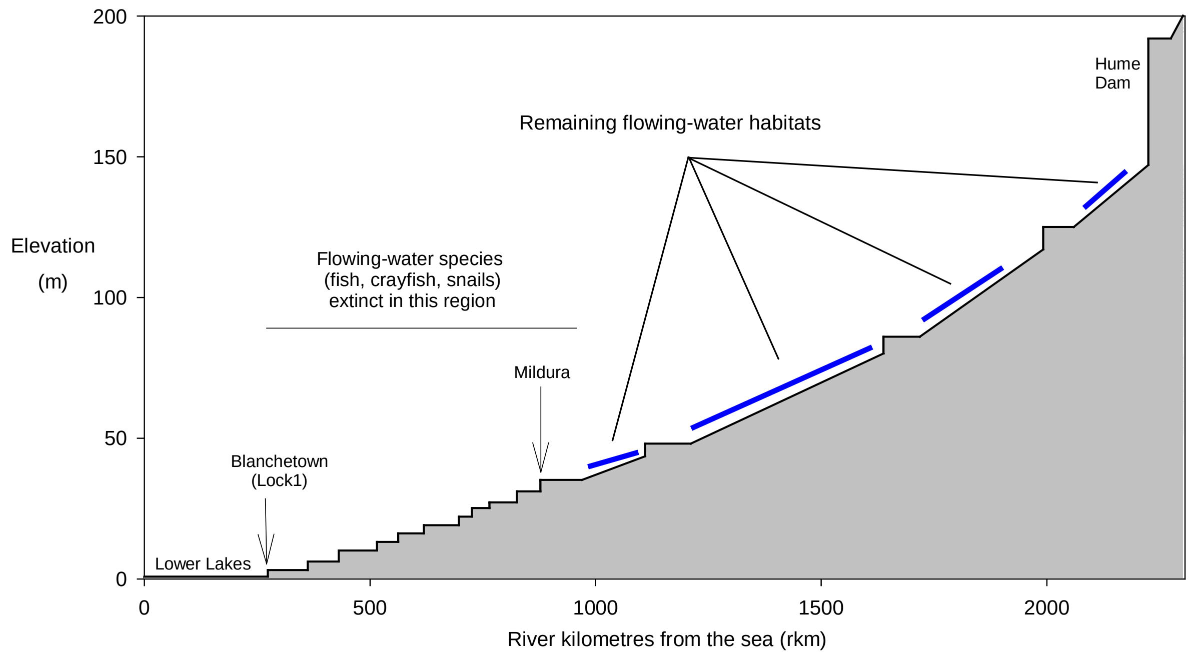

Figure 1. Profile of the Murray River showing elevation from the sea to Hume Dam (from Appendix 2).

3.2 Basin Plan - Schedule 6 - SDL Adjustments – Ecological Elements Methodology

Schedule 6 of the Basin Plan describes the framework for a method for adjustments in the Sustainable Diversion Limit. Schedule 6 emphasizes hydrology and Sections S6.01 to S6.04 discuss "environmental outcomes" as the goal. In S6.05, however, the scoring method is narrowed to flood dependent area, applying "fit for purpose preference curves", and "fit for purpose metrics".

The emphasis on flood-dependent area has arisen from decades of work on floodplains degraded from reduced flooding frequency. It does not, however, consider the reasons for the loss of aquatic species that live in the river channel, such as trout cod and Murray crayfish in the lower 700 km of the Murray River, or the loss of other aquatic species elsewhere in the Basin. Importantly, this emphasis on flood-dependent area has led to the present Ecological Elements Methodology (EEM), developed by CSIRO (Overton *et al*. 2014), having severe limitations and potentially added risks for the rehabilitation of aquatic biota.

There are three fundamental ecological principles missing from EEM:

1. recognition of the primary division in aquatic ecology between flowing water (lotic) habitats and stillwater water (lentic) habitats [i.e. hydraulics or hydrodynamics[1]],
2. spatial scale and connectivity, and
3. integrity of flow.

[1] Hydrodynamics is the variation of hydraulics over space and time

Not incorporating the first principle overlooks that many aquatic biota are flowing water (lotic) specialists (e.g. snails, mussels, fish [Murray cod, silver perch, trout cod, Macquarie perch and blackfish]). Flowing water habitats have declined due to weirpools and dams throughout the Basin, and hence *flowing water* biota have declined, as per the example of the lower Murray River above. Importantly, natural floods include a diversity of *flowing water* and *stillwater* habitats; that is, they have hydrodynamic diversity in which diverse aquatic biota thrive (Mallen-Cooper *et al*. 2011). SDL projects have tended to use inundated area as the key metric but a still, backwatered pond on a floodplain does not have the dynamics (throughput, hydraulics, flowing water) of a natural flood or the same ecological value.

Not incorporating the second principle overlooks that different species have life cycles that function over different spatial scales. Generalist fish species (spawn in rivers, wetlands and floodplains) can complete their life cycle over small spatial scales (e.g. single wetland or weirpool); while riverine specialist species complete their life cycle over varying spatial scales of <10 km (e.g. Murray cod) to 100s km (e.g. silver perch and golden perch). Critically, ignoring spatial scale in aquatic ecology overlooks that populations function over large spatial scales of whole catchments; including those species that may move little within a generation. Local and regional watering needs to be considered on a system or catchment scale to achieve the objectives of the Basin Plan; this has started to become part of the policy discussion.

Integrity of flow refers to the value of flow that maintains a hydrograph over a specific spatial scale. A flow that is unaltered along a river channel has high longitudinal integrity and a channel flow that is synchronised with floodplain inundation has high lateral integrity. The same flow volume that is stored and used at a later time, or is compartmentalised and used at different sites, at different times has a lower integrity of flow and a lower value for the river ecosystem. Integrity of flow acknowledges that river nutrients, carbon, chemical cues for spawning, plankton and propagules are transported by flow over wide spatial scales; and this large-scale interaction is essential for riverine function. Ignoring integrity of flow leads to further compartmentalisation of flow.

Hence, the <u>expected outcomes for fish and other aquatic biota with an unaltered SDL EEM program are</u>: more disconnected wetland /floodplain habitats, that are stillwater habitats without the hydrodynamics of a natural flood; supported by fragmented hydrology (i.e. not synchronised with river hydrology); with the continued loss of *flowing water* habitats.

Although the policy may improve localised abundances or health of terrestrial fauna and flora it predictably will favour generalist native and non-native fish species – both of which have abundant populations under present regulated conditions - and further disadvantage *flowing-water* specialist biota, especially those with large-scale life histories that have declined. In sum, more carp and common native fish, and threatened species become more threatened.

4. Way forward

The following is a framework for a new approach to using Basin Plan water more effectively:

1. Recognise the dependence of aquatic biota on hydraulic conditions (often called *ecohydraulics*) and the fundamental division in aquatic ecology between flowing water (lotic) and stillwater (lentic) habitats. This opens up a range of new opportunities to use the Basin Plan more effectively and highlights risks to minimize.

2. Urgently revise the SDL EEM to incorporate hydraulics, spatial scale and connectivity.
3. Integrate hydrodynamic objectives into flow management (see Appendix 3 for examples).
4. Incorporate 'integrity of flow' as a value in flow management (se Appendix 4 for further detail).
5. To assess the benefits of flow/hydraulic measures for aquatic biota, utilise guilds of fish and other aquatic biota based on hydraulics and spatial scale of the life cycle (e.g. Appendix 3).
6. The Natural Flow Paradigm underpins much of the Basin Plan thinking and river management in general; yet some of our most threatened fish species are in the most hydrologically-impacted reaches because there are suitable hydraulics, habitat and connectivity (see Appendix 4 for examples). Models of natural flows are a powerful tool but "*in some cases, the most productive restoration path may be to decouple a site from its hydrological and hydrodynamic history, pool the past regional ecological values and impose a hydrodynamic regime to target the values that have been lost. For example, where lotic habitats have been lost from the main river channel and it is impractical for them to be restored, these habitats can be created in anabranches where they may not have been an original feature of the habitat template, thereby creating new lotic refugia*" (Mallen-Cooper and Zampatti, in press). This concept needs to be explored within the context of the Basin Plan.
7. Aquatic biota require three aspects to complete their life cycles and thrive: flow, habitat and connectivity. The Basin Plan provides only flow. Complementary measures of habitat and connectivity are also required. Hydraulic habitats described above should be integral with flow but are related to infrastructure such as weirs, so will overlap with complementary measures.
8. Establish aquatic reserves based on hydrodynamics, scale and connectivity (see Appendix 4).
9. Manage weirpools to create hydrodynamic diversity. Lowering or removing a weir re-creates hydraulic complexity at the same discharge (Figure 2). Applying this to the lower Murray River is potentially one of the largest and most effective river rehabilitation projects globally, because removing or significantly lowering a weir will provide 10s or 100s km of flowing water habitat with no extra environmental water (Appendix 2).

References

Mallen-Cooper M, Zampatti B, Hillman T, King A, Koehn J, Saddlier S, Sharpe S, Stuart I. (2011). Managing the Chowilla Creek Environmental Regulator for Fish Species at Risk. Report prepared for the South Australian Murray-Darling Basin Natural Resources Management Board. 128 p.

Overton IC, Pollino CA, Roberts J, Reid JRW, Bond NR, McGinness HM, Gawne B, Stratford DS, Merrin LE, Barma D, Cuddy SM, Nielsen DL, Smith T, Henderson BL, Baldwin DS, Chiu GS and Doody TM. (2014) Development of the Murray-Darling Basin Plan SDL Adjustment Ecological Elements Method. Report prepared by CSIRO for the Murray-Darling Basin Authority Authors:

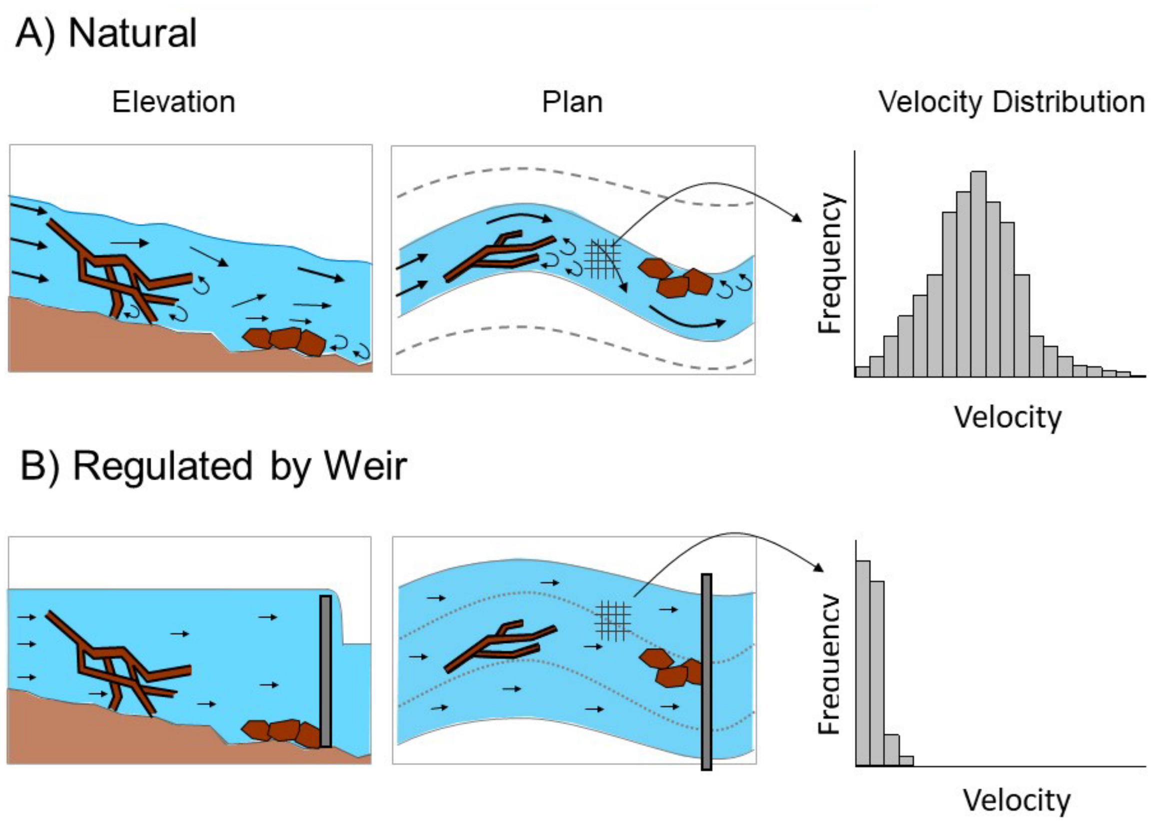

Figure 2. Conceptual diagram of hydraulic diversity in (a) a natural river and (b) the same river with the same discharge but with a weir added.

Appendix 1. Curriculum Vitae of Martin Mallen-Cooper

Dr Martin Mallen-Cooper

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Institute for Land Water and Society
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Director, OzFish Unlimited

Qualifications: **BAppSc**, 1979, University of Technology

PhD, 1996, Title: 'Fishways and freshwater fish migration in south-eastern Australia', University of Technology, Sydney.

Summary of experience

Dr Martin Mallen-Cooper has 30 years experience in fish ecology and fish passage research, management and fishway design, with 10 years at NSW Department of Primary Industries – Fisheries, Australia and the latter 20 years as a consultant.

In 1996 Dr Mallen-Cooper completed a PhD on 'Fishways and Freshwater Fish Migration in South-Eastern Australia'. The thesis was on fish ecology, and specifically on migration biology and its application to fishway design. Dr Mallen-Cooper has published his findings in national and international journals, workshops, and symposia. His early research on fish swimming ability and behaviour enabled him to design the first effective fishways for native fish in Australia. Prior to Dr Mallen-Cooper's work, fishways in Australia were designed for salmon and not for native fish. The research also led to the first effective fishways in Bangladesh. He is now a specialist in providing fish passage in rivers with diverse species and continues to do research on fishway design.

Dr Mallen-Cooper has provided design criteria for over 200 fish passage projects. He has been responsible for the biological performance of these projects, which have included pool-type, Denil and nature-like fishways for small weirs (AUD $0.02 to $5 mil. for individual sites and up to AUD $75 mil for large projects) to fish locks and fish lifts (up to AUD $20 mil) for high dams. The success of these projects is due to his approach of:

i) Providing biological design criteria specific to the river system and fish species,
ii) Integrating hydrology, biology, hydraulics, and dam and weir management,
iii) Identifying and managing knowledge gaps and risks,
iv) Evaluating fishway options,
v) Optimising fishway design,
vi) Maintaining the objective of providing practical solutions that pass fish.

Clients have included state and federal government agencies, engineering firms, local councils, and community groups. This work has mainly been in Australia, but also in New Zealand, China, Bangladesh, Laos (Mekong River Commission) and Cambodia; work in the last two countries has been dealing with large hydropower development as well as fish passage at wetlands.

Dr Mallen-Cooper's work on fishways is aimed at developing designs through a process that is consultative, transparent, and assesses the project through measurable and quantitative performance indicators, within the broader objective of ensuring ecologically sustainable fish populations.

Expert Panels / Steering Committees / Research Reviews

Habitat and Movement Requirements of Fish (Vic. Dept. Conservation and Natural Resources); 1994-1998
Review of Queensland Fishway Research (Qld DPI); 1997
Point Source Management of Carp (Vic DNRE); 1999-2001
Downstream Migration of Adult Fish (Vic DNRE); 1999-2001
Fish Passage Task Force (Murray-Darling Basin Authority); 2001-12
Carp Ecology Project (ARI); 2002
Downstream Migration Project (ARI); 2002
Protection and Enhancement of Murray cod Populations (DSE); 2004-05
Native Fish in Irrigation Supply Offtakes (NSW DPI); 2004-06
Eidsvold Fish Passage Monitoring Plan (Burnett Water); 2005
Native Fish Strategy - Drought Expert Panel (Murray-Darling Basin Authority); 2007
Lower Lakes Fish Risk Assessment (SARDI); 2008
Impacts of Irrigation on Fish (NSW DPI); 2008
Development of Fish Screening Criteria for Water Diversions in the Murray-Darling Basin (NSW DPI); 2008-11
Mitigation of Fish losses in Irrigation Offtakes (NSW DPI); 2009
Environmental requirements for managing successful fish recruitment in the Murray River Valley – Review of existing knowledge (DSE); 2009
Edward-Wakool Fish Monitoring (Murray CMA); 2010-2012
Murray River - Steering committee for fishway assessments; 2003-12
Mekong: Australian Centre for International Agricultural Research (ACIAR) – Fish Passage: Proof of Concept (FIS-2006-183); 2006-08
Mekong: ACIAR – Development of fish passage criteria for floodplain species of Central Laos (FIS-2007-076); 2007-09
Mekong: ACIAR – Development of fish passage technology to increase fisheries production on floodplains in the lower Mekong and Murray-Darling River basins (FIS-2009-041) 2009-11.
Mekong: ACIAR – Improving the design of irrigation infrastructure to increase fisheries production in floodplain wetlands of the Lower Mekong and Murray-Darling Basins (FIS-2012-100) 2012-present.

Examples of fish passage projects in Australia

Project	Client
MURRAY-DARLING BASIN	
Murray Barrage fishway options / concepts / detailed designs	Murray-Darling Basin Authority
Lock 1 fishway	Murray-Darling Basin Authority
Lock 2 fishway	Murray-Darling Basin Authority
Lock 3 fishway	Murray-Darling Basin Authority
Lock 4 fishway	Murray-Darling Basin Authority
Lock 5 fishway	Murray-Darling Basin Authority
Lock 6 fishway	Murray-Darling Basin Authority
Lock 7 fishway	Murray-Darling Basin Authority
Lock 8 fishway	Murray-Darling Basin Authority

Lock 9 fishway	Murray-Darling Basin Authority
Lock 10 fishway	Murray-Darling Basin Authority
Lock 11 Mildura Denil fishway	Murray-Darling Basin Authority
Lock 15 Euston Weir Denil fishway	Murray-Darling Basin Authority
Lock 15 Euston Weir fish lock	Murray-Darling Basin Authority
Lock 26 Torrumbarry fishway	Murray-Darling Basin Authority
Lock 26 Torrumbarry fishway	Murray-Darling Basin Authority
Yarrawonga Weir fishway	Murray-Darling Basin Authority
Liaison with CFD modellers	Murray-Darling Basin Authority
Black Engine Creek	Murray-Darling Basin Authority
Gulpa Creek	Murray-Darling Basin Authority
Lake Victoria fish passage options	Murray-Darling Basin Authority
Review of Fish Counters	Murray-Darling Basin Authority
Nigra Creek wetland	Murray-Darling Basin Authority

NEW SOUTH WALES

Review of fish passage in NSW	NSW Fisheries
Manyweathers weir, Richmond river	NSW Fisheries
Balranald fish lock	NSW Fisheries
Buckenbowra Weir	Eurobodalla Shire Council
Review of the proposed Pump Fishway for Audley Weir, Hacking River	NSW Fisheries
Lower Gwydir Floodplain, NSW	Wetland Care Australia
Jerry's Plains Weir, Hunter River	NSW Fisheries
Lower Ourimbah Weir	Wyong Shire Council
Colongolook River	Great Lakes Council
Tarabah Weir	NSW Fisheries
Brewarrina Weir, Barwon River	NSW Fisheries
Burtundy Weir, Darling River	NSW Fisheries
Weir 32, Darling River	NSW Western Local Land Services

VICTORIA

Hollands Creek Diversion Weir, Broken River	Goulburn Broken Catchment Management Authority (CMA)
Gowangardie Weir, Broken River	Goulburn Broken CMA
Latrobe River	West Gippsland CMA
Euroa and Benalla fishways	Sinclair Knight Merz
Katandra Weir fishway, Nine Mile Creek	Goulburn-Murray Water, Victoria
Broken Creek Offtake fishway	Goulburn-Murray Water
Caseys Weir	Goulburn Broken Catchment

TASMANIA

Workshop on fish passage in northern Tasmania	Inland Fisheries Service of Tasmania
Little Swanport River- rock-ramp fishway	Private landholder
Second River- rock-ramp fishway	Private landholder

Black River- rock-ramp fishway	Private landholder

SOUTH AUSTRALIA

Fish passage at culverts and regulators in wetlands of the lower Murray River	Wetland Care Australia
Fish Passage and Paiwalla Wetland	Mannun to Wellington Local Action Planning Committee Inc
Fishway Design for Hunters Creek Causeway	Dept for Environment and Heritage

AUSTRALIAN CAPITAL TERRITORY

Casuarina Sands and Cotter Campground weirs, Murrumbidgee River	G K Ellery and Associates
Cotter River, Vanities Crossing	ACT Environment
Cotter River, Pipeline Crossing	ACT Environment

QUEENSLAND

Cedar Grove Weir fishway, south-eastern Queensland	PPK Environmental & Infrastructure
Design of vertical-slot fishways in the Murray-Darling river system in Queensland	Queensland Department of Primary Industries
Proposed Bedford Weir and Bingegang Weir fish locks, Fitzroy River	State Water Projects – Engineering Services, Queensland
Eidsvold Weir fish lock	SMEC
Paradise Dam fish lift and downstream fish lock	Burnett Dam Alliance
Wyaralong Dam fish lift	Wyaralong Dam Alliance

Other clients have included URS, GHD, SMEC, SKM, Hydro Tasmania Consulting, Sunwater, NSW Public Works, Victorian Department of Natural Resources and Environment, Northern Territory Department of Transport and Works.

Fish passage projects overseas

Project	Client
New Zealand - Mararoa Weir fishway	Meritec (Worley Consultants)
Bangladesh - Manu River fishway	Canadian International Development Agency
China – Yangtze and Pearl rivers	China Australia Agricultural Cooperation Agreement
USA & France – study tour	Sydney Catchment Authority
Laos – Mekong River Dams & Fish Workshop	Mekong River Commission
- Review of Xayaburi Dam	Mekong River Commission
- Review of Don Sahong	Mekong River Commission
Cambodia – Sambor Dam Design to optimise fish outcomes	Natural Heritage Institute (USAID & Macarthur Foundation)

- Xekong R. – strategic hydropower to optimise power production and minimise fish impacts	Natural Heritage Institute (USAID & Macarthur Foundation)
- Lower Sesan 2 Review	Natural Heritage Institute (USAID & Macarthur Foundation)
- Lower Sesan 2 Fishpass design	Cambodian Inland Fisheries Research and Development Institute (EuAID)

Publications (listed chronologically)

2017 Bice, C. M., Gibbs, M. S., Kilsby, N. N., Mallen-Cooper, M., & Zampatti, B. P. (2017). Putting the “river” back into the lower River Murray: quantifying the hydraulic impact of river regulation to guide ecological restoration. *Transactions of the Royal Society of South Australia*, *141*(2), 108-131.

2017 Bice, C. M., Zampatti, B. P., & Mallen-Cooper, M. Paired hydraulically distinct vertical-slot fishways provide complementary fish passage at an estuarine barrier. *Ecological Engineering*, *98*, 246-256.

2016 Zampatti B. and Mallen-Cooper, M. Making fish ‘happen’. *Rip Rap*. **39**, 1-3.

2016 Mallen-Cooper, M. Can we have dams and maintain most of the fishery? *Catch and Culture* 22 (3). 48-50.

2015 O’Connor, J., Mallen-Cooper, M., and Stuart, I. Performance, Operation and Maintenance Guidelines for Fishways and Fish Passage Works. Technical Report No. 262 for the Water and Catchments Group, Department of Environment, Land Water and Planning.

2014 Koehn, J.D., King, A.J., Beesley, L., Copeland, C., Zampatti, B.P., and Mallen-Cooper, M. Flows for native fish in the Murray-Darling Basin: lessons and considerations for future management. *Ecological Management & Restoration* **15**(s1), 40-50.

2014 Baumgartner, L., Zampatti, B., Jones, M., Stuart, I., and Mallen-Cooper, M. Fish passage in the Murray-Darling Basin, Australia: Not just an upstream battle. *Ecological Management & Restoration* **15**, 28-39.

2014 Brown, R.S., Colotelo, A.H., Pflugrath, B.D., Boys, C.A., Baumgartner, L.J., Deng, Z.D., Silva, L.G.M., Brauner, C.J., Mallen-Cooper, M., Phonekhampeng, O., Thorncraft, G., and Singhanouvong, D. Understanding Barotrauma in Fish Passing Hydro Structures: A Global Strategy for Sustainable Development of Water Resources. *Fisheries* **39**(3), 108-122.

2014 Slarke, S., Mallen-Cooper, M., Giurgis, M., Keepit Fishway Offsets: Mollee Weir fish lock and downstream multi-function migration gate – integrating form and function. 2014 ANCOLD Conference, Canberra, ACT. 10 p.

2013 Baumgartner LJ, Conallin J, Wooden I, Campbell B, Gee R, Robinson WA, Mallen-Cooper M. Using flow guilds of freshwater fish in an adaptive management framework to simplify environmental flow delivery for semi-arid riverine systems. *Fish and Fisheries* DOI: 10.1111/faf.12023

2012 Barrett, J. and Mallen-Cooper, M. Fish finding a new way from the sea to Hume Dam. RipRap 34:

2010 Maher G, Mallen-Cooper M, Herweynen R. A Bi-Directional Fishlift – An Innovative Solution for Fish Passage. 2010 ANCOLD Conference, Hobart, Tasmania. 11 p.

2010 Slarke S, Mallen-Cooper M, Prentice J, Mildura Weir Denil Fishway; an Innovative Fish Passage Solution for a Unique Site. 2010 ANCOLD Conference , Hobart, Tasmania. 11 p.

2010 Dugan PJ , Barlow C, Agostinho AA, Baran E, Cada GF, Chen D, Cowx IG, Ferguson JW, Jutagate T, Mallen-Cooper M, Marmulla G, Nestler J, Petrere M, Welcomme RL and Winemiller KO. Fish migration, dams, and loss of ecosystem services in the Mekong Basin. *Ambio* DOI 10.1007/s13280-010-0036-1

2010 Mallen-Cooper M, Zampatti B. Delivering environmental flows for fish; have we got the scales right? Murray-Darling Basin Commission Fish Forum 2010, held at the National Museum, Canberra 15-16 September 2010. Pp. 49-51.

2009 King, A.J., Ramsey, D., Baumgartner L., Humphries P., Jones M., Koehn J., Lyon J., Mallen-Cooper M., Meredith S., Vilizzi L., Ye Q., Zampatti, B. 'Environmental requirements for managing successful fish recruitment in the Murray River Valley: review of existing knowledge' Technical Report Series No. 197. (Arthur Rylah Institute for Environmental Research, Department of Sustainability and Environment: Melbourne, Australia)

2009 Prentice J, Barrett J, Mallen-Cooper M. The River Murray – Providing Fish Passage from the

Sea to Hume Dam. ANCOLD 2009 Conference. 9 p.

2009 Paul T, Deen A, Mallen-Cooper M, Smit K. Delivering environmental flows and fish passage to the Nepean River. AWWA 2009 Conference, November 2009. 5 p.

2008 Baumgartner LJ, Mallen-Cooper M, Zampatti B, Stuart I, Jones M. Learning through Monitoring: The Sea to Hume Program. Murray-Darling Basin Commission Fish Forum 2008, held at the National Convention Centre, Canberra 9-10 September 2008. 5 p.

2007d Lintermans M. Cottingham P. (eds) with Gehrke P., Hillman, T., Jackson, T. Koehn, J Mallen-Cooper, M. McMahon T. and Walker K. 2007. Fish out of water – lessons for managing native fish during drought. Final Report of the Drought Expert Panel. Murray-Darling Basin Commission, Canberra.

2007d Mallen-Cooper, M and Brand, D.A. Non-salmonids in a salmonid fishway: what do 50 years of data tell us about past and future fish passage? *Fisheries Management and Ecology* **14**, 319-332.

2007c Mallen-Cooper, M and Stuart, I.G. Optimising Denil fishways for passage of small and large fishes. *Fisheries Management and Ecology* **14**, 61-71.

2007b Stuart, I.G., Berghuis, A.P., Long P.E., and Mallen-Cooper, M. Do fish locks have potential in tropical rivers? *River Research and Applications*

2007a Barrett, J. and Mallen-Cooper, M. The 'Sea to Hume Dam' program – retrofitting fishways along Australia's greatest river. International Association of Hydraulic Engineering and Research (IAHR) 32nd Biennial Congress, Venice, July 1-7, 2007, 'Harmonizing the Demands of Art and Nature in Hydraulics', Special Session - Retrofitting Existing Dams with Fish Passes, 10 p.

2006b Barrett, J. and Mallen-Cooper, M. The Murray River's 'Sea to Hume Dam' fish passage program: progress to date and lessons learned. *Ecological Management and Restoration* **7** (3), 173-183.

2006a Mallen-Cooper, M. and Stuart, I.G. Fish, Floods and Fallacy. *Australasian Science* **27** (5), 19-22.

2004c Mallen-Cooper, M. Fish passage – from go to whoa needs flow to go. National Symposium on Ecosystem Research and Management of Fisheries, Adelaide 20-21 September 2004. (Abstract).

2004b Mallen-Cooper, M. Wetland Connectivity and Fish Passage. Workshop on Management of Fish in Wetlands in South Australian. Adelaide, 23 April 2004, 6 pp.

2004a Greene, G.R., Smit, K. and Mallen-Cooper, M. Minimising the uncertainties surrounding the successful delivery of a high-level fishway at Tallowa Dam. Rivers Symposium.

2003 Mallen-Cooper, M. and Stuart, I.G. Age, growth, and non-flood recruitment of two potamodromous fishes in a large semi-arid / temperate river system. *River Research and Applications* **19**, 697-719.

2001 Smit, K., Mallen-Cooper, M., Walker, S. Greene, G. High-level fishway options for Tallowa Dam. Proceedings of the Third National Fishway Technical Workshop. 11 p. (Queensland Department of Primary Industries: Rockhampton.)

2000 Mallen-Cooper, M. Taking the mystery out of migration. *in* D.A. Hancock, D.C. Smith and J.D. Koehn (eds.). Fish Movement and Migration, Australian Society for Fish Biology Workshop Proceedings. pp. 101-111.

1999b Stuart, I.G. and Mallen-Cooper, M. An assessment of the effectiveness of a vertical-slot fishway for non-salmonid fish at a tidal barrier on a large tropical/sub-tropical river. *Regulated Rivers* **15**, 575-590.

1999a Mallen-Cooper, M. Developing fishways for nonsalmonid fishes: a case study from the Murray River in Australia. pp. 173-195 *in* M. Odeh (ed.). Innovations in Fish Passage Technology. (American Fisheries Society: Bethesda, Maryland.)

1997b Mallen-Cooper, M. Priorities for fishways in semi-arid and tropical streams. *Proceedings of the Second National Fishway Technical Workshop.* pp. 27-34. (Queensland Department of Primary Industries: Rockhampton.)

1997a Mallen-Cooper, M. and Copeland, C. Science and the management of freshwater fish: a case study of fishways and fish migration in the Murray-Darling Basin. In 'Saving our natural heritage? The role of science in managing Australia's ecosystems' [Eds. C. Copeland and D. Lewis] pp. 262-271.

1996 Mallen-Cooper, M. Fishways and freshwater fish migration in south-eastern Australia. PhD thesis. University of Technology , Sydney, 377 p.

1994c Mallen-Cooper, M. Swimming ability of adult golden perch, *Macquaria ambigua* (Percicthyidae), and adult silver perch, *Bidyanus bidyanus* (Teraponidae), in an experimental vertical-slot fishway. *Australian Journal of Marine and Freshwater Research* **45**, 191-8.

1994b Mallen-Cooper, M. How high can a fish jump? *New Scientist* [16 April 1994]. **142** (1921), 32-7.

1994a Harris, J.H. and Mallen-Cooper M. Fish passage development in the rehabilitation of fisheries in mainland south-eastern Australia. *Proceedings of the International Symposium and Workshop on Rehabilitation of Inland Fisheries, Hull, 6-10 April, 1992* (Ed. I. Cowx) pp. 185-193.

1993b Mallen-Cooper, M. Fishways in Australia; past problems, present success and future opportunities. *ANCOLD Bulletin* **93,** 22-33.

1993a Mallen-Cooper, M. Habitat changes and declines of freshwater fish in Australia: what is the evidence and do we need more? *in* D.A. Hancock (ed.). Sustaining fisheries through sustaining habitat, Australian Society for Fish Biology Workshop Proceedings. Australian Government Publishing service: Canberra. pp. 118-123.

1992 Mallen-Cooper, M. Swimming ability of juvenile Australian bass, *Macquaria novemaculeata* (Steindachner), and juvenile barramundi, *Lates calcarifer* (Bloch), in an experimental vertical-slot fishway. *Australian Journal of Marine and Freshwater Research* **43**, 823-34.

1990 Mallen-Cooper, M. and Harris, J.H. Fishways in mainland south-eastern Australia. *Proceedings of the International Symposium on Fishways '90 in Gifu.* pp. 221-229.

1989 Mallen-Cooper, M. Fish passage in the Murray-Darling Basin. In: *Proceedings of the Workshop on Native Fish Management* (Ed. B. Lawrence). Murray-Darling Basin Commission. pp. 123-136.

Reports for consultancies and grants (listed chronologically)

2017 Natural Heritage Institute (multiple authors). Xekong hydropower master plan. Report to the Government of Laos PDR

2017 Natural Heritage Institute (multiple authors). Lower Sesan 2 Fishpass Concept Design. Report to the Cambodian Government.

2017 Natural Heritage Institute (multiple authors). Sambor Dam concept design. Report to the Cambodian Government.

2011 Mallen-Cooper M, Stuart IG, Sharpe C. Optimising Outcomes for Native Fish in Managed Inundations of the Gunbower Forest. Report prepared for the North Central Catchment Management Authority. 31 p.

2011 Mallen-Cooper M, Zampatti B, Hillman T, King A, Koehn J, Saddlier S, Sharpe S, Stuart I. 2011. Managing the Chowilla Creek Environmental Regulator for Fish Species at Risk. Report prepared for the South Australian Murray-Darling Basin Natural Resources Management Board. 128 p.

2010 Mallen-Cooper M, King AJ, Koehn JD, Saddlier S, Sharpe C, Stuart IG, Zampatti BP. 2010. Fish requirements for the proposed upper Lindsay watercourse enhancement project. Report prepared for the Mallee Catchment Management Authority. 45 p.

2009 King AJ, Ramsay D, Baumgartner L, Humphries P, Jones M, Koehn J, Lyon J, Mallen-Cooper

M, Meredith S, Vilizzi L, Ye Q, Zampatti B. Environmental Requirements for managing successful fish recruitment in the Murray River Valley - review of existing knowledge. Department of Sustainability and Environment, Heidelberg, Victoria. Arthur Rylah Institute for Environmental Research, Technical Report Series No. 197.

2008 Mallen-Cooper, M. Koehn, J., King A., Stuart I. & Zampatti, B. Risk assessment of the proposed Chowilla Regulator and managed floodplain inundations on fish. Department of Water, Land and Biodiversity Conservation, South Australia. 86 p.

2008 Mallen-Cooper M, Zampatti BP, Stuart IG, & Baumgartner LJ. Innovative fishways – manipulating turbulence in the vertical-slot design to improve performance and reduce cost. Report to the Murray-Darling Basin Commission. 24 p.

2008 Howland, M, Jackson P. and Mallen-Cooper M. Fishway Effectiveness for High Dams. Report for Queensland Water Infrastructure. 52 p.

2006 O'Brien T., Mallen-Cooper, M., Pitman, K. Instream barriers of the Loddon and Campaspe catchments: assessment and prioritisation for fish passage. Report to the North Central Catchment Management Authority. 85 p.

2006 Mallen-Cooper, M and Smit, K. Fishway options for Karangi Gauge Weir (Skews Crossing), Orara River. 14 p.

2006 Mallen-Cooper, M. Fishway Design for Hunters Creek Causeway. Report to Dept for Environment and Heritage. 9 p.

2006 Mallen-Cooper, M. Fish Passage and Paiwalla Wetland. Report to Mannun to Wellington Local Action Planning Committee. 3 p.

2005 Eidsvold Weir Fish Passage Monitoring Plan. Report to Burnett Water. 28 p.

2005 Mallen-Cooper, M. Background material and fishway options for Lock 11 Mildura, Murray River. Report to the Murray-Darling Basin Commission. 9 p.

2005 Mallen-Cooper, M. Fish passage options for a causeway on the Urumbilum River. Report for the NSW Dept of Primary Industries – Fisheries. 7 p.

2005 Mallen-Cooper, M. Design of a rock-ramp fishway at Skews Crosssing, Orara River. Report for the NSW Dept of Primary Industries – Fisheries. 15 p.

2005 Mallen-Cooper, M. Review of fish passage on bed control structures in the Orara and lower Urumbilum rivers. Report for the NSW Dept of Primary Industries – Fisheries. 7 p.

2004 Mallen-Cooper, M. Concept design for a fishway on the Torrens River Outlet Weir (Breakout Creek). Report for the Torrens Catchment Management Board. 7 p.

2004 Smit, K., Mallen-Cooper, M. Tallowa Dam high level fishway pre-design report. Report to the Sydney Catchment Authority. 22 p.

2004 Mallen-Cooper, M. Initial Recommendations for Fish Passage at Locketts's Crossing, Colongolook River. Report to Great Lakes Council. 4 p.

2004 Mallen-Cooper, M. Fish passage in the Nigra Creek wetland complex. Report to the Nigra Creek Wetland Committee. 4 p.

2004 Mallen-Cooper, M. Fish passage at selected sites in the Gunbower Forest. Report to the North Central Catchment Management Authority. 5 p.

2004 Mallen-Cooper, M. Eidsvold Weir Fish Passage Monitoring Plan. Report to Burnett Water. 23 pp.

2004 Mallen-Cooper, M. Background Paper on Biological Inputs into Fishway Design for the lower Murray River. Paper prepared for Murray-Darling Basin Commission's Value Management Workshop. 37 p.

2004 Mallen-Cooper, M and Smit, K. Design of a sloping fish lock for Eidsvold Weir, Burnett River. Report to SMEC. 10 p.

2004 Howland, M. Mallen-Cooper, M, Neumaier, A. Burnett River Dam Fishway Monitoring Framework. Burnett Dam Alliance. 23 p.

2004 Giudici. C., Howland, M. Mallen-Cooper, M, Neumaier, A. Managing fish passage during flood

events. Burnett Dam Alliance. 25 p.

2004 Giudici. C., Howland, M. Mallen-Cooper, M, Neumaier, A. Design, Operation and Management of the Burnett Dam Fishway. Burnett Dam Alliance. 18 p.

2003 Smit. K., Mallen-Cooper, M. Successful delivery of a fishway at Tallowa Dam. Report to the Sydney Catchment Authority. 55 pp.

2003 Mallen-Cooper, M. Options for excluding large carp from the Main Eastern Irrigation channel at Maffra Weir. Report to Southern Rural Water. 11p.

2003 Mallen-Cooper, M. Fishway design criteria for a proposed earthen dam on East Creek, Black River catchment, north-western Tasmania. Report to landholder Bob Parr. 5 p.

2002. SMEC and Fishway Consulting Services. Design of fishways for four weirs on the upper Parramatta River. Report to the Upper Parramatta River Trust. 17 p.

2002 Mallen-Cooper, M., in conjunction with Brian Cooper. Monitoring fish movements - literature and equipment review. Report to the Murray-Darling Basin Commission. 39 p.

2002 Mallen-Cooper, M. Fishway options for Brewarrina Weir. Report to NSW Fisheries. 34 p.

2002 Mallen-Cooper, M. Fishway options for Manyweathers Weir, Richmond River. Report to NSW Fisheries. 26 p.

2002 Mallen-Cooper, M. Fish passage options for Tea Garden Creek Weir, Ovens River. Report to the Victorian North East Catchment Management Authority. 16 p.

2002 Mallen-Cooper, M. Assessment of fish habitat and fish passage needs in the Second River, near ‘Hawkspur’ (Tasmania). Report to Tony Botsman. 4 p.

2002 Mallen-Cooper, M. Assessment of fish habitat and fish passage needs in the Little Swanport River, near ‘Stonehenge’ (Tasmania). Report to RW McShane Trust. 6 p.

2002 Mallen-Cooper, M. and Klaas Smit. Prospective cost of a fishway at Mullet Creek, Lake Illawarra. Report to NSW Fisheries. 5 p.

2002 Fish Passage Reference Group. Review of a proposed Denil fishway on the Gulpa Creek Offtake Regulator. Report to NSW State Water. 12 p.

2002 Fish Passage Reference Group. Proposed regulator on Black Engine Creek – comments from the fish passage reference group of the Murray-Darling Basin Commission. 8 p.

2002 Brief for design of a fishway for Stevens Weir, Edwards River. Report to NSW Fisheries. 4 p.

2001 Smit, K., Mallen-Cooper, M. Tallowa Dam high-level fishway feasibility study. Report to the Sydney Catchment Authority. 39 p.

2001 Mallen-Cooper, M. Fishway options for two weirs on the Upper Parramatta River. Report to the Upper Parramatta River Catchment Trust. 11 p.

2001 Mallen-Cooper, M. Fish passage options for the Murray River Barrages. Report to the Murray-Darling Basin Commission. 26 p.

2001 Mallen-Cooper, M. Fish passage in off-channel habitats of the lower River Murray. Report to Wetland Care Australia. 57 p.

2001 Mallen-Cooper, M. Design criteria for a fishway at Vanities Crossing, Cotter River, ACT. Report to Environment ACT. 4 p.

2001 Mallen-Cooper, M. Optimising passage of fish and other fauna in the settling pond of Eraring Power Station. Report for Water Research Laboratory and Eraring Energy 2 p.

2001 Mallen-Cooper, M. Conceptual designs for fishways at two sites in northern Tasmania. Report to Inland Fisheries Service. 17 p.

2001 Mallen-Cooper, M. Assessment of Nepean River fishways. In: Nepean Weirs Assessment (SMEC). Report to Sydney Catchment Authority.

2000 Mallen-Cooper, M. Review of barriers to fish passage in the Lower Gwydir Floodplain. Report to Wetland Care Australia. 40 p.

2000 Mallen-Cooper, M. Field inspections of Euroa and Benalla fishways. Report to the Goulburn

Broken Catchment Management Authority. 6 p.

2000 Mallen-Cooper, M. Fish passage options for Hollands Creek diversion Weir, Broken River catchment. Report to the Goulburn Broken Catchment Management Authority. 4 p.

2000 Mallen-Cooper, M. Fish passage options for Gowangardie Weir, Broken River. Report to the Goulburn Broken Catchment Management Authority. 3 p.

2000 Mallen-Cooper, M. Fishway options for Buckenbowra Weir. Report to Eurobodalla Shire Council. 22 p.

2000 Mallen-Cooper, M. Review of fish passage in NSW. Report to NSW Fisheries. 86 p.

1999 Mallen-Cooper, M. A review of the proposed Pump Fishway for Audley Weir. Report to NSW Fisheries. 8 p.

1999 Mallen-Cooper, M. Design of vertical-slot fishways in the Murray-Darling river system in Queensland, and fishway options for Nangram Weir, Condamine River. Report to Queensland Department of Primary Industries. 15 p.

1999 Mallen-Cooper, M. A review of fishway options for the Casuarina Sands and Cotter Campground weirs, Australian Capital Territory. Report to G K Ellery and Associates. 10 p.

1999 Mallen-Cooper, M. A review of fish passage options for Jerry's Plains Weir, Hunter River. Report to NSW Fisheries. 15 p.

1999 Mallen-Cooper, M. Review of the design of the Cedar Grove Weir fishway, south-eastern Queensland. Report to PPK Environmental & Infrastructure. 4 p.

1999 Mallen-Cooper, M. Biological design criteria for the proposed Euroa and Benalla fishways. Report to Sinclair Knight Merz. 10 p.

1999 Mallen-Cooper, M. Review of the design of the Katandra Weir fishway, Nine Mile Creek. Report to Goulburn-Murray Water. 3 p.

1999 Mallen-Cooper, M. Review of the design of the Broken Creek Offtake fishway, Nine Mile Creek. Report to Goulburn-Murray Water. 3 p.

1999 Mallen-Cooper, M. Biological considerations of the proposed Bedford Weir and Bingegang Weir fish locks, Fitzroy River, Central Queensland 8 p.

1998 Mallen-Cooper, M. Fish passage options at tidal barrages in the Mary River Wetlands, Northern Territory. Report to the Northern Territory Department of Transport and Works. 23 p.

1998 Mallen-Cooper, M. A comparison of vertical-slot fishways and fish locks and their application in south-eastern Queensland. Report to the South-East Queensland Water Board. 6 p.

1998 Mallen-Cooper, M. Evaluation of fishway options for the proposed Cedar Grove Weir. Report to Gutteridge, Haskins and Davey for EIS on Cedar Grove Weir. 6 p.

1997 Boyd, G.J. and Mallen-Cooper, M. Manapouri Lake Control Residual Flow and Fish Pass Concept Design Report. Report to the Electricity Corporation of New Zealand. 25 p.

1997 Mallen-Cooper, M. Research priorities and some suggested experimental designs for the Southern Fishway Team. Report to the Queensland Department of Primary Industries. 14 p.

1997 Mallen-Cooper, M. Review of fishway plans for Schier's Weir, Broken Creek, Victoria. Report to Goulburn-Murray Water. 5 p.

1996 Mallen-Cooper, M. Assessment of the design of the Loudoun Weir fishway on the Condamine River in southern Queensland. Report to the Queensland Department of Primary Industries. 4 p.

1996 Mallen-Cooper, M. Review of fishway assessment in the Fitzroy River, central Queensland. Report to the Queensland Department of Primary Industries. 13 p.

1996 Mallen-Cooper, M. Background and rationale for the design of the fishway on the Nicholson River anabranch in the Shire of Burke (Queensland). Report to the Council of the Shire of Burke. 12 p.

1995 Mallen-Cooper, M., Stuart, I.G., Hides-Pearson, F., and Harris, J.H. Fish migration in the Murray River and assessment of the Torrumbarry fishway. Final report for the Natural Resources

Management Strategy Project N002. 149 pp.

1994 Mallen-Cooper, M. Assessment of a rock-ramp fishway at Dight's falls on the Yarra River. Report to the Melbourne Water Corporation. 8 p.

1993 Mallen-Cooper, M. 'Proceedings of the Workshop on Fish Passage in Australia.' (editor) 21 p.

1993 Mallen-Cooper, M. and Harris, J.H. Fish passage options for Eden Bann Weir on the Fitzroy River, Queensland. Report to the Queensland Department of Primary Industry. 4 p.

1992 Mallen-Cooper, M. Progress report on NRMS project N002 for November 1990 to January 1992 - Fish migration in the Murray River and assessment of the Torrumbarry fishway. 12 p.

1992 Mallen-Cooper, M., Harris, J.H. and Thorncraft, G.A. Enhancing upstream passage of fish through a navigation lock on the River Murray. Report to the Murray-Darling Basin Commission. 16 p.

1992 Mallen-Cooper, M. and Thorncraft, G.A. Fish passage and fish abundance at Brewarrina Weir following a bloom of blue green algae. Fisheries Research Institute Internal Report. 12 p.

1992 Mallen-Cooper, M. and Brand D. Assessment of two fishways on the River Murray and historical changes in fish movement. Report to the Murray-Darling Basin Commission. 38 p.

1991 Mallen-Cooper, M. and Edwards, E. Fish passage through the Main Weir at Menindee Lakes during the flood of September 1990. Fisheries Research Institute Internal Report. 17 p.

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RESEARCH ARTICLE

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History, hydrology and hydraulics: Rethinking the ecological management of large rivers

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Abstract
Climatic extremes capture imaginations and provide a fundamental premise for biologists—that ecosystems are adapted to natural variability. Hence, understanding past extremes provides a template for contemporary ecological models and management. Nevertheless, myths can develop around historical climatic events, distorting perceptions of the past. The mythology of the Murray River in Australia is that over 100 years ago, it naturally "dried to a series of pools" in drought; therefore, the biota are flexible and adapted to hydrological variability and lentic habitats.
Analysis of historical and modelled hydrology and hydrodynamics, however, demonstrates that: (a) cease-to-flow events were not natural and were instead caused by multiple small-scale irrigation diversions; and (b) the Murray River had widespread perennial lotic habitats. Within a generation, the spatial, temporal, and causal context was lost and with it, the links between preregulation hydrology and hydraulics, and river ecology.
From an intermittently lentic system, we propose an alternative model which integrates ecohydrology and ecohydraulics. Specifically, the model incorporates: (a) persistence of lotic in-channel and lentic off-channel refugia, even in droughts; and (b) a reliable spring flow pulse that increases hydrodynamic complexity, promotes longitudinal integrity of lotic conditions and replenishes low-lying wetlands. The model helps explain the decline of lotic biota, suggesting that hydraulic change has had a greater impact on aquatic biodiversity than changes in hydrology.
Being mindful of historical conditions and considering spatio-temporal ecohydraulics provides new opportunities for the rehabilitation of highly modified rivers and may assist the strategic development of large rivers, including for hydropower.

KEYWORDS
drought, ecohydraulics, ecohydrology, fish, hydropower, lotic, Murray River, rehabilitation

1 | INTRODUCTION

Anthropogenic modification of rivers has a profound effect on ecosystem integrity (Richter & Postel, 2004) and is arguably the world's greatest threat to aquatic biodiversity (Dudgeon et al., 2006; Vörösmarty et al., 2010). Contemporary approaches to aquatic ecosystem restoration involve the reinstatement of functionally important aspects of the natural (unaltered) flow regime (Poff et al., 1997; Richter, Mathews, Harrison, & Wigington, 2003). Such approaches, however, require a fundamental knowledge of preregulation hydrology and river dynamics (Galat & Lipkin, 2000).

In regulated rivers, perceptions of predevelopment flow regimes serve as benchmarks that shape conceptual models of biology and ecosystem function, influence research, and guide management and restoration (Kennard et al., 2010; Poff & Zimmerman, 2010). The periodicity and magnitude of extreme natural events (such as droughts and floods) are of particular interest, as they are often associated with a strong biological response and hence are considered ecologically important facets of the natural flow regime (Lake, 2000). These events capture imaginations and provide a fundamental premise for biologists—that ecosystems are inherently adapted to natural variability.

Ecosystem restoration also relies on an understanding of historical ecology (Jackson & Hobbs, 2009). Perceptions of predisturbance condition, however, are often clouded by the passage of time, and along with the variability of terrestrial and aquatic ecosystems, can lead ecologists and managers to suffer from "temporal myopia" (Silvertown et al., 2010). Multidecadal ecological datasets are unusual, so ecological history needs to be evaluated using available documentary and archival evidence, time-series of instrument-based data (e.g., stream gauging records), and palaeoecological approaches (Swetnam, Allen, & Betancourt, 1999). Nonetheless, even where there is an appreciation of the need for a long-term ecological perspective, quantitative monitoring and ecological theory can postdate anthropogenic changes to fluvial systems by decades or centuries and changing human perceptions can create false impressions of past conditions, that is, the "shifting baseline syndrome" (Ehlmann & Criss, 2006; Papworth, Rist, Coad, & Milner-Gulland, 2009; Pauly, Watson, & Alder, 2005; Ward, Tockner, Uehlinger, & Malard, 2001).

The Murray River in south-eastern Australia forms part of Australia's longest river system, the Murray–Darling, and has been regulated for consumptive use for 130 years. The Murray River is generally categorized as a semiarid, dryland river characterized by highly variable hydrology (Maheshwari, Walker, & McMahon, 1995; Walker, 1992), and it has recently experienced an unprecedented (since records began) drought with consistently low rainfall and flow from 2001 to 2009, including a 4-year period when no flow reached the sea (Dijk et al., 2013; Zampatti, Bice, & Jennings, 2010). The variable hydrology of the Murray River, and other dryland rivers, is often associated with biota that are flexible, opportunistic, and eurytopic (Kingsford, Lemly, & Thompson, 2006; Puckridge, Sheldon, Walker, & Boulton, 1998; Walker, 2006); including that they are adapted to drought (Lake, 2003; Lytle & Poff, 2004). Hydrological variability, in concert with documentary evidence of intermittent flow (e.g., photographs and written accounts), has fostered an ecohydrological paradigm for the Murray River that suggests that, under natural conditions (i.e., prior to regulation of flow by main-stem dams), the river: (a) would cease-to-flow and dry to a "series of pools" during drought, and (b) during low flows the low gradient lower reaches of the river were slow flowing, low energy environments, (Goode & Harvey, 2009; Jacobs, 1990). This model incorporates the notion that aquatic biota in the Murray River have evolved in these conditions and are adapted to them. Ultimately, this thinking underpins contemporary models of aquatic ecology which directly influence research, management, and rehabilitation (Murray–Darling Basin Commission, 2005; Young, Schiller, Harris, Roberts, & Hillman, 2001).

Our objective is to review the contemporary ecohydrological paradigm for the Murray River by examining historical streamflow and water velocity data, combined with recent hydrological and hydrodynamic models. We explore two propositions, that under natural conditions: (a) the Murray River did not stop flowing and that early irrigation, before main-stem upland dams and lowland weirs, at times diverted all flow; and (b) the lower reaches of the river were characterized by hydraulically complex, perennial lotic habitats, even in droughts, and there was a *regular seasonal pulse* of increased hydraulic complexity in spring associated with increased discharge and water velocity. We suggest that these predictable aspects of the Murray's unregulated flow regime are key features in the development and maintenance of a lotic ecosystem. We discuss the influence of present ecological models of drought on research and management and suggest that a revised view of past conditions would provide new opportunities to improve the ecological integrity of the Murray River. We also suggest that consideration of spatio-temporal ecohydraulics has significant global potential to improve rehabilitation of highly modified rivers and the strategic development of large tropical rivers.

2 | BACKGROUND

2.1 | Study area

Australia is the second driest continent (after Antarctica) and is characterized by highly variable rainfall and rivers with profound hydrological variability (Chiew, Piechota, Dracup, & McMahon, 1998; Puckridge et al., 1998; Verdon, Wyatt, Kiem, & Franks, 2004). The Murray–Darling river system is well-known for experiencing these extremes as it is the birthplace of irrigation in Australia, and now supports 40% of the nation's agricultural production (Crase, Pagan, & Dollery, 2004). The river system provides strong ongoing cultural links for Aboriginal people who have inhabited the region for at least 40,000 years (Bowler et al., 2003).

The Murray–Darling Basin (MDB) drains approximately one seventh of the Australian continent (1,073,000 km^2), and the combined length of the two major rivers, the Murray and the Darling, is ~5,500 km (Figure 1). The Murray River rises in the Great Dividing Range in eastern Australia at 2,228 m elevation but quickly falls over the first 300 km from its source to an elevation of 150 m at 2,225 rkm (river km from the sea), and then gradually decreases in gradient from 29 to 3 cm km^{-1} (Mackay & Eastburn, 1990). In the lower reaches, at 72 rkm, the Murray River passes into two large connected lakes, Alexandrina and Albert (750 km^2; McJannet, Webster, Stenson, & Sherman, 2008), which then contract to multiple paths between islands to the Coorong, an elongated coastal estuarine lagoon system, which discharges to the sea through a narrow mouth (Figure 1). Under natural conditions, the Murray River was hydrologically variable, but relatively seasonal with high winter/spring and low summer/autumn flows (Maheshwari et al., 1995).

Two large dams, Hume and Dartmouth, were built in headwaters of the Murray in 1936 and 1979 resulting in storages of 1,540 GL (3,038 GL following augmentation in 1961) and 4,000 GL, respectively. In addition, a series of 14 downstream weirs were built from 1922 to 1939, for navigation and to provide gravity diversion or pumping pools for irrigation and water supply. The lower 11 weirs form a series of contiguous weirpools for 700 km (Walker, 2006). The Lower Lakes of the Murray River are also used for irrigation, with tidal barrages preventing loss of freshwater and intrusion of seawater (Close, 1990).

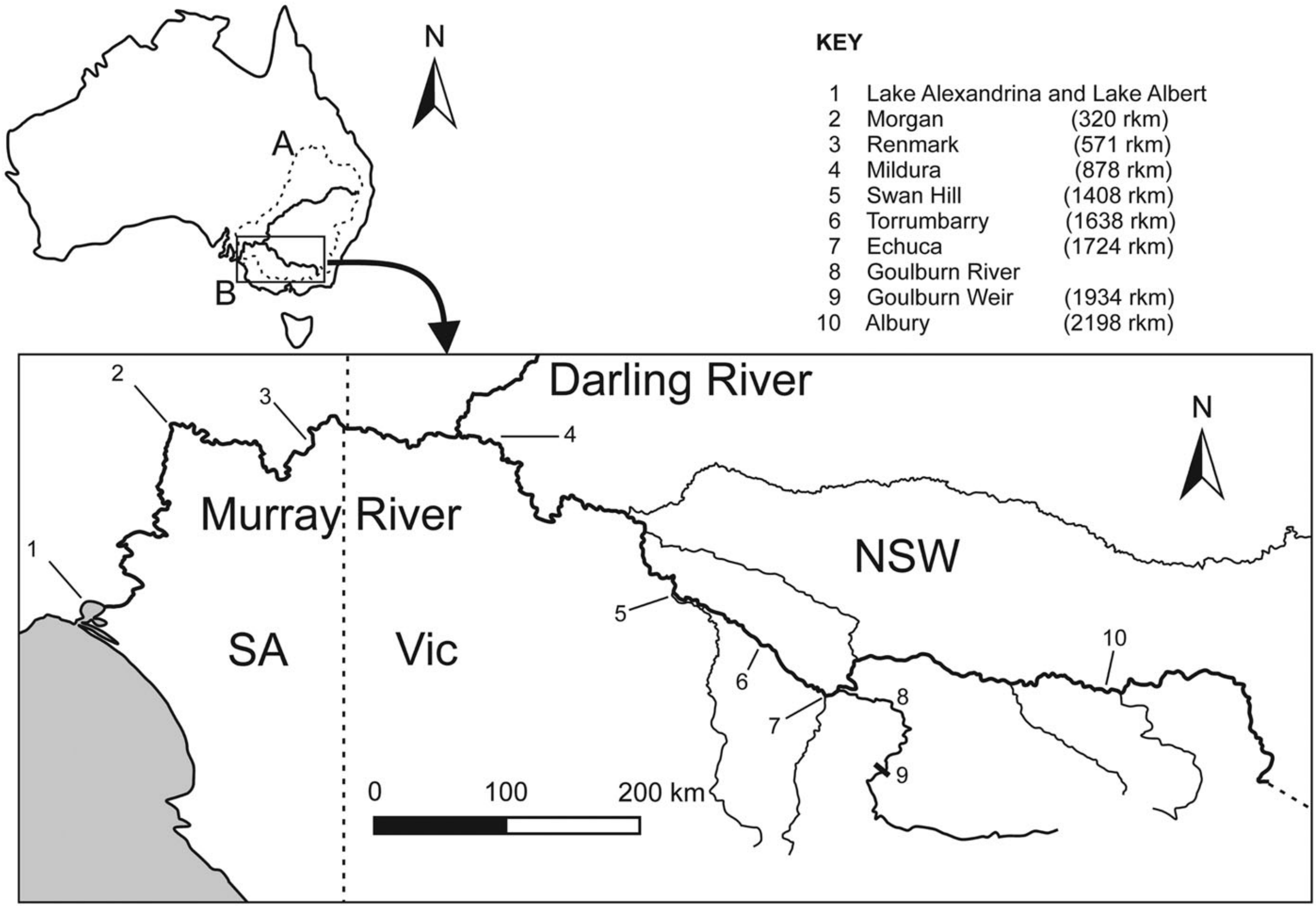

FIGURE 1 Map of the study area depicting: (a) the Murray-Darling Basin, and (b) the Murray River and sites mentioned in the text. The Murray River flows through three States: New South Wales, Victoria and South Australia

Diversion of flow has reduced mean annual discharge of the Murray River to the sea by 61% from 12,233 to 4,723 GL (CSIRO, 2008). The upland dams store winter/spring flows and release these for consumptive use which reverses the natural seasonality below the dams and suppresses the seasonality downstream of major irrigation offtakes (Jacobs, 1990; Maheshwari et al., 1995).

2.2 | Present perceptions of the unregulated Murray River at low flows

Droughts are a salient feature of Australia's climate and the universal description of the Murray River in extreme droughts, prior to the construction of dams and weirs, is that it stopped flowing and was reduced to “a series of pools.” This is part of Australian folklore; appearing in a range of sources from scientific (Chessman, 2011; Lake, 1967a; Lake, 2011) to popular literature (Bureau of Meteorology, 2013; Encyclopaedia Britannica, 1911; Wikipedia, 2013). Indeed, climate modellers have used it as a point for comparison to calibrate models, assuming it to be a natural occurrence (Draper & Mills, 2008). The impression that the Murray River naturally stopped flowing in droughts is reinforced by the description of the Murray River as semiarid or arid, and its grouping with dryland rivers that have extensive periods of low and intermittent flow (Gawne et al., 2007; Walker, 1992).

Commonly, there is no temporal or spatial context for the descriptions of cease-to-flow events in the Murray River. This leaves the perception that they extended for a substantial period of the droughts, which can be multiple years in the Murray River catchment (Verdon-Kidd & Kiem, 2009), and that they occurred over a major portion of the river length in unison with the spatial scale of prevailing terrestrial drought. The evidence for cease-to-flow events is compelling and irrefutable: there are dated photographs of the dry, or almost dry, bed of the Murray River (e.g., National Library of Australia[1]), historical gauge data recording zero flows (Bibra, 1964; Johnston, 1913), newspaper articles,[2] and parliamentary proceedings (Acting Commissioner of Water Conservation and Irrigation, 1915).

With intermittent flow comes the loss of lotic habitats and increased lentic habitats (Lake, 2003); both considered to be features of the Murray River channel, prior to main-stem dams. The low channel gradient (<5 cm km^{-1}) of the Murray River is often emphasized (Shiel, Walker, & Williams, 1982; Thoms, Rayburg, & Neave, 2008) and the unregulated Murray River is characterized as slow-flowing (Reid & Brooks, 2000).

River flow also directly influences the extent of the estuary and the intrusion of saltwater (Geddes, 1987). Perceptions of the Lower Lakes of the Murray River prior to regulation fall into two groups: (a)

[1]www.nla.gov.au

[2]The Advertiser (Adelaide, SA: 1889–1931), December 18, 1914, p. 8.The Sydney Morning Herald (Sydney, NSW: 1831–), December 7, 1914, p. 7.The Argus (Melbourne, Vic.: 1848–1957), December 9, 1914, p. 10.

the scientific literature (e.g., Close, 1990; Fluin, Gell, Haynes, Tibby, & Hancock, 2007) which describes a relatively freshwater system in the past 2,000 years that was occasionally brackish; and (b) published opinions on water management (Marohasy, 2012) which describe the Lower Lakes as estuarine.

It is consistently reported that the first significant diversions of water from the Murray River occurred after 1920, following the completion of major storages (Maheshwari et al., 1995), and that the primary impacts of river regulation on river ecology occurred after this time (Bren, 1988; Leslie, 2001; Walker & Thoms, 1993). Whilst it is well known that irrigation was active prior to the construction of main-stem dams and weirs (Eaton & River Murray Commission, 1945), we propose that a focus on the impacts of large-scale diversions has overlooked the impact of pumping and early tributary dams on low flows, and the ecological significance of these flows.

3 | METHODS

To support the proposition that the Murray River did not stop flowing under natural conditions, we use: (a) historical gauging records, and (b) modelled natural daily flows.

Gauging of streamflow commenced in 1865 with sites in the upper Murray River at Albury (2,198 rkm) from 1877 (McKay, 1903); the middle Murray at Echuca (1,724 rkm) from 1865 to 1905, Torrumbarry (1,638 rkm) from 1906, Swan Hill (1,415 rkm) from 1884, and Mildura (878 rkm) from 1865 (Bibra, 1964) which from 1891 were the sum of streamflow gauging and irrigation diversions immediately upstream of the gauge; and the lower Murray at Renmark (571 rkm) from July 1901, Overland Corner (425 rkm) from 1878 to 1886, and Morgan (320 rkm) from 1886 (Johnston, 1913; Stephens, 1974, unpublished data of South Australian Department of Environment, Water and Natural Resources) (Figure 1). Flow data for Renmark from December 1914 to June 1915 inclusive is recorded as “ambiguous” and only total monthly flow and mean monthly flow are provided, with no minima or maxima (Stephens, 1974). We evaluated records up to 1925 which is prior to main-stem dams and the majority of weirs.

Modelled natural daily flows were derived from the MSM–BIGMOD model that employs a water balance approach and integrates hydrological, climatic, and consumptive (e.g., irrigation diversions and losses) data, and storage and water-sharing operating rules (Close & Sharma, 2003). Modelled data were available from 1895 to 2009 from the Murray–Darling Basin Authority (MDBA, unpublished data), for five locations, at 320, 887, 1,415, 1,638, 2,198 rkm; corresponding to Morgan, Mildura, Swan Hill, Torrumbarry, and Albury.

We used the historical and modelled data to examine the following:

1. *Temporal and spatial scale of zero-flow events*, to clarify historical occurrence and demonstrate that these events were very rare and only occurred after irrigation commenced.
2. *Capacity and diversions of early irrigation*, to show that there was sufficient infrastructure to divert all of the low flows.
3. *Hydrology of zero-flow events*, to demonstrate that, rather than natural channel and evaporative losses, it was the longitudinal truncation of flow by key irrigation regions that was the likely cause of cease-to-flow events.
4. *Seasonality of hydrology in drought years*, to show that zero or low flows were highly seasonal and that an annual regime of high and low flows persisted in droughts.
5. *Lower river and estuary*, to show that the Lower Lakes were predominantly fresh and became brackish only in droughts and only in the summer-autumn period.

To support the proposition that the lower river was hydraulically complex, we analysed: (a) historical rating curves (velocity vs. river discharge) combined with gauged data for 1886–1913, and (b) contemporary hydrodynamic modelling of 135 km of the lower Murray River.

Historical rating curves, determined prior to river regulation, are available for the Murray River at Morgan (320 rkm; Johnston, 1913), Mildura (878 rkm; Murray, 1892), and near Euston (1,110 rkm; New South Wales Royal Commission Conservation of Water, 1886). We selected Morgan as it is in the lower river reaches (Figure 1) where the gradient is least (3.4 cm km^{-1}), so it could be expected to be the slowest-flowing region of the Murray River with the least hydrodynamic diversity. Monthly discharge data from 1886 to 1913 (Stephens, 1974) were used, a period that includes the Federation Drought and a cease-to-flow event. Discharge data were converted to mean channel velocity for each month using the rating curves.

The historical rating curves represent a single cross-section of the river with no weirs. To improve spatial resolution and understand the impact of weirs, we used hydrodynamic modelling (MIKE11 [DHI, Hørsholm, Denmark]) to develop two sets of rating curves, with and without weirs, of 119 cross-sections of the Murray River main channel from 562 to 697 rkm (Lock 5 to Lock 7). The rating curves used mean channel velocity at 10 flows from 1,000 to 80,000 ML d^{-1}. We applied this hydrodynamic model to three scenarios: (a) modelled natural flows (MDBA, unpublished data) with no weirs, (b) existing flows and weirs, and (c) existing flows with no weirs. We used flow data from 1995 to 2003, which includes 3 years of drought, and applied mean daily flow for each month, to be comparable with the historical data. Additional hydrodynamic data were obtained for 142 km of an adjoining anabranch channel system (Chowilla and associated creeks) using 595 cross-sections, under the same three scenarios.

4 | RESULTS

4.1 | Hydrology

4.1.1 | Temporal and spatial extent of zero-flow events

European settlement of the Murray River valley commenced in the 1830s. Prior to regulation of flow by main-stem dams, droughts were reported in 1851, 1881–1882, 1884–1886, 1895–1903 (Federation Drought), 1911–1915, 1923, and 1927–1929. There were three confirmed occurrences of zero flow, at Morgan in 1901, and at Swan Hill in 1914–1915 and in 1923, and one unconfirmed occurrence at Morgan in 1915. One of the confirmed events occurred for more than a month at Swan Hill in April 1915; all others were less than a month and mean daily flows in each month were 40 to 676 ML d^{-1}. The ambiguous data from Renmark in 1914–1915 has mean flows of 194 to 1,036 ML d^{-1} in the dry months of December 1914 to May 1915, and 3,333 ML d^{-1} in June 1915 (Stephens, 1974); these could include zero flows either at this site or downstream at Morgan, and are discussed below.

There were several parliamentary reports, commissions, and conferences on irrigation and navigation of the Murray River prior to these zero-flow events (e.g., New South Wales Royal Commission Conservation of Water, 1886; Select Committee on the Navigation of the Murray & c, 1858; South Australia Royal Commission, 1891). Most of these specifically examined flow data but none report periods of zero flow in any reach of the Murray River. Historical newspaper reports and photographs[3] of a dry river bed, where date and location is recorded, are all from the same times and locations as the cease-to-flow events outlined above, or downstream of these sites when the flow was less than 500 ML d^{-1}. The common feature of all these sites is that they were, and still are, downstream of major irrigations areas, which raises two questions: (a) did irrigation developments have the capacity to influence low flows in the river and (b) if so, were they diverting water in the peak of a drought?

4.1.2 | Flow diverted for irrigation

An indication of the extent of water diversions leading up to and including most of the Federation Drought (1895–1903) can be seen in Figure 2 (Davis, Murray, & Burchell, 1902). These data are approximate; they underestimate unauthorized diversions, but also do not include return flows from irrigation areas. Nevertheless, they demonstrate that irrigation diversions rapidly increased in 1893 and were sustained throughout the drought. The sudden increase was largely due to the construction of Goulburn Weir on the Goulburn River—the largest irrigation diversion weir in Australia at the time, on one of the largest contributing tributaries of the Murray River. In 1901, it was estimated that 598 GL was diverted for irrigation from the Murray River and tributaries; 95% of this was from the middle reaches of the Murray River and the Victorian tributaries. All diversions were upstream of Morgan (320 rkm), where one or potentially two zero-flow events occurred, and over 400 GL $year^{-1}$ was diverted upstream of Swan Hill where the other zero-flow events occurred (Davis et al., 1902).

Irrigation demand varied considerably between wet and dry years. The area of irrigated land in the Murray catchment in Victoria from 1907 (the earliest records of this type) to 1923 peaked in droughts (Figure 3; State Rivers and Water Supply Commission, 1908). Irrigation diversions were higher in years when natural streamflows were lower, and these high-demand periods also coincide with the zero flow events.

Using a conservative irrigation season of 9 months (Davis et al., 1902), the *per annum* figure converts to a daily mean diversion of over 2,000 ML d^{-1} in 1901, when the first zero-flow occurred (Figure 2). In the summers of droughts, there were also unrecorded diversions from small pumps; in the Federation Drought in 1903, there were reportedly 150 pumps in one river reach[4] (1,400 to 1,700 rkm), each with a capacity of 10 ML d^{-1} (Ferguson, 1988) potentially diverting 1,500 ML d^{-1}; all upstream of the sites with zero flow.

[3] www.trove.nla.gov.au

[4] The Advertiser (Adelaide, SA: 1889–1931), Tuesday, October 27, 1903, p. 7.

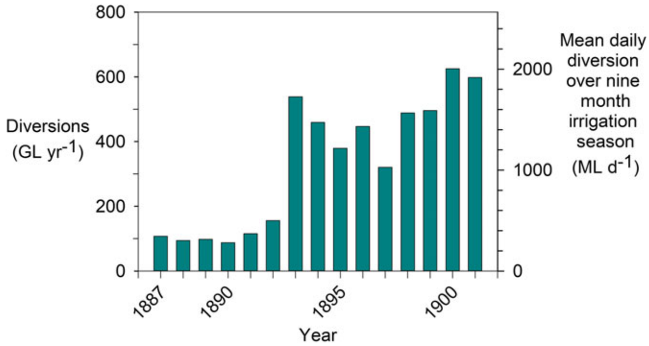

FIGURE 2 Growth of irrigation diversions in the Victorian reaches and tributaries of the Murray River from 1887 to 1901

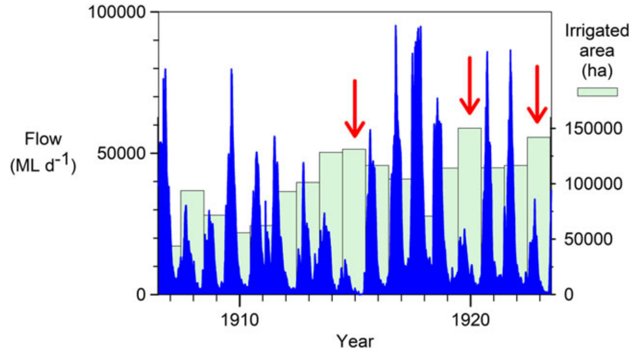

FIGURE 3 Annual irrigated area in Victoria in the catchment of the Murray River from 1907 to 1923 plotted with daily flow. NSW data not available. Arrows show peaks of irrigated area coinciding with low river flow in late summer

4.1.3 | Hydrology of zero-flow events

The first documented zero-flow event in the Murray River occurred in April 1901 at Morgan (320 rkm) while the minimum flow upstream at Mildura (880 rkm) was 1,199 ML d^{-1} (Figure 4). Losses can potentially be to groundwater, evaporation, or diversions. At low flows, however, river levels are lower than surrounding groundwater so there is net

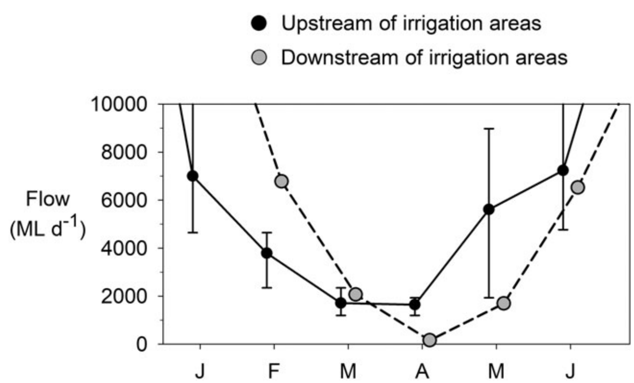

FIGURE 4 Mean daily flow for each month from January to June 1901, at Mildura gauge (878 rkm; solid symbols), upstream of irrigation areas at Mildura and Renmark; and Morgan gauge (320 rkm; grey symbols), downstream of irrigation areas. Maximum and minimum daily flow for Mildura shown and only mean available for Morgan

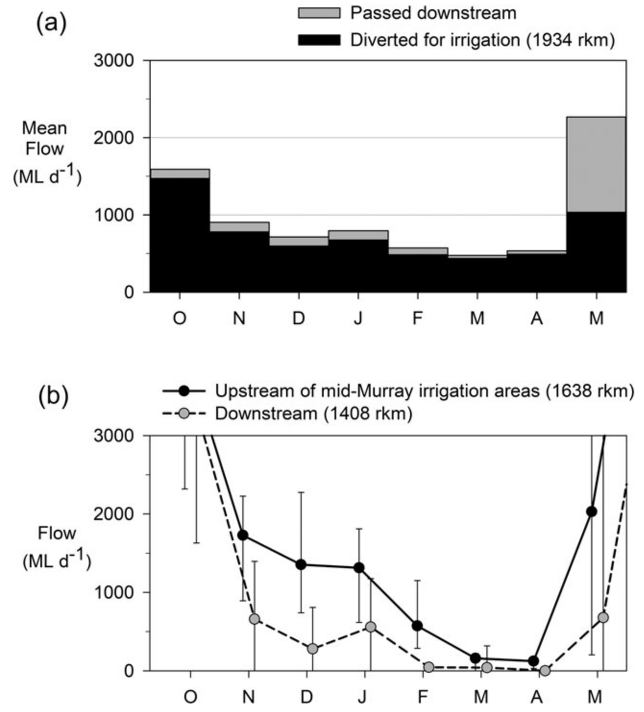

FIGURE 5 Flow in the 1914–1915 drought: (a) irrigation diversions from a major upstream tributary (Goulburn Weir, Goulburn River, 1,934 rkm; mean daily flow); (b) mean daily flow (including maximum and minimum) for each month from October 1914 to May 2015, upstream (Torrumbarry, 1,638 rkm, solid symbols) and downstream (Swan Hill, 1408 rkm, grey symbols) of mid-Murray irrigation areas

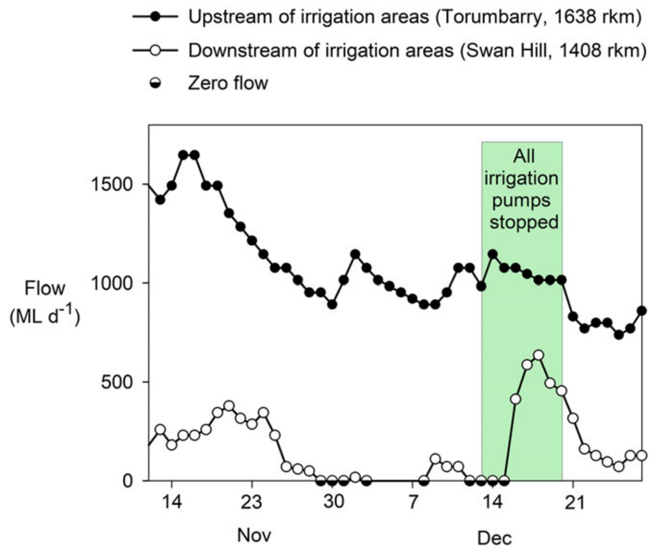

FIGURE 6 Hydrograph of the 1914–1915 drought showing daily flow upstream (Torrumbarry, 1,638 rkm, solid symbols) and downstream (Swan Hill, 1,408 rkm, open symbols and half-filled symbols for zero flow) of mid-Murray irrigation areas, with a shaded period when irrigation pumps on the Murray upstream of Swan Hill were stopped

gain from groundwater (Mackay & Eastburn, 1990). Evaporative losses can be as high as 434 ML d^{-1} (using Modern Class A pan evaporation rates with a conservative coefficient of 0.8) in this river reach, but this does not explain the total loss of flow. Diversions were made for stock and domestic purposes, up to 55 ML d^{-1}, between these two gauges, but the major users were the large irrigation areas at Mildura and Renmark. These had a combined pumping capacity in 1901 of 661 ML d^{-1} (Davis et al., 1902) and were actively pumping at the time.[5] Evaporation would have reduced the low flow, but the most likely explanation for the complete loss of flow downstream is that diversions, particularly for irrigation, used the remaining flow.

The second confirmed zero-flow event occurred at Swan Hill in the 1914–1915 drought. In the Goulburn River, 526 km upstream, up to 94% of flow was being diverted for irrigation over this period (Bibra, 1964; Figure 5). In the Murray River at Torrumbarry, 230 km upstream of Swan Hill, from November 1914 to February 1915, flow was 500–1,000 ML d^{-1} higher upstream of main-stem irrigation areas compared with downstream (Figure 5). In March and April 1915, both Torrumbarry and Swan Hill gauges recorded zero or close to zero flow while irrigation diversion in the Goulburn River continued upstream (Figure 5). Small irrigation pumps were also common at this time, indicated by the growth in annual permits in Victoria from 469 in 1909–1910, the year licensing of small pumps started, to 945 in 1914–1915 (State Rivers and Water Supply Commission, 1908).

A comparison of daily flow data between the Torrumbarry and Swan Hill gauges shows the direct impact of pumping on a finer temporal scale (Figure 6). The State governments of the day made the unprecedented agreement to cease all pumping for irrigation, but not domestic supplies, in this reach for short periods to allow flow to downstream settlements (Acting Commissioner of Water Conservation and Irrigation, 1915; State Rivers and Water Supply Commission, 1908). When pumping ceased, the river downstream increased in flow from zero to over 500 ML d^{-1}, providing comparative data of the same river reach with similar inflows and evaporation, with only the impact of irrigation pumps removed.

It is likely that zero flow also occurred in the lower river downstream of Renmark (571 rkm) in 1915. In this drought, 11 temporary sandbag dams were built on the main-stem of the Murray River between 1,638 rkm (Torrumbarry) and 320 rkm (Morgan) at all major irrigation settlements[6]; one at 878 rkm (Mildura) reportedly backing water up for 40 km and storing 2 weeks supply for irrigation.[7] All low flows were regulated between settlements and diverted for irrigation and town water (e.g., Acting Commissioner of Water Conservation and Irrigation, 1915) and pumping reportedly diverted all flow causing short-term, localized zero flow downstream of individual dams.[8]

The temporary dams are the likely source of the "ambiguous" data at Renmark (571 rkm) because (a) flows were fully regulated between dams and (b) the Renmark dam would have backed water up to the gauge (5.5 km upstream) rendering the rating curve inapplicable. The diversions in the lower river, from 571 to 384 rkm, all reported brackish water at these low flows, but still suitable for irrigation,[9] so

[5]The Mildura Cultivator (Victoria.: 1888–1920), April 20, 1901, p. 7.Renmark Pioneer (SA: 1892–1913), March 8, 1901, p. 3.

[6]Murray Pioneer and Australian River Record (Renmark, SA.: 1913–1942), January 21, 1915, p. 4

[7]Murray Pioneer and Australian River Record (Renmark, SA.: 1913–1942), December 3, 1914, p. 2

[8]Daily Herald (Adelaide, SA: 1910–1924) January 1, 1915, p. 2

[9]Kadina and Wallaroo Times (SA: 1888–1954) May 1, 1915, p. 4

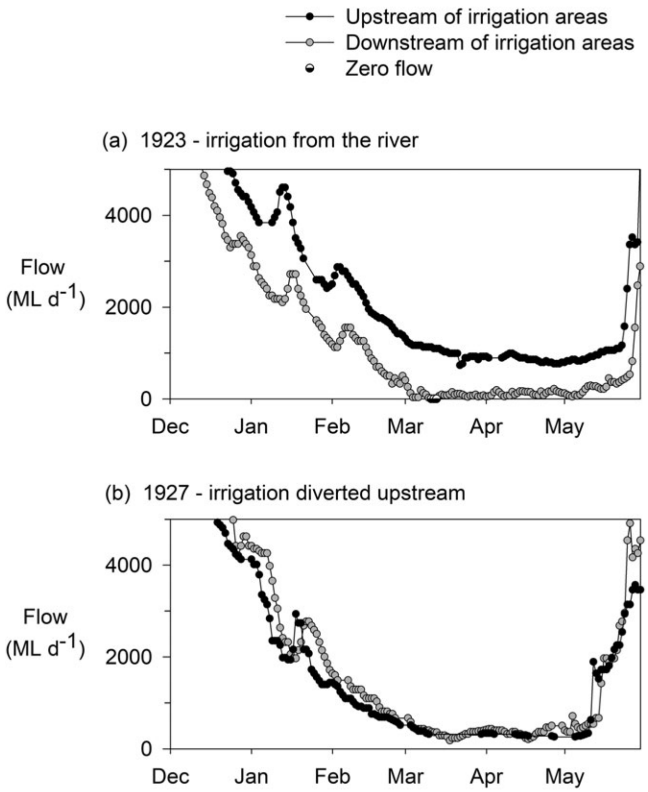

FIGURE 7 Discharge at Torrumbarry (1,638 rkm) and Swan Hill (1,408 rkm): (a) in 1923 when irrigation was by pumps from the river and (b) in 1927 when irrigation was by gravity diversion upstream of the Torrumbarry gauge

saline groundwater likely contributed to these flows (Mackay & Eastburn, 1990).

There was sufficient flow, using inflows and storage in the temporary dams, to complete the irrigation season in the lower river[9], but there are no specific flow data in the lower river for 1915 to compare with and without pumping or to quantitatively assess the cumulative effects of multiple diversions. Hence, it is unknown whether, under natural conditions, total inflows for the system would have exceeded evaporative losses along the entire river length and maintained flow. It appears likely, however, that groundwater would have at least provided a "trickle"—a common description of the lower river at that time[10]—and maintained some riffles.

The third confirmed zero-flow event was in 1923 at Swan Hill. When this event occurred, discharge 230 km upstream (Torrumbarry) was approximately 1,000 ML d^{-1} (Figure 7). Further upstream, in the Goulburn River, there were diversions with monthly averages in March and April 1923 over 900 ML d^{-1} (Water Conservation and Irrigation Commission, 1924). Channel losses may explain some of the discrepancy between the Torrumbarry and Swan Hill gauges. Nevertheless, by 1927, all diversion for irrigation between Torrumbarry and Swan Hill was by gravity from the new Torrumbarry Weir, and there would have been only a few irrigation pumps between these two gauges; in 1927, there were very low flows that remained similar at the two sites, confirming that channel losses at low flows in this reach were minimal. These data also suggest that in this era, return flows from irrigation during droughts was minimal.

[10]Murray Pioneer and Australian River Record (Renmark, SA.: 1913–1942), March 25, 1915, p. 4

4.1.4 | Modelled natural flows

Modelled natural daily flow from 1895 to 2009 show the river is perennial at upstream sites (1,415, 1,638, and 2,198 rkm), which includes Swan Hill, but not at the most downstream sites at 320 and 887 rkm (Morgan and Mildura); here, the model shows six events of zero flow over 114 years, with spells of 17 to 160 days, while being perennial for up to 53 and 88 years (Morgan and Mildura). The river is perennial throughout the historical droughts in 1902 and 1923 but has zero flow at 320 rkm in 1915 for 44 days, which overlaps with the "ambiguous" gauged data for the same period. Outside of the historical droughts, the predicted zero flows in modern droughts were prevented by regulated flow from upstream dams. The modelled data predict longer spell periods of zero flow for recent droughts than experienced historically, but generally align with the gauged data, providing further evidence that these events, if they occurred naturally, were rare, of short duration and over a small spatial scale.

Modelled natural flow data provide a salient contrast to the perception of the Murray River drying to a series of pools during drought. One of the most recognizable photos of the Murray River in drought is that of Commissioner Sir Ronald East (Victorian State Rivers and Water Supply Commission) standing astride a dwindling Murray River in 1923 (Figure 8). If, however, the lowest modelled natural flow in that year is considered, the water level would have been approaching the top of Sir Ronald's legs (Figure 8).

4.1.5 | Seasonality of hydrology in droughts

Stating that the Murray River "dried to a series of pools" in droughts infers that the temporal extent of drought on the land was reflected in the hydrology of the river, so that multi-year droughts resulted in multi-year suppression of flows and loss of seasonality. We compared gauged flows at Mildura (880 rkm) for 3 years preceding the peaks of the three major droughts discussed above, which were prior to the establishment of upland main-stem dams (Figure 9). Low flows did not extend more than late summer and autumn, whereas seasonality was retained with significant increases in flows over winter and spring, every year. Modelled data of natural flows (Close & Sharma, 2003) from 1895 to 2009 (MDBA, unpublished data) suggest that the lowest peak flow in spring (September–November) downstream of the Darling River junction (838 km rkm), was 8,553 ML d^{-1} and that 99% of the time, it was greater than 13,570 ML d^{-1}, even in extreme droughts.

4.1.6 | Lower river and estuary

We used two hydrological datasets to examine the impact of low flows on net flow to the sea: (a) historical gauging from Overland Corner (425 rkm) and Morgan (320 rkm) from 1876 to 1913, a 37-year period that is prior to upland main-stem dams and lowland weirs, and includes the Federation Drought (1895–1903); and (b) modelled natural flows (MDBA, unpublished data) to assess long term trends (1895–2009). These flows were incorporated in a water balance model using modern estimates of monthly evaporation from the lower

FIGURE 8 Photograph of the Murray River near Nyah, Victoria during the drought of 1923. The left photograph is zero flow and the right is shown with an extrapolated water level from the lowest modelled natural flow (without diversions) in 1923 (1,394 ML d^{-1}, MDBA unpublished data). The river is 70 m wide; if the flow was passing at 0.3 m s^{-1}, it would conservatively have been 0.7 m deep in the middle. Photograph reproduced with permission of Goulburn-Murray Water

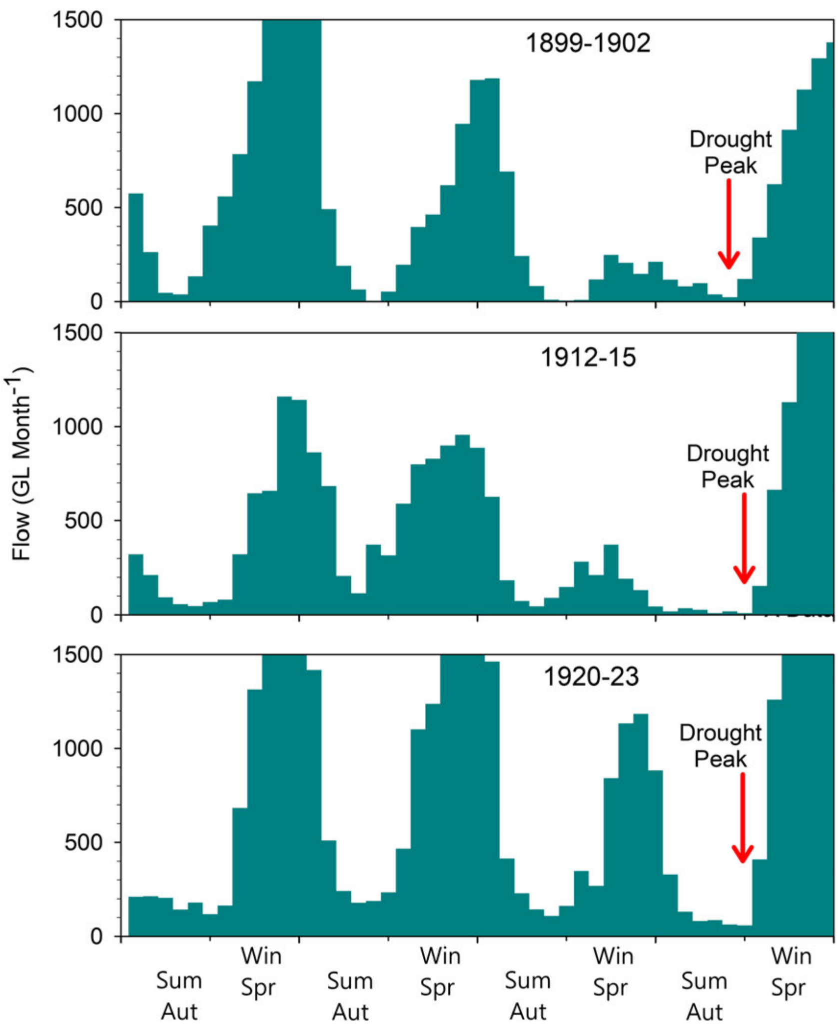

FIGURE 9 Monthly discharge (GL) at Mildura (878 rkm) for the 3 years preceding the peaks of the three major droughts prior to the construction of large upstream dams from the mid-1930s

lakes (McJannet et al., 2008) and river (Gippel, 2006). For the historical data, we also separately applied estimates of irrigation diversions to the model.

In the 37-year historical dataset, without diversion estimates, inflows exceeded evaporation for 94.6% of the time resulting in net freshwater flow through the Lower Lakes to the river mouth. For the remaining 5.4%, evaporation exceeded inflows, initially in the mid-1880s, prior to the expansion of irrigation, which happened twice for 2 months duration in autumn, and then in the Federation Drought for 2 to 5 months duration each year from 1900 to 1903 (Figure 10). These periods were always in late summer and autumn. Incorporating irrigation diversions (estimated from Figure 2) into the water balance model for this period reduces the total number of months in the Federation Drought where evaporation exceeds inflows from 13 to 5. Other notable periods of flow deficit occurred in 1915 and 1923, coinciding with low river flows and irrigation peaks (Figure 3).

Modelled natural flows produced very similar results: 96.5% of the time, there was a net flow to the sea. In droughts, evaporation exceeds inflows into the Lower Lakes for a maximum continuous period of 5 months, leading to saltwater intrusion and brackish salinities, but over the long-term the lakes could be fresh for up to 22 years continuously.

4.2 | Hydrodynamics

4.2.1 | Modelling of historical data

Seasonal hydrodynamics for Morgan (320 rkm) from 1886 to 1913 are shown in Figure 11. For comparison, lotic conditions are indicated with a mean channel velocity greater than 0.3 m s^{-1} and lentic conditions less than 0.15 m s^{-1} (from Vardakas et al., 2017). These data show a strong seasonal trend in mean channel water velocities with (a) higher velocities and predominantly lotic conditions in spring and (b) lower velocities and a mix of lotic and lentic conditions in late summer and autumn, directly reflecting reduced discharge

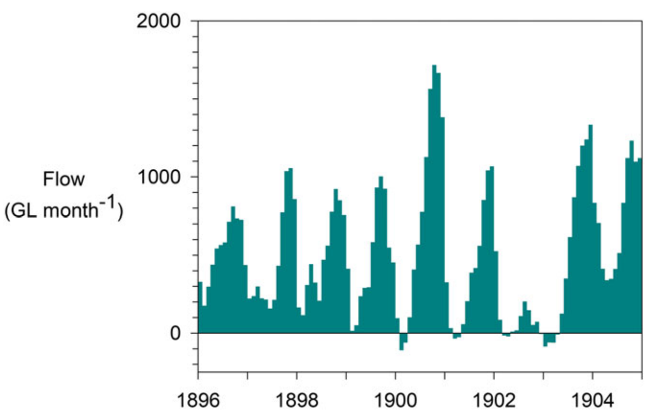

FIGURE 10 Net flow at the Murray mouth during the Federation drought from 1896 to 1903 using monthly gauged flow at Morgan (320 rkm) less evaporation from the river and Lower Lakes. Negative values indicate a net inflow of seawater into the Lower Lakes

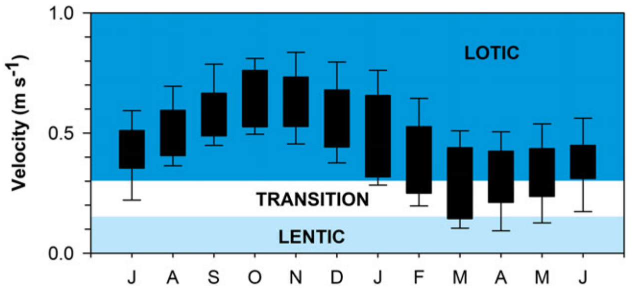

FIGURE 11 Box plot (5, 25, 75, 95 percentiles) of monthly channel velocity, using mean flow, of the Murray River at Morgan (320 rkm) from 1886 to 1913. For comparison, lotic and lentic are shaded dark blue and light blue, while transition between the two is unshaded

(Figure 11). Historical data from Mildura and Euston, upstream of Morgan, show similar results.

4.2.2 | Mike 11 modelling

Seasonal hydrodynamics for the main-stem of the Murray River (562 to 697 rkm) are shown in Figure 12 under three scenarios: (a) natural, (b) existing flows and weirs, and (c) existing flows with no weirs. The same lotic and lentic thresholds as above are used. The natural flows show the same pattern as the historical data from Morgan, Mildura, and Euston; strong seasonality with consistently high mean channel velocities every spring, as well as temporal and spatial continuity of lotic habitats throughout the year (Figure 12a). Modelling of the adjoining anabranch system shows lotic habitats in large creeks all year in wet periods, which become seasonally disconnected in the summer–autumn of dry years (Murray River discharge <5,000 ML d^{-1}). Small anabranch creeks were disconnected every summer—forming a series of in-channel pools—and reconnected only in the winter/spring of wet years when flows were high (>40,000 ML d^{-1}). A few low-lying wetlands were reconnected every year (>15,000 ML d^{-1}).

In the model with existing weirs and flows (Figure 12b), spatial and temporal integrity of lotic habitats has been lost—that is, they are fragmented and reduced by lentic weirpools with less flow; and are largely absent from mid-summer to autumn every year. These modelled data are reinforced by contemporary data collected in three sequential weirpools (1, 2, and 3) in the lower Murray which demonstrate that median water velocities in the lower Murray River at flows of 3,000–6,000 ML d^{-1} are ≤0.1 m s^{-1} (Bice, Zampatti, & James, 2016). With the weirs in the model, the major and minor creeks of the adjacent anabranch system become permanently lotic due to elevated backwater from the weirs providing inflow at the inlets, while connected wetlands have stable depth.

Removing the weirs in the model (Figure 12c), while keeping gauged flows, increases water velocities and substantially improves the temporal and spatial integrity of lotic habitats. These habitats become present throughout the year, and in spring and summer most sites are lotic, although mean channel velocities are lower than the model of natural flows. There are, however, less lentic or transition sites in summer compared with natural because flows are higher due to regulation. With no weirs, but less total flow, the anabranch system

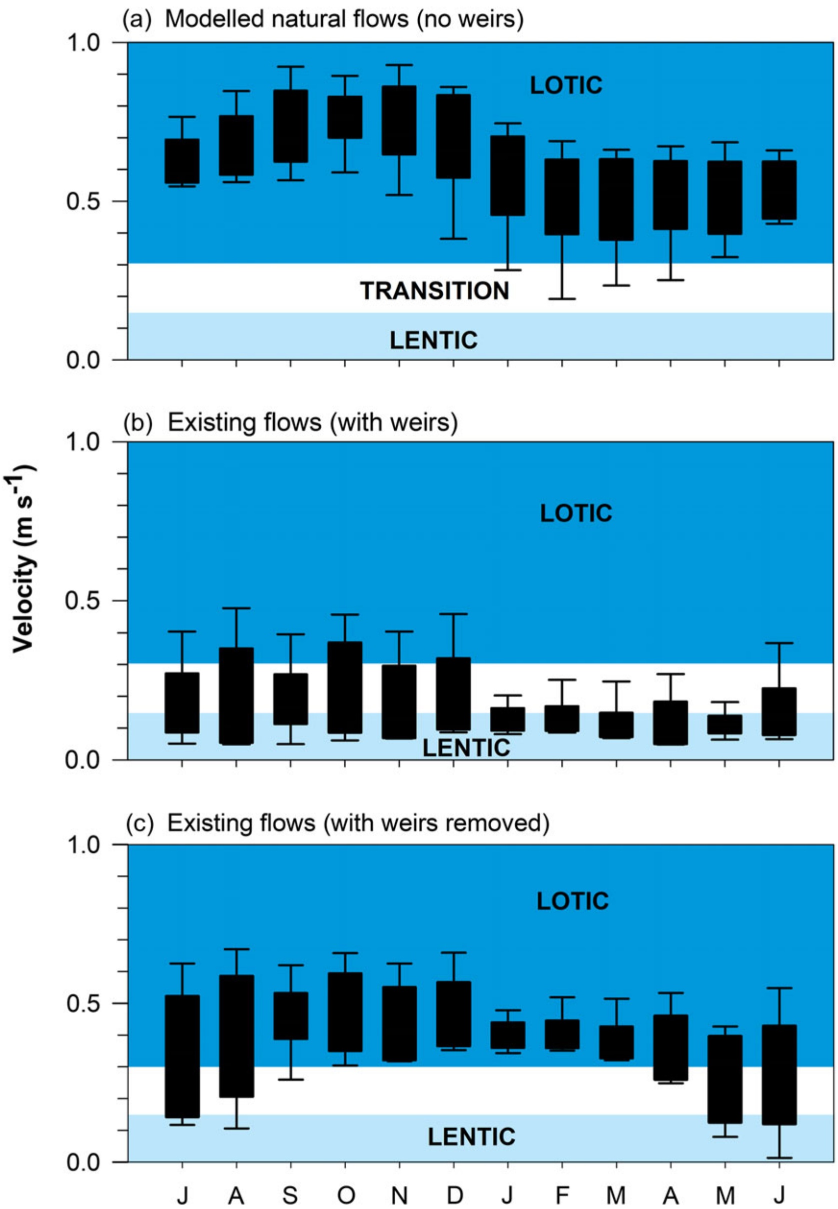

FIGURE 12 Box plot (5, 25, 75, 95 percentiles) of monthly channel velocity using a mean of 119 cross-sections of the Murray River from 562 to 697 rkm and mean monthly flow, from 1995 to 2003: (a) modelled natural flows with no weirs, (b) existing flows and weirs, and (c) existing flows with weirs removed. For comparison, lotic and lentic are shaded dark blue and light blue, while transition between the two is unshaded

becomes more intermittent with longer disconnection of minor creeks, compared with modelled natural.

In this analysis, we are using mean cross-sectional channel velocity to infer hydrodynamic diversity. In low gradient rivers, a low mean cross-sectional velocity has less variation in velocity and will inherently have less turbulence and complexity, whilst a high mean velocity will have increased complexity and turbulence (Bice et al., 2016; Tiffan, Kock, Haskell, Connor, & Steinhorst, 2009). The modelling results are consistently supported by early descriptions of the Murray River, reporting hydraulic complexity caused by rocky bars and extensive timber in the river, with velocities between 0.6 and 1.3 m s^{-1} at higher flows (Coyle, 1889; Hays, 1956; Johnston, 1913; Select Committee on the Navigation of the Murray & c, 1858; Sturt, 1833).

5 | DISCUSSION

In rivers with long histories of regulation, perceptions of natural preregulation hydrology frame contemporary views of aquatic ecology (Ward et al., 2001). A primary tenet is that biota that have evolved under natural conditions remain adapted to them (Poff et al., 1997). Hence, understanding historical conditions provides a foundation for ecological models that inform present-day management (Galat & Lipkin, 2000; Swetnam et al., 1999). The Murray River and perceptions of its preregulation hydrology not only provide an excellent example of this, but also the risks of "shifting baseline syndrome" where recent history dilutes perceptions of the past (Pauly, 1995).

The context of the cease-to-flow events in the Murray River over 100 years ago was undisputed at the time, but lost in a generation. The impacts of irrigation diversions on low flows were well acknowledged by the governments and water authorities of the day, and all publications and newspaper reports at the time attributed these conditions to irrigation.

The present study reveals that, contrary to the widely held belief, it is extremely unlikely that the Murray River naturally ceased to flow in historical droughts and if it did, it would have been only for days, not months–years. This supports the findings of early hydrological modelling which demonstrates a perennial river (Close, 1990). There are no reports of the Murray River ceasing to flow until irrigation capacity had reached 500 GL year^{-1} by the late 19th century and during every recorded zero-flow event after this time, water was actively diverted for irrigation. Land clearing at the time may have impacted runoff, but it would more likely have increased flow and reduced zero flow periods (Silberstein, Best, Hickel, Gargett, & Adhitya, 2004; Siriwardena, Finlayson, & McMahon, 2006). Conservative estimates of channel losses do not account for complete loss of flow, and we conclude that irrigation diversions tipped the water balance at low flows, diverting the remaining flow. Despite the severity of historical climatic droughts, flow in the Murray River was perennial and seasonality of flows was retained every year, with significantly higher winter/spring flows. Modern hydrological modelling suggests a similar picture, with the addition of seasonal periods of zero flow in the lower reaches in extreme droughts (e.g., Millenium Drought).

Here, we present the case that a perennial, seasonal hydrology, with permanent lotic habitats, was the dominant force that structured aquatic ecosystems in the Murray River, rather than intermittent and variable hydrology. We first establish key differences in the hydrology of the Murray River compared with other dryland rivers, then describe the significance of hydrodynamics in a regulated river, before discussing the implications of the present study on riverine ecology. We use this to develop an ecohydraulic conceptual model of the river and demonstrate how this knowledge can contribute to new and practical directions for river restoration. We then discuss at a global scale the urgent need to consider spatio-temporal ecohydraulics in large rivers.

5.1 | Hydrology of dryland rivers

The rivers of the MDB, including the Murray River, are commonly categorized as *dryland* rivers; a grouping that includes intermittently flowing rivers without dominant, regular, annual, or seasonal cycles (Davies, Thoms, Walker, O'Keeffe, & Gore, 2009; Walker, Sheldon, & Puckridge, 1995). Two key characteristics, however, differentiate the Murray from other dryland rivers of the MDB and many others worldwide: perenniality and seasonality.

Poff and Ward (1989) used "the degree of intermittency" as a primary dichotomy in classifying rivers, which would be directly applicable to dryland rivers. Rivers in the Murray–Darling system can have intermittent flow along their entire length (McKay, 1903). Nevertheless, perennial flow sets the Murray apart from other dryland rivers, providing the potential for a lotic ecology to develop.

Seasonality is a key ecological driver. Although the natural and altered seasonality of the Murray River is well known (Close, 1990; Maheshwari et al., 1995), comparative analyses of the hydrology of dryland rivers only rarely assess seasonality (see Sheldon & Thoms, 2006; Webb, Thoms, & Reid, 2012) although it is used for MDB rivers (Davies, Harris, Hillman, & Walker, 2010). Measures of seasonality, such as Colwells Index (e.g., Webb et al., 2012) or other metrics (Davies et al., 2010), often equally weight all months. In the Murray River, where many species of fish spawn in spring and early summer (Lintermans, 2007), it is the strength and predictability of these specific seasonal flows that are the most ecologically relevant. Hydrological variability is often emphasized in ecological studies of the Murray River (e.g., Gawne et al., 2007; Humphries, King, & Koehn, 1999) which in turn emphasizes the flexibility of the biota. Seasonally predictable flows in the Murray, however, have an inherent stability—they form the heartbeat of the river—a reliable pulse that occurs every spring.

In the unregulated Murray River, perennial and seasonal flow was available to enable the development of an ecosystem that could utilize: (a) permanent lotic habitats, (b) a predictable in-channel increase in hydrodynamic complexity each spring, and (c) a range of permanent off-channel habitats (e.g., low-lying wetlands and disconnected anabranches) maintained by spring flows. The hydrological impact on spring flows in the Murray River by flow regulation has been severe. For example, despite the severity of the Millenium Drought (2001–2009)—possibly a 1:1,500 year event (Dijk et al., 2013)—modelled natural flows (MDBA, unpublished) shows that spring flows over 20,000 ML d^{-1} would have occurred every year except one, if there was no storage and diversions (Figure 13). Climatic drought in the MDB is a natural phenomenon, but multi-year suppression of spring flows in the Murray River is not.

5.2 | Hydrodynamics

The term *flow* in river ecology has a broad context, which at a high level incorporates volume and timing (hydrology) and the physical characteristics of flowing water (hydraulics). In the context of river regulation and restoration, analysis of hydrological deviation is commonplace (e.g., Richter, Baumgartner, Powell, & Braun, 1996), yet the impact of river regulation on hydraulics and the physical interaction between flowing water and organisms/physico-chemical processes is less well considered (Bockelmann, Fenrich, Lin, & Falconer, 2004; Clarke, Bruce-Burgess, & Wharton, 2003). Hydrological analysis is a powerful tool in ecology, but it is the hydraulic characteristics of flow (velocity, depth, and turbulence) that determine habitats and it is hydrodynamics—the change in hydraulics over space and time—that determines ecological processes.

The key feature that governs fluvial hydrodynamics is the physical habitat template of the river (Poff & Ward, 1990; Southwood, 1977), including channel gradient, cross-section, sinuosity, roughness (e.g., woody debris, rocks, and aquatic plants), and floodplain connections.

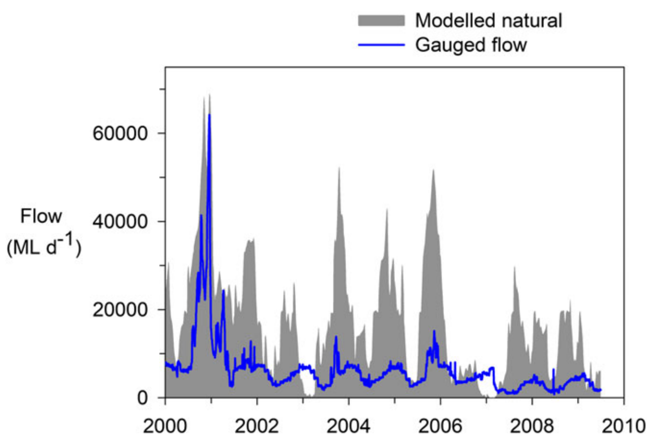

FIGURE 13 Comparison of gauged and natural daily flow (ML d^{-1}) in the lower Murray River (South Australia border) in the recent Millenium Drought (Zampatti & Leigh, 2013)

Modification of the physical template interrupts fluvial processes and streamflow dynamics, negatively impacting biodiversity (Poff, Olden, Merritt, & Pepin, 2007).

In the Murray River, the physical template has been affected by removal of large woody debris—initially to mitigate navigation hazards (South Australia Royal Commission, 1891) and subsequently to increase channel conveyance (Ladson & Chong, 2005)—and the construction of dams and weirs. Despite the impact of removing large woody debris on habitat and hydrodynamics, and the notable impacts of flow regulation, it is dams and weirs that have, by far, had the greatest impact on river channel hydrodynamics. The low gradient of the river in the lower reaches ensures the hydraulic impact of backwater from low-level weirs is extensive; creating contiguous lentic habitats for 700 km at low flows (Walker, 2006). Any variation in the natural physical template, including rock bars present in early descriptions of the Murray (Sturt, 1833), is drowned out, further simplifying hydrodynamics. The creation of weirpools has also simplified the channel cross-section, resulting in greatly reduced benches (Thoms & Walker, 1993). In dryland rivers without weirs, these benches are exposed at low flows and become important stores of terrestrial carbon (leaf litter) that may ultimately fuel productivity during higher flows (Francis & Sheldon, 2002).

The lower Murray River now only regains its original lotic character when the weirs are removed at high flows of 40–60,000 ML d^{-1} (exceeded 11% and 6% of the time; 1980–2011 [post-Dartmouth Dam] gauged flow at SA border, 650 rkm) although some lotic habitats are restored at intermediate flows (15,000–40,000 ML d^{-1}; Bice, Gibbs, Kilsby, Mallen-Cooper, & Zampatti, 2017). The middle reaches of the Murray River are substantially less affected by weirpools and generally retain much of their lotic character (Figure 14). The substantial hydrodynamic alteration and resultant habitat homogenization in the lower river has had a profound effect on ecosystem function and form.

5.3 | Ecology

Assuming that the Murray River ceased to flow naturally in droughts greatly influences the ecological view of the significance of hydrodynamic diversity and habitat heterogeneity. Primarily it supports the impression that lentic habitats were a natural feature of the system

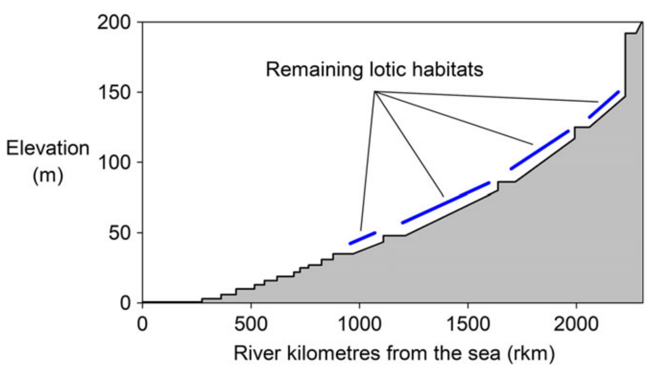

FIGURE 14 Profile of the Murray River showing weirpools and remaining lotic habitats in the main channel at low and regulated flows (<10,000 ML d^{-1}). At high flows (>50,000 ML d^{-1}) the lower weirs are removed and the channel becomes entirely lotic for the lower 1,992 km

and that permanent lotic habitats, with associated hydrodynamic diversity, are not critical for native aquatic biota and cannot be relied upon seasonally for critical stages of the life cycle. The present study provides the opportunity to reconsider the ecology of droughts in this dryland river and to evaluate the ecohydraulics of the three broad components of the ecosystem: river channel, floodplain (including wetlands), and the Lower Lakes and estuary.

5.4 | Droughts

Riverine drought can be defined as "extremely low levels [of discharge] for an extended period of time … [where] hydrological connectivity is disrupted" (Lake, 2003). Discussions of riverine drought frequently include cessation of flow as a criterion or descriptor (Lake, 2007; Magoulick & Kobza, 2003), and they often describe a concurrent loss of lotic habitats (Lake, 2003). In Australian rivers, multi-year periods of low flows are not unusual, often occurring with decadal cycles (McMahon & Finlayson, 2003).

A common theme in the discussion of riverine drought, both in Australia and internationally, is that these events are natural and the biota are adapted to them (Lake, 2003; McMahon & Finlayson, 2003). In the Murray–Darling river system, research related to drought and aquatic biota has focused on invertebrates in intermittently flowing streams (Boulton, 2003; Boulton & Lake, 1992; Closs & Lake, 1996; Dexter, Bond, Hale, & Reich, 2014; Reich, McMaster, Bond, Metzeling, & Lake, 2010), the plankton seedbank of dry wetlands (Brock, Nielsen, Shiel, Green, & Langley, 2003; Nielsen, Smith, Hillman, & Shiel, 2000) and floodplains (Boulton & Lloyd, 1992; Jenkins & Boulton, 2003), physiological tolerances of small-bodied adult fish (McMaster & Bond, 2008; McNeil & Closs, 2007) and lentic refugia for fish and invertebrates either instream in waterholes (Balcombe et al., 2006; Bond & Lake, 2005; Sheldon et al., 2010; Webb et al., 2012), or in off-channel habitats such as billabongs (ox-bow lakes; McNeil, 2004).

Despite the recent decade-long drought (Dijk et al., 2013) and the literature on biotic responses to riverine drought (Humphries & Baldwin, 2003), the ecological relevance of permanent lotic habitats (lotic refugia) and a predictable spring pulse during drought in perennial rivers remains unexplored, leaving an impression that these are not key aspects of the ecology of perennial Australian dryland rivers in droughts. The historical perspective of the Murray River receding to a series of pools in severe droughts further supports this view. Given that lentic and lotic are fundamental divisions in aquatic ecology, the division between permanent and intermittently-flowing dryland rivers is equally important. If the Murray River is perennial, as we suggest, then lotic habitats were available to exploit as a niche and would have persisted as low-flow refugia.

5.5 | River channels and lotic ecology

In lotic ecosystems, specific biota are well recognized, including biofilms (Lear, Anderson, Smith, Boxen, & Lewis, 2008), diatoms (Passy, 2001), plankton, meiofauna (Dole-Olivier, Galassi, Marmonier, & Creuzé des Châtelliers, 2000), worms (Traunspurger, 2000), aquatic insects (Gratton & Zanden, 2009), snails (Cross & Benke, 2002), bivalves (Sheldon & Walker, 1989), crustacea (Girard et al., 2014), and fish (Schlosser & Angermeier, 1995). In dryland rivers, lotic biota and ecology are less well acknowledged. Lotic bivalves and macroinvertebrates are recognized in the Murray River (Richardson & Cook, 2006; Sheldon & Walker, 1989; Sheldon & Walker, 1998), but it is the loss of a suite of species that reveals the greatest dependency on lotic habitats. Murray crayfish (*Euastacus armatus*), trout cod (*Maccullochella macquariensis*), river blackfish (*Gadopsis marmoratus*), Macquarie perch (*Macquaria australasica*), and river snail (*Notopala sublineata*) are now extinct from the lower river where 700 km of contiguous weirpools occur (Mallen-Cooper & Brand, 2007; Sheldon & Walker, 1997; Walker, 1985). The first four species have contracted to lotic environments elsewhere in the river system (Lintermans, 2007). The loss of river snail and decline of other snails is attributed to a change of biofilms from predominantly bacterial to algal in the hydraulically homogenized weirpools (Sheldon & Walker, 1997). Other species such as Murray cod (*Maccullochella peelii peelii*) and silver perch (*Bidyanus bidyanus*) have also declined in the weirpools and are more abundant in lotic habitats (Mallen-Cooper, 1999; Walker, 2006).

The importance of lotic habitats, in particular water velocity, is specifically recognized for some fish species in the Murray River (Jones & Stuart, 2007; Koehn, 2009; Koehn et al., 2008). Nevertheless, against the historical background of the river in drought, and the fact that most adult fish can, at some time, be collected in lentic habitats, the importance of lotic habitats in the life cycle is less recognized. Spawning and recruitment patterns, however, reveal where fish have flexible or specific hydrodynamic requirements.

Three broad models of recruitment presently apply to wholly freshwater fish in the Murray River, which are related to low flows (Humphries et al., 1999), in-channel flows (Mallen-Cooper & Stuart, 2003), and floods (Lake, 1967b). The generalization of the Murray River and its lowland tributaries as slow-flowing has, in part, led to the *low flow recruitment model* which proposes that recruitment of some native species is likely to occur in the warmer months that correspond with slow-flowing, low flows (Humphries et al., 1999). The model appears to work well for the generalist species that have protracted spawning periods, that can overlap with both high and low flows, and spawn in both lotic riverine and lentic off-channel habitats (Humphries, Serafini, & King, 2002; Koehn & Harrington, 2005; Vilizzi, 2012). This flexibility has, arguably, maintained high abundances of these species in this regulated river system, including the weirpools in the lower Murray River (Bice et al., 2013; Cheshire, Ye, Gillanders, & King, 2016).

In contrast, riverine specialist species (Murray cod, trout cod, golden perch *Macquaria ambigua*, silver perch, Macquarie perch, and river blackfish) have all declined in range and abundance, and a more complex pattern of recruitment and habitat use is emerging, which incorporates flow, hydrodynamics, and spatial scale. The riverine species mostly spawn from spring to early summer (September–December; Humphries, 2005; King, Tonkin, & Mahoney, 2009; Puckridge & Walker, 1990; Rowland, 1998; Zampatti & Leigh, 2013) which, under natural conditions in the Murray River, overlaps with the period of greatest discharge and hydrodynamic diversity (Figure 11). Larval drift is a key life history process for these species, with the exception of river blackfish, and recruitment has been associated with flows that are contained within the river channel (*in-channel recruitment* model, where a pulse of flow inundates benches and increases in-channel carbon and aquatic productivity; leading to greater larval survival) and, for most species, overbank floods (*flood recruitment* model, where floodplain carbon increases productivity). In both cases, lotic habitats and hydrodynamic diversity are key characteristics of channel and floodplain habitats.

For these species, the use of lotic habitats for recruitment does not reflect flexibility in a river with highly variable flow, but specialist strategies that exploit a permanent or seasonal hydrodynamic feature of a lotic ecosystem. Elsewhere in regions with Mediterranean climates, spatio-temporal maintenance of lotic habitats has been associated with the restoration of native fish populations in regulated streams (Kiernan, Moyle, & Crain, 2012).

5.6 | Wetlands

Perspectives of wetland ecology in the Murray River are greatly influenced by an emphasis on the variability of the unregulated flow regime and the two major impacts of regulation: (a) permanent inundation of low-lying wetlands caused by weirpools (Walker et al., 1995) and (b) reduced inundation frequency of higher level floodplains, caused by water diversions and storage upstream (Maheshwari et al., 1995; Walker, 2006). Under natural conditions, it is perceived that there was widespread desiccation of floodplains and wetlands under low flows; hence, reinstating a wetting and drying cycle has become the dominant theme in wetland management (Jensen, 2002; Pressey, 1986; Thomson, 1986). Nevertheless, historical diatom assemblages in wetland sediments indicate a range of hydrological regimes (Gell & Reid, 2014). Modelled natural flow data and river geomorphology also suggest a range of wetland inundation, including low-lying wetlands that were connected to the river each year (Robinson et al., 2015), indicating permanency if evaporation did not exceed wetland volume. At low flows, anabranches could also disconnect from the main channel, transitioning from a lotic channel to a series of disconnected pools at a lower elevation than surrounding wetlands, thus providing additional off-channel lentic habitats.

These off-channel habitats that persisted during low river flows historically supported three wetland specialist fish species—flat-headed galaxias (*Galaxias rostratus*), southern purple spotted gudgeon (*Mogurnda adspersa*), and southern pygmy perch (*Nannoperca australis*; Hammer & Walker, 2004; Lloyd & Walker, 1986). All three are now extinct from these highly altered habitats in the lower Murray and threatened elsewhere along the river (Hammer & Walker, 2004; Lloyd & Walker, 1986). Small perennial wetlands, with variable water levels, were likely heavily vegetated with submerged macrophytes (Kattel et al., 2015; Reid, Sayer, Kershaw, & Heijnis, 2007) and harboured low abundances of large piscivorous fish, thus providing a unique refuge for small-bodied fish away from the main river channel. Consequently, small-bodied wetland specialist fishes, like the channel specialists, employed a specific strategy adapted to a river with predictable seasonal flow; in this case exploiting a habitat niche of wetland refugia.

5.7 | Estuary and Lower Lakes

The view that the Murray River "naturally dried to a series of pools" has also diminished the importance of freshwater flow to maintain the estuarine ecosystem and provide connectivity with the sea. Reduced flow has seen the brackish-estuarine interface compress to an extent that the tidal barrages sometimes separate completely marine and completely freshwater environments leaving an estuarine ecosystem in peril (Kingsford et al., 2011; Zampatti et al., 2010). Fragmentation and a diminished estuary are particularly reflected in the diadromous and estuarine fish fauna of the system. The six diadromous fish in the region—pouched lamprey *Geotria australis*, short-headed lamprey *Mordacia mordax*, common galaxias *Galaxias maculatus*, short-finned eel *Anguilla australis*, estuary perch *Macquaria colonorum*, and congolli *Pseudaphritis urvilii*—have all declined and three are endangered in the Murray River (Bice, Hammer, Wedderburn, Ye, & Zampatti, in press). The estuarine specialist, estuary perch, has declined substantially since barrage construction and has been rarely recorded in the past two decades; similarly, commercial catches of marine species that use the remnant estuary, such as Mulloway *Argyrosomus japonicus*, have reduced dramatically (Ferguson, Ward, & Geddes, 2008).

The present study shows that prior to river regulation, the lakes were predominantly freshwater, with net flow to the sea for more than 95% of the time. During these times an estuarine ecosystem, characterized by variable salinities, would have existed in the coastal lagoons and channels between the lakes and the sea (Fluin et al., 2007; Reeves, Haynes, García, & Gell, 2015). For the remaining 5% of the time, without net flow to the sea, the estuarine interface would have moved into the lakes. These periods would have been characterized by brackish salinities in the lakes, and occurred during very low flows in summer/autumn. Hence, the estuarine interface was dynamic and flow dependent.

Paleolimnological and documentary evidence support this conclusion. Studies of diatoms in sediments show that prior to river regulation, Lake Alexandrina was characterized by "relatively freshwater conditions with longstanding and major inputs from the River Murray, particularly after ca. 2,000 years b.p." (Fluin et al., 2007); the northern regions of the lake, near the river, are dominated by freshwater and oligosaline diatoms; whereas the southern, seaward, regions of the lake have freshwater and some marine/brackish diatoms indicating intrusion of an active estuarine interface. In contrast, the northern coastal lagoon of the Coorong has more persistent estuarine conditions, characterized by marine–estuarine diatoms, indicative of salinities typically below seawater (Fluin et al., 2007).

Historical reports also describe the northern regions of the lake as fresh all year for 40 years prior to the expansion of irrigation in the late 1890s and the Federation Drought (Davis et al., 1902), whereas the southern regions of the lake were described as a fluctuating estuary during low flows. Brackish periods in the lake were only reported as occurring during low flows in late summer and autumn, whereas prior to significant diversions upstream, Lake Alexandrina remained suitable for stock and agriculture, even in droughts (Davis et al., 1902). Charles Sturt, the first European explorer to navigate down the Murray River (Sturt, 1833), reached Lake Alexandrina during a drought in late summer (February) of 1830 and found the body of the lake brackish but drinkable, while the southern channel leading to the sea was tidal.

The three lines of evidence (hydrological, palaeoecological, and anecdotal) present a consistent ecohydrological model for the Lower Lakes. Prior to irrigation, the estuary was coastal, whereas the lakes were fresh with occasional incursions of the estuary in the southern, seaward regions during droughts and low flows. Like the hydrology of the river, the hydrology of the Lower Lakes is sensitive to small changes in discharge at low flows; hence, following irrigation development, diversions upstream tipped the evaporation/outflow balance and created longer periods of higher salinity in the lakes in droughts. This cause of increasing lake salinities was first suggested in 1902 (Davis et al., 1902), and the trend continued with increasing upstream diversions up to 1940, when the tidal barrages were completed to address the issue (Jacobs, 1990).

Recent developments aim to address two key impacts of diminished freshwater flow and connectivity in the present-day estuary of the Murray River, downstream of the barrages, and the Lower Lakes. Fish passage is being reinstated to link estuarine and freshwater habitats (Barrett & Mallen-Cooper, 2006; Bice, Zampatti, & Mallen-Cooper, 2017), and greater volumes of freshwater are proposed for the Lower Lakes and Coorong estuary as part of a broader flow management plan for the MDB (Murray–Darling Basin Commission, 2012). Rehabilitation of the estuarine ecosystem will depend on sustaining a permanent, if spatially reduced, estuarine gradient. In concert, operating the tidal barrages to be more permeable, allowing exchange of seawater and freshwater—similar to the growing trend in tidal floodgates (Boys & Pease, 2017; Jacobs et al., 2009)—may assist in restoring estuarine function in this highly regulated river system.

5.8 | An ecohydraulic model of a perennial dryland river

The aquatic ecology of the Murray River is underpinned, and frequently associated with, the river's natural and contemporary hydrology. Yet considering hydrology alone overlooks the hydraulic attributes of flowing water that govern ecosystem function and form. We propose an ecological model for this perennial dryland river that integrates ecohydraulics, ecohydrology, habitat, and spatial scale. It provides a tier of detail that helps explain ecological processes and the distribution of biota, and presents new opportunities for rehabilitation.

The premise of the model is that, under natural conditions, the Murray River was hydrodynamically diverse at all flows, along almost its entire length, with lotic habitats a permanent feature of the river, even in severe droughts. These conditions enabled a specific lotic ecology to develop in the river channel and an estuarine ecology to develop at the river terminus. Figure 15 shows the model under pre-regulated and post-regulated conditions, with three flows: (a) low flows, (b) a spring pulse within the channel, and (c) an overbank flood.

Under pre-regulated conditions, the river channel at low flows (a) would have been a series of pools and connecting sections of lotic habitats that were rocky bars, runs, or riffles, as described by Charles Sturt in 1830 (Sturt, 1833). These conditions represent a contraction of lotic habitats in dry periods, providing refugia for lotic biota that, in the Murray River, would likely include biofilms, diatoms, zooplankton, aquatic insects, snails, mussels, crustaceans, and fish (Walker, 2006). Outside of the main channel, large floodplain lakes and elevated wetlands become dry; a few low-lying wetlands may remain and anabranches cease to flow, becoming a series of pools. These small off-channel lentic habitats provide refuge for wetland specialist fish species. In low flows, river benches and dry anabranches provide a

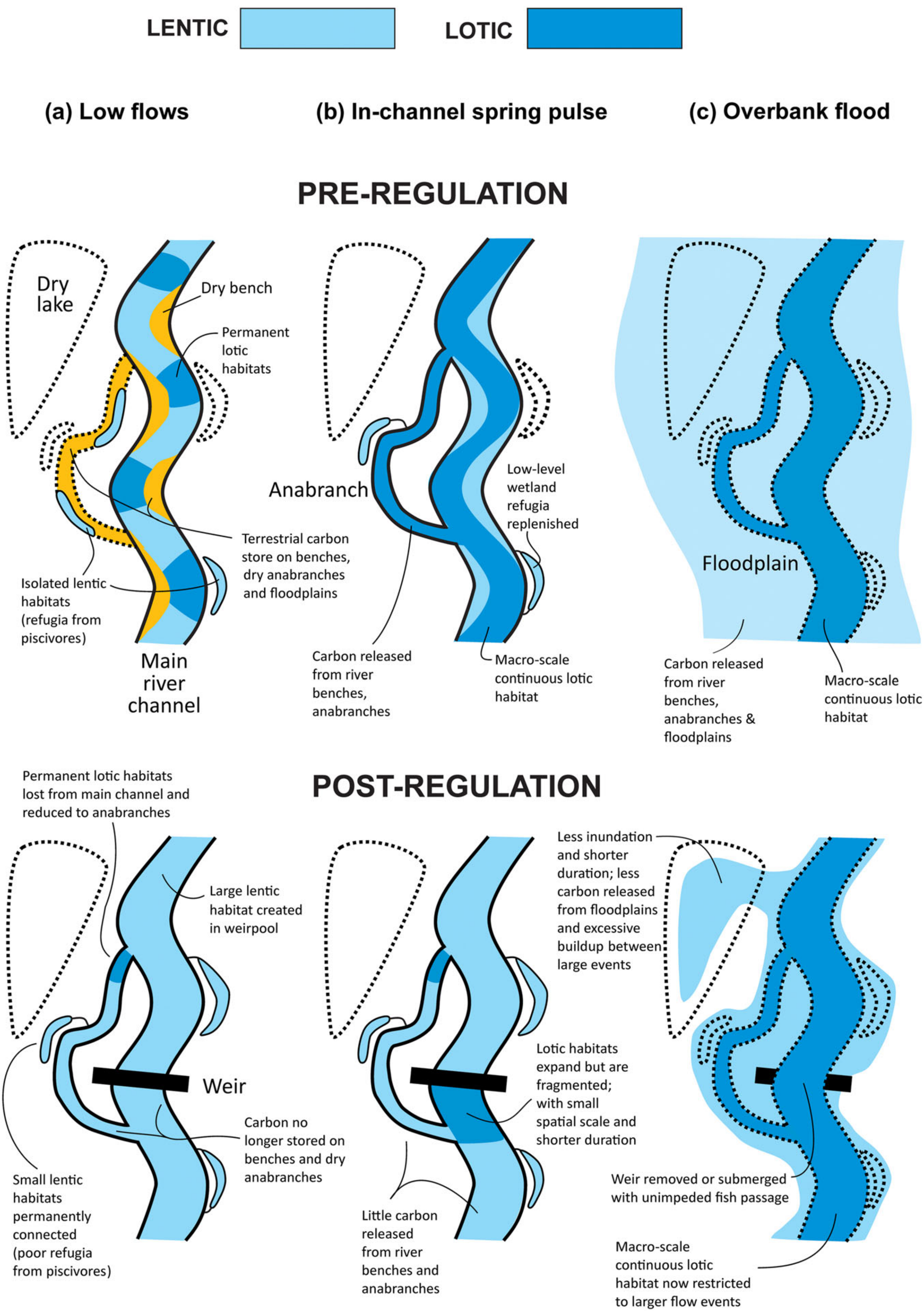

FIGURE 15 A model of a perennial dryland river integrating ecohydraulics and ecohydrology

low-lying terrestrial carbon store, whereas floodplains provide a store at a higher elevation.

The in-channel spring pulse (b) releases low-lying carbon stores to the river, increasing productivity; and the flow replenishes low-lying wetlands and intermittently flowing anabranches, thereby maintaining permanent off-channel habitats for wetland specialists. Large-scale flooding (c) would mobilize carbon from the floodplain and enable wetland specialist species to disperse, reconnecting larger metapopulations.

The spatial scale and integrity of lotic habitats changes with discharge. The in-channel pulse promotes continuous macro-scale (100–1,000s km) lotic hydrodynamics. Many fish, crustacean, and mussel species have drifting larvae that would use these conditions; but for at least two fish species, golden perch and silver perch, the hydrodynamics, and large spatial scale appear to be essential for recruitment and strong year classes (Mallen-Cooper & Stuart, 2003). Large-scale floods provide the same opportunities with the added advantage of access to ephemeral habitats for feeding. These events provide a large release of carbon and productivity, as per the Flood Pulse Concept (Junk, Bayley, & Sparks, 1989).

The model demonstrates that under regulated conditions the river loses lotic habitats in the main channel—the fragmentation and extent depending on the distance between weirs and the river gradient—and in some cases small lotic habitats are created in anabranch channels that by-pass weirs. The spring pulse is reduced in magnitude and frequency, and no longer provides macro-scale lotic habitats, while weirs reduce aquatic connectivity, both for upstream migration and downstream drifting life stages in large, lentic weirpools. The frequency and spatial scale of large floods is reduced but, when they occur, they maintain continuous lotic habitats and connectivity because the weirs are submerged.

The model offers an explanation for the loss of lotic biota in contiguous weirpools (Walker, 2006); the retention of some lotic biota in flowing anabranches; the episodic recruitment of golden perch in the lower Murray (Zampatti & Leigh, 2013); and the more frequent recruitment in the mid-Murray (Mallen-Cooper & Stuart, 2003; Zampatti et al., 2015) which retains macro-scale lotic conditions under all flows (Figure 14). Although much has been written about the altered hydrology of the Murray River, it is altered hydrodynamics and fragmentation of the river that have had an equal or greater impact on aquatic biota, causing reduced biodiversity and biotic homogenization. These changes have not only led to a loss of native species but also provided conditions conducive to non-native species—predominantly common carp (*Cyprinus carpio*), redfin perch (*Perca fluviatilis*), gambusia (*Gambusia holbrooki*), and oriential weatherloach (*Misgurnus anguillicaudatus*)—that further impact native fishes (Lintermans, 2007; Wedderburn et al., 2017).

Expanding the model to a larger spatial scale of thousands of kilometres and temporal scale of 10,000 years (Holocene) provides a broader framework. The wet periods in the early to mid-Holocene (Stanley & De Deckker, 2002) would have provided well-distributed and numerous lotic habitats enabling the development of a lotic ecology. After the mid-Holocene, there was a phase of more arid and variable climate in south-eastern Australia (Stanley & De Deckker, 2002) when periods of zero flow, potentially widespread, could have occurred. Under these conditions, lotic biota would contract from a large spatial scale to a few remaining refugia; in the Murray River system, these would likely be in upper catchments, as per the drought model proposed by Lake (2003). Once conditions became wetter, lotic biota would expand their distribution, so large-scale spatial variation could be expected over long time periods.

The aquatic biota that appear reliant on lotic habitats for spawning and recruitment, such as golden perch and silver perch, live for over 20 years (Mallen-Cooper & Stuart, 2003), so that adults of these species could potentially tolerate years of zero flow, and extensive lentic habitats, which may have occurred in the Holocene. The short-lived species that are present in the lowlands of the Murray River appear to be flexible, spawning and recruiting in lentic or lotic habitats; hence, they could also persevere through variable climate in the Holocene. Correspondingly, the persistence of oligosaline and freshwater diatoms in sediments where the river enters the lower lakes (Fluin et al., 2007), indicates that consecutive years or decades of zero flow were unlikely in the last 5,000 years.

5.9 | Applying ecohydraulic models to rehabilitation and river management

Using spatio-temporal ecohydraulics provides the opportunity to re-examine river rehabilitation in the Murray River and highly modified rivers globally. Furthermore, it provides an important perspective for rivers where regulation is evolving, for example, due to the growth of hydropower (Winemiller et al., 2016).

In the Murray River, an emphasis on large-scale patterns of hydrologic change has led to rehabilitation focused on restoring the duration and frequency of floodplain inundation especially through the use of purpose–built regulators (Pittock, Finlayson, & Howitt, 2013); and establishing drying regimes in floodplain habitats that are considered unnaturally perennial. Ephemeral floodplains in semiarid/dryland systems can provide a "boom" in aquatic productivity when inundated, but unlike highly seasonal rivers with permanent floodplains, such as large tropical rivers (Welcomme 1979), they make little contribution to aquatic species diversity. In dryland river systems, in-channel fluvial dynamics provide the repeatable multi-year conditions for spawning and recruitment, which determine and sustain aquatic biodiversity; in the same way that low-flow hydrology shapes the fish assemblages of dryland tropical streams (Arthington, Rolls, Sternberg, Mackay, & James, 2014).

Contemporary restoration initiatives in the MDB aim to use environmental water allocations more effectively by artificially inundating floodplains with regulating structures and measuring response of biota, particularly overstorey vegetation, at the local scale (Overton et al., 2014). The strategy may improve localized abundances and health of terrestrial floodplain flora, but the risk of focusing on site-specific hydrological or floodplain-inundation targets is that the extent and integrity of lotic habitats is reduced and meso-scale (1s-10s km) lentic habitats with fragmented hydrology increase. The latter will favour generalist native and non-native fish species and disadvantage specialized lotic biota, especially those with macro-scale life histories. We suggest that including objectives for hydrodynamics and spatial integrity of flow in the MDB would greatly help achieve restoration goals, and we consider that in some cases these objectives would be compatible with modifications of present policies.

Integrating ecohydraulics into river rehabilitation presents major new opportunities that, in many cases, use little or no additional water. For example, lowering the water level in weirpools creates lotic habitats upstream, with no change in discharge. This could be implemented permanently or seasonally; and mostly, does not require new infrastructure (Bice et al., 2017; Bice et al., 2016). Recognizing ecohydraulics also increases the importance of preserving existing lotic habitats. In some cases, the most productive restoration path may be to decouple a site from its hydrological and hydrodynamic history, pool the past regional ecological values and impose a hydrodynamic regime to target the values that have been lost. For example, where lotic habitats have been lost from the main river channel and it is impractical for them to be restored, these habitats can be created in tributaries and anabranches where they may not have been an original feature of the habitat template, thereby creating new lotic refugia.

Spatio-temporal ecohydraulics has broader application in assessing *river ecosystem health*, determining *environmental flows*, and in *strategic development* of global water resources. In the MDB, assessment of river ecosystem health uses fish, macroinvertebrates, and hydrology (Davies et al., 2010) which reflects river health criteria worldwide (Chakona, Phiri, Chinamaringa, & Muller, 2009; Oberdorff, Pont, Hugueny, & Porcher, 2002; Schneider, Laizé, Acreman, & Florke, 2013). A useful adjunct to river health assessment would be the inclusion of hydraulics. Biotic patterns are often a product of the hydrodynamics of rivers (not flow volume per se), hence characterizing hydraulic change may assist in determining the mechanisms underlying changes in river health, and in turn inform rehabilitation. Likewise, the environmental flow requirements of riverine ecosystems are commonly determined using a hydrological approach and ecohydrological models (Swirepik et al., 2016). Incorporating spatio-temporal hydrodynamic thresholds into environmental flows could provide useful and quantifiable measures more aligned with ecological processes. In this case, past hydrology would remain important, but hydraulics would provide the metrics for management. Currently, environmental flows are managed by measuring river discharge through networks of gauging stations. Discharge at these points is calculated using water velocity and cross-sectional stream area, which provides a ready-made tool for initial feedback on changes in hydraulics in real time. A long-term goal could be to link these gauging stations with regional hydrodynamic modelling to provide a broader spatial perspective.

Reinstating or protecting ecologically relevant aspects of the flow regime (environmental flows) is one of the most powerful tools for managing rivers. Quantifying the flow requirements of riverine ecosystems started with simple hydrologic rules, such as proportions of mean flow (Tennant, 1976), and expanded to include detailed ecohydraulics (e.g., PHABSIM™), an acknowledgement that biota respond to the hydraulics of discharge. Nevertheless, hydraulic considerations were focused on preference curves of water depth and velocity for adult and juvenile fish of individual species which were not practical in diverse rivers, and did not consider the hydrodynamic requirements for all life-stages (e.g., larval survival). Recognition of the complexity of flow-ecology relationships and the need for urgent answers for water managers led to the growth of holistic methods (Arthington & Zalucki, 1998). These techniques were based on the premise that hydrology has a primary influence on a range of biotic and abiotic factors. They combined readily available hydrological and biological data with expert opinion and stakeholder values; either "top down," using the hydrology of modelled natural flows or reference streams, or "bottom up," building a flow regime for different functional objectives. These methods also vary from solely hydrological to those that integrate specific hydraulic attributes (Acreman & Dunbar, 2004). In most cases, however, hydraulics are not the endpoint for management. Furthermore, the approaches are often used at the site or reach scale (e.g., identifying riffles and pools) and in small rivers (i.e., wadeable at low flows; e.g., Brizga et al., 2002; King, Brown, & Sabet, 2003).

The ecological implications of riverine hydraulics over large spatial scales are often discussed (notably Poff et al., 2010), but they are not explicitly addressed in any present environmental flow method. This aspect becomes increasingly important in large rivers where the annual life cycles of biota, with specific hydraulic requirements, can occur over large spatial scales (100–1,000s km). The loss of pelagophils in large fragmented rivers is testament to this (Dudley & Platania, 2007; Wilde & Urbanczyk, 2013). In these systems, where the hydrodynamic integrity of the river is fundamentally impacted (i.e., through weirpools and reservoirs), reinstatement of aspects of the natural hydrological regime is unlikely to recover lost species.

Modern hydrodynamic modelling tools provide the potential to assess large spatial scales and deliver a powerful adjunct to environmental flow methods, especially in large rivers. In the present study, these tools enabled the past and present hydrodynamics to be assessed in a large river and, when combined with present ecological knowledge, provide new directions for environmental flow management.

A pressing need in global water resource management is strategic planning in those regions where development of large rivers and hydropower is rapid, which includes Southeast Asia, South America, and Africa (Winemiller et al., 2016). Hydrological impacts vary from storage reservoirs that provide short-term daily peaks of flow to run-of-river dams with minimal change in flow. All these structures, however, have considerable hydrodynamic impact, transforming lotic habitats to lentic.

In the large rivers of these tropical regions, migratory fish form an important part of the fish assemblage and support fisheries that provide essential food and livelihoods (Winemiller et al., 2016). Many of these fish migrate over large distances (100s km) and have a drifting larval stage (Agostinho, Pelicice, & Gomes, 2008; Cowx et al., 2015). Despite the growing recognition that drifting larvae have poor survival in reservoirs (Pelicice, Pompeu, & Agostinho, 2015), the issue is ignored in dam design (Baumann & Stevanella, 2012) and hydropower planning; leaving the focus to site-based impacts and upstream fish passage. Recognition of the hydrodynamic integrity of rivers and the requirement to maintain sufficient spatial scales for life cycles and riverine processes provides an urgently needed perspective for hydropower planning, and potentially for dam design, to minimize impacts on aquatic biota and food security. Brazil provides an example of the value of this direction, creating a protected reserve of 230 km of free-flowing river between two dams to maintain valuable populations of migratory fishes (Pelicice & Agostinho, 2008).

6 | CONCLUSION

The Murray River provides a telling example of temporal myopia in ecology, emphasizing the need to consider historical conditions as well as contemporary knowledge. By integrating these factors, we propose an ecohydraulic model for this perennial dryland river that presents new prospects for improving the integrity of the river's aquatic ecosystems. As part of this, restoration of riverine hydrodynamics, and the annual spring-flow pulse—the heartbeat of the river—are primary considerations. For global river management, we hope our study raises the profile of hydrodynamics, especially in highly modified—but not necessarily hydrologically impacted—rivers, where the impact of altered hydrodynamics on river ecology may be equal or greater than changes to hydrology. This perspective provides opportunities to refine flow management using ecologically relevant hydraulic objectives; and aid strategic water resource development that values hydrodynamics as a keystone of aquatic ecosystems.

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REFERENCES

Acreman, M., & Dunbar, M. J. (2004). Defining environmental river flow requirements: A review. *Hydrology and Earth System Sciences*, *8*(5), 861–876.

Acting Commissioner of Water Conservation and Irrigation (1915). Report of the acting Commissioner for water conservation and irrigation for the year ended 30th June, 1915. NSW Government Printer: Sydney.

Agostinho, A., Pelicice, F., & Gomes, L. (2008). Dams and the fish fauna of the Neotropical region: Impacts and management related to diversity and fisheries. *Brazilian Journal of Biology*, *68*(4), 1119–1132.

Arthington, A. H., Rolls, R. J., Sternberg, D., Mackay, S. J., & James, C. S. (2014). Fish assemblages in subtropical rivers: Low-flow hydrology dominates hydro-ecological relationships. *Hydrological Sciences Journal*, *59*(3–4), 594–604. https://doi.org/10.1080/02626667.2013.844345

Arthington, A. H., & Zalucki, J. M. (1998). Comparative evaluation of environmental flow assessment techniques: Review of methods. 149 p. Canberra: Land and Water Resources Research and Development Corporation Occasional Paper 27/98.

Balcombe, S. R., Arthington, A. H., Foster, N. D., Thoms, M. C., Wilson, G. G., & Bunn, S. E. (2006). Fish assemblages of an Australian dryland river: Abundance, assemblage structure and recruitment patterns in the Warrego River, Murray–Darling Basin. *Marine and Freshwater Research*, *57*(6), 619–633.

Barrett, J., & Mallen-Cooper, M. (2006). The Murray River's 'Sea to Hume Dam'fish passage program: Progress to date and lessons learned. *Ecological Management & Restoration*, *7*(3), 173–183.

Baumann, P., & Stevanella, G. (2012). Fish passage principles to be considered for medium and large dams: The case study of a fish passage concept for a hydroelectric power project on the Mekong mainstem in Laos. *Ecological Engineering*, *48*, 79–85. https://doi.org/10.1016/j.ecoleng.2011.06.032

Bibra, E. E. (1964). *Victorian river gaugings to 1960: Stream gauging and compilation of information carried out by the Hydrographic Section of the State Rivers and Water Supply Commission, in collaboration with the Water Resources Section, Investigations and Designs Division*. (p. 562). Melbourne: State Rivers and Water Supply Commission.

Bice, C. M., Gehrig, S., Zampatti, B., Nicol, J., Wilson, P., Leigh, S., & Marsland, K. (2013). Flow-induced alterations to fish assemblages, habitat and fish–habitat associations in a regulated lowland river. *Hydrobiologia*, *722*, 205–222.

Bice, C. M., Gibbs, M. S., Kilsby, N. N., Mallen-Cooper, M., & Zampatti, B. P. (2017). Putting the "river" back into the Lower River Murray: Quantifying the hydraulic impact of river regulation to guide ecological restoration. *Transactions of the Royal Society of South Australia*, *141*(2), 108–131.

Bice, C. M., Hammer, M. P., Wedderburn, S. D., Ye, Q., & Zampatti, B. P. (in press). Fishes of the Lower Lakes and Coorong. In R. Fitzpatrick, L. Mosley, Q. Ye, S. Hemming, S. Shepherd, & D. Rigney (Eds.), *Natural history of the Coorong, Lower Lakes and Murray mouth*. Royal Society of South Australia: Adelaide.

Bice, C. M., Zampatti, B. P., & James, C. (2016). The influence of weirpool raising on main channel hydraulics in the lower River Murray, South Australia, in 2015. *South Australian Research and Development Institute (Aquatic Sciences), Adelaide. SARDI Publication No. F2015/000381–2. SARDI Research Report Series No. 904. 40 pp*.

Bice, C. M., Zampatti, B. P., & Mallen-Cooper, M. (2017). Paired hydraulically distinct vertical-slot fishways provide complementary fish passage at an estuarine barrier. *Ecological Engineering*, *98*, 246–256.

Bockelmann, B. N., Fenrich, E. K., Lin, B., & Falconer, R. A. (2004). Development of an ecohydraulics model for stream and river restoration. *Ecological Engineering*, *22*(4), 227–235.

Bond, N. R., & Lake, P. S. (2005). Ecological restoration and large-scale ecological disturbance: The effects of drought on the response by fish to a habitat restoration experiment. *Restoration Ecology*, *13*(1), 39–48. https://doi.org/10.1111/j.1526-100X.2005.00006.x

Boulton, A. J. (2003). Parallels and contrasts in the effects of drought on stream macroinvertebrate assemblages. *Freshwater Biology*, *48*(7), 1173–1185.

Boulton, A. J., & Lake, P. S. (1992). The ecology of two intermittent streams in Victoria, Australia. *Freshwater Biology*, *27*(1), 99–121.

Boulton, A. J., & Lloyd, L. N. (1992). Flooding frequency and invertebrate emergence from dry floodplain sediments of the river murray, Australia. *Regulated Rivers: Research & Management*, *7*(2), 137–151. https://doi.org/10.1002/rrr.3450070203

Bowler, J. M., Johnston, H., Olley, J. M., Prescott, J. R., Roberts, R. G., Shawcross, W., & Spooner, N. A. (2003). New ages for human occupation and climatic change at Lake Mungo, Australia. *Nature*, *421*(6925), 837–840.

Boys, C. A., & Pease, B. (2017). Opening the floodgates to the recovery of nektonic assemblages in a temperate coastal wetland. *Marine and Freshwater Research*, *68*(6), 1023–1035.

Bren, L. J. (1988). Effects of river regulation on flooding of a riparian red gum forest on the River Murray, Australia. *Regulated Rivers: Research & Management*, *2*(2), 65–77. https://doi.org/10.1002/rrr.3450020202

Brizga, S. O., Arthington, A. H., Choy, S. C., Kennard, M. J., Mackay, S. J., Pusey, B. J., & Werren, G. L. (2002). Benchmarking, a 'top-down' methodology for assessing environmental flows in Australian rivers. Paper presented at the proceedings of the international conference on environmental flows for river systems, Southern Waters, University of Cape Town, South Africa.

Brock, M. A., Nielsen, D. L., Shiel, R. J., Green, J. D., & Langley, J. D. (2003). Drought and aquatic community resilience: The role of eggs and seeds in sediments of temporary wetlands. *Freshwater Biology*, *48*(7), 1207–1218. https://doi.org/10.1046/j.1365-2427.2003.01083.x

Bureau of Meteorology (2013). Climate Education; the 1914–15 drought. http://www.bom.gov.au/lam/climate/levelthree/c20thc/drought2.htm. Melbourne. Viewed 27 November 2013. : Australian Government.

Chakona, A., Phiri, C., Chinamaringa, T., & Muller, N. (2009). Changes in biota along a dry-land river in northwestern Zimbabwe: Declines and improvements in river health related to land use. *Aquatic Ecology*, *43*(4), 1095–1106. https://doi.org/10.1007/s10452-008-9222-7

Cheshire, K. J. M., Ye, Q., Gillanders, B. M., & King, A. (2016). Annual variation in larval fish assemblages in a heavily regulated river during differing hydrological conditions. *River Research and Applications*, *32*(6), 1207–1219. https://doi.org/10.1002/rra.2946

Chessman, B. C. (2011). Declines of freshwater turtles associated with climatic drying in Australia's Murray–Darling Basin. *Wildlife Research*, *38*(8), 664–671. https://doi.org/10.1071/WR11108

Chiew, F. H., Piechota, T. C., Dracup, J. A., & McMahon, T. A. (1998). El Nino/Southern Oscillation and Australian rainfall, streamflow and drought: Links and potential for forecasting. *Journal of Hydrology*, *204*(1), 138–149.

Clarke, S. J., Bruce-Burgess, L., & Wharton, G. (2003). Linking form and function: Towards an eco-hydromorphic approach to sustainable river restoration. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *13*(5), 439–450.

Close, A. (1990). The impact of man on the natural flow regime. In N. Mackay, & D. Eastburn (Eds.), *The Murray* (pp. 60–74). Canberra, Australia: Murray-Darling Basin Commission.

Close, A., & Sharma, P. (2003). *Hydrologic models used for water resource and salinity management in the River Murray system*. Australia: Institution of Engineers.

Closs, G. E., & Lake, P. S. (1996). Drought, differential mortality and the coexistence of a native and an introduced fish species in a south east Australian intermittent stream. *Environmental Biology of Fishes*, *47*(1), 17–26.

Cowx, I. G., Kamonrat, W., Sukumasavin, N., Sirimongkolthawon, R., Suksri, S., & Phila, N. (2015). *Larval and juvenile fish communities of the Lower Mekong Basin*. *MRC Technical Paper No. 49*. Mekong River Commission, Phnom Penh, Cambodia. *100 pp. ISSN: 1683–1489*.

Coyle, J. E. F. (1889). River Murray. *NSW Legislative Council Journals*, *45*(2), 581–604.

Crase, L., Pagan, P., & Dollery, B. (2004). Water markets as a vehicle for reforming water resource allocation in the Murray-Darling Basin of Australia. *Water Resources Research*, *40*(8), 1–10.

Cross, W. F., & Benke, A. C. (2002). Intra- and interspecific competition among coexisting lotic snails. *Oikos*, *96*(2), 251–264.

CSIRO (2008). Water availability in the Murray-Darling Basin. Report to the Australian government from the CSIRO Murray-Darling Basin sustainable yields project. CSIRO, Australia. 217pp.

Davies, B. R., Thoms, M. C., Walker, K. F., O'Keeffe, J. H., & Gore, J. A. (2009). Dryland rivers: Their ecology, conservation and management. In P. C. Calow, & G. E. Petts (Eds.), *The Rivers Handbook*. Oxford: Blackwell Science.

Davies, P., Harris, J., Hillman, T. J., & Walker, K. F. (2010). The sustainable rivers audit: Assessing river ecosystem health in the Murray–Darling Basin, Australia. *Marine and Freshwater Research*, *61*(7), 764–777.

Davis, J., Murray, S., & Burchell, F. (1902). *Interstate Royal Commission on the River Murray*. (p. 359). Melbourne: Sands and McDougall Limited Printers.

Dexter, T., Bond, N., Hale, R., & Reich, P. (2014). Dispersal and recruitment of fish in an intermittent stream network. *Austral Ecology*, *39*(2), 225–235. https://doi.org/10.1111/aec.12064

Dijk, A. I., Beck, H. E., Crosbie, R. S., Jeu, R. A., Liu, Y. Y., Podger, G. M., … Viney, N. R. (2013). The Millennium Drought in southeast Australia (2001–2009): Natural and human causes and implications for water resources, ecosystems, economy, and society. *Water Resources Research*, *49*(2), 1040–1057. https://doi.org/10.1002/wrcr.20123

Dole-Olivier, M. J., Galassi, D., Marmonier, P., & Creuzé des Châtelliers, M. (2000). The biology and ecology of lotic microcrustaceans. *Freshwater Biology*, *44*(1), 63–91.

Draper, C., & Mills, G. (2008). The atmospheric water balance over the semiarid Murray–Darling River Basin. *Journal of Hydrometeorology*, *9*, 521–534.

Dudgeon, D., Arthington, A. H., Gessner, M. O., Kawabata, Z. I., Knowler, D. J., Lévêque, C., … Stiassny, M. L. (2006). Freshwater biodiversity: Importance, threats, status and conservation challenges. *Biological Reviews*, *81*(2), 163–182.

Dudley, R. K., & Platania, S. P. (2007). Flow regulation and fragmentation imperil pelagic-spawning riverine fishes. *Ecological Applications*, *17*(7), 2074–2086. https://doi.org/10.1890/06-1252.1

Eaton, J. H. O., & River Murray Commission (1945). *A short history of the River Murray works*. Adelaide: Government Printer.

Ehlmann, B. L., & Criss, R. E. (2006). Enhanced stage and stage variability on the lower Missouri River benchmarked by Lewis and Clark. *Geology*, *34*(11), 977–980.

Encyclopaedia Britannica (1911). *Encyclopaedia britannica. A dictionary of arts, science, literature and general information* (Vol. 11). Cambridge: University Press.

Ferguson, G. J., Ward, T. M., & Geddes, M. C. (2008). Do recent age structures and historical catches of mulloway, *Argyrosomus japonicus* (Sciaenidae), reflect freshwater inflows in the remnant estuary of the Murray River, South Australia? *Aquatic Living Resources*, *21*(02), 145–152.

Ferguson, J. M. (1988). Irrigation development in Victoria: 1881-1890: A resource for tourism and education. *Proceedings of the Fourth National Conference on Engineering Heritage, Sydney, 5–8 December 1988*, 23–25.

Fluin, J., Gell, P., Haynes, D., Tibby, J., & Hancock, G. (2007). Palaeolimnological evidence for the independent evolution of neighbouring terminal lakes, the Murray Darling Basin, Australia. *Hydrobiologia*, *591*(1), 117–134.

Francis, C., & Sheldon, F. (2002). River Red Gum (*Eucalyptus camaldulensis* Dehnh.) organic matter as a carbon source in the lower Darling River, Australia. *Hydrobiologia*, *481*(1–3), 113–124. https://doi.org/10.1023/A:1021269205983

Galat, D. L., & Lipkin, R. (2000). Restoring ecological integrity of great rivers: Historical hydrographs aid in defining reference conditions for the Missouri River. *Hydrobiologia*, *422–23*, 29–48.

Gawne, B., Merrick, C., Williams, D. G., Rees, G., Oliver, R., Bowen, P. M., … Frankenberg, J. (2007). Patterns of primary and heterotrophic productivity in an arid lowland river. *River Research and Applications*, *23*(10), 1070–1087.

Geddes, M. (1987). Changes in salinity and in the distribution of macrophytes, macrobenthos and fish in the Coorong Lagoons, South Australia, following a period of River Murray flow. *Transactions of the Royal Society of South Australia*, *111*(4), 173–182.

Gell, P., & Reid, M. (2014). Assessing change in floodplain wetland condition in the Murray Darling Basin. *The Anthropocene*, *8*, 39–45.

Gippel, C. (2006). *Scoping study of operational changes to reduce river and storage losses along the River Murray system*. Canberra: Murray-Darling Basin Commission.

Girard, V., Monti, D., Valade, P., Lamouroux, N., Mallet, J. P., & Grondin, H. (2014). Hydraulic preferences of shrimps and fishes in tropical insular rivers. *River Research and Applications*, *30*(6), 766–779.

Goode, J. R., & Harvey, P. D. (2009). Water Resources. In J. T. Jennings (Ed.), *Natural history of the Riverland and Murraylands* (pp. 162–177). Adelaide: Royal Society of South Australia.

Gratton, C., & Zanden, M. J. V. (2009). Flux of aquatic insect productivity to land: Comparison of lentic and lotic ecosystems. *Ecology*, *90*(10), 2689–2699.

Hammer, M. P., & Walker, K. F. (2004). A catalogue of South Australian freshwater fishes, including new records, range extensions and translocations. *Transactions of the Royal Society of South Australia*, *128*, 85–97.

Hays, W. B. (1956). *Engineering in South Australia: Being an account of the principal public works now executed: Preceded by a historical sketch of the colony, from its foundation to the present time*. London: John Knott.

Humphries, P. (2005). Spawning time and early life history of Murray cod, *Maccullochella peelii* (Mitchell) in an Australian river. *Environmental Biology of Fishes*, *72*(4), 393–407.

Humphries, P., & Baldwin, D. (2003). Drought and aquatic ecosystems: An introduction. *Freshwater Biology*, *48*(7), 1141–1146.

Humphries, P., King, A., & Koehn, J. (1999). Fish, flows and flood plains: Links between freshwater fishes and their environment in the Murray-Darling River system, Australia. *Environmental Biology of Fishes*, *56*(1), 129–151.

Humphries, P., Serafini, L. G., & King, A. J. (2002). River regulation and fish larvae: Variation through space and time. *Freshwater Biology*, *47*(7), 1307–1331.

Jackson, S. T., & Hobbs, R. J. (2009). Ecological restoration in the light of ecological history. *Science*, *325*(5940), 567–569.

Jacobs, S., Beauchard, O., Struyf, E., Cox, T., Maris, T., & Meire, P. (2009). Restoration of tidal freshwater vegetation using controlled reduced tide (CRT) along the Schelde Estuary (Belgium). *Estuarine, Coastal and Shelf Science*, *85*(3), 368–376.

Jacobs, T. (1990). River regulation. In N. Mackay, & D. Eastburn (Eds.), *The Murray*. Murray-Darling Basin Commission: Canberra, Australia.

Jenkins, K., & Boulton, A. (2003). Connectivity in a dryland river: Short-term aquatic microinvertebrate recruitment following floodplain inundation. *Ecology*, *84*(10), 2708–2723.

Jensen, A. (2002). Repairing wetlands of the Lower Murray: Learning from restoration practice. *Ecological Management & Restoration*, *3*(1), 5–14. https://doi.org/10.1046/j.1442-8903.2002.00092.x

Johnston, E. N. (1913). *Captains Johnston's report of the general scheme for the improvement of the River Murray*. North Terrace, Adelaide: Government Printer.

Jones, M., & Stuart, I. (2007). Movements and habitat use of common carp (*Cyprinus carpio*) and Murray cod (*Maccullochella peelii peelii*) juveniles in a large lowland Australian river. *Ecology of Freshwater Fish*, *16*(2), 210–220.

Junk, W., Bayley, P., & Sparks, R. (1989). The flood pulse concept in river-floodplain systems. *Canadian Special Publications in Fisheries and Aquatic Sciences*, *106*, 110–127.

Kattel, G., Gell, P., Perga, M. E., Jeppesen, E., Grundell, R., Weller, S., … Barry, L. (2015). Tracking a century of change in trophic structure and dynamics in a floodplain wetland: Integrating palaeoecological and palaeoisotopic evidence. *Freshwater Biology*, *60*(4), 711–723.

Kennard, M. J., Pusey, B. J., Olden, J. D., MacKay, S. J., Stein, J. L., & Marsh, N. (2010). Classification of natural flow regimes in Australia to support environmental flow management. *Freshwater Biology*, *55*(1), 171–193.

Kiernan, J. D., Moyle, P. B., & Crain, P. K. (2012). Restoring native fish assemblages to a regulated California stream using the natural flow regime concept. *Ecological Applications*, *22*(5), 1472–1482.

King, A. J., Tonkin, Z., & Mahoney, J. (2009). Environmental flow enhances native fish spawning and recruitment in the Murray River, Australia. *River Research and Applications*, *25*(10), 1205–1218. https://doi.org/10.1002/rra.1209

King, J., Brown, C., & Sabet, H. (2003). A scenario-based holistic approach to environmental flow assessments for rivers. *River Research and Applications*, *19*(5–6), 619–639.

Kingsford, R., Lemly, A., & Thompson, J. (2006). Impacts of dams, river management and diversions on desert rivers. In R. Kingsford (Ed.), *Ecology of desert rivers* (pp. 203–247). Cambridge: Cambridge University Press.

Kingsford, R. T., Walker, K. F., Lester, R. E., Young, W. J., Fairweather, P. G., Sammut, J., & Geddes, M. C. (2011). A Ramsar wetland in crisis–the Coorong, Lower Lakes and Murray Mouth, Australia. *Marine and Freshwater Research*, *62*(3), 255–265.

Koehn, J. (2009). Multi-scale habitat selection by Murray cod *Maccullochella peelii peelii* in two lowland rivers. *Journal of Fish Biology*, *75*(1), 113–129. https://doi.org/10.1111/j.1095-8649.2009.02270.x

Koehn, J. D., & Harrington, D. J. (2005). Collection and distribution of the early life stages of the Murray cod (*Maccullochella peelii peelii*) in a regulated river. *Australian Journal of Zoology*, *53*, 137–144.

Koehn, J. D., Nicol, S. J., McKenzie, J. A., Lieschke, J. A., Lyon, J. P., & Pomorin, K. (2008). Spatial ecology of an endangered native Australian Percichthyid fish, the trout cod *Maccullochella macquariensis*. *Endangered Species Research*, *4*(1–2), 219–225.210.

Ladson, A. R., & Chong, J. (2005). Unseasonal flooding of the Barmah-Millewa forest. *Proceedings of the Royal Society of Victoria*, *117*(1), 127–137.

Lake, J. S. (1967a). Rearing experiments with five species of Australian freshwater fishes. II. Morphogenesis and ontogeny. *Marine and Freshwater Research*, *18*(2), 155–176. https://doi.org/10.1071/MF9670155

Lake, J. S. (1967b). Rearing experiments with five species of Australian freshwater fishes. I. Inducement to spawning. *Marine and Freshwater Research*, *18*(2), 137–154.

Lake, P. S. (2000). Disturbance, patchiness, and diversity in streams. *Journal of the North American Benthological Society*, *19*(4), 573–592.

Lake, P. S. (2003). Ecological effects of perturbation by drought in flowing waters. *Freshwater Biology*, *48*(7), 1161–1172. https://doi.org/10.1046/j.1365-2427.2003.01086.x

Lake, P. S. (2007). Flow-generated disturbances and ecological responses: Floods and Droughts. In P. J. Wood, D. M. Hannah, & J. P. Sadler (Eds.), *Hydroecology and ecohydrology: Past, present, and future* (pp. 75–92). West Sussex, England: John Wiley & Sons Ltd.

Lake, P. S. (2011). *Drought and aquatic ecosystems: Effects and responses*. Oxford, England: Wiley-Blackwell.

Lear, G., Anderson, M. J., Smith, J. P., Boxen, K., & Lewis, G. D. (2008). Spatial and temporal heterogeneity of the bacterial communities in stream epilithic biofilms. *FEMS microbiology ecology*, *65*(3), 463–473.

Leslie, D. J. (2001). Effect of river management on colonially-nesting waterbirds in the Barmah-Millewa forest, south-eastern Australia. *Regulated Rivers: Research & Management*, *17*(1), 21–36.

Lintermans, M. (2007). *Fishes of the Murray-Darling Basin: An introductory guide*. Canberra, ACT: Murray-Darling Basin Commission.

Lloyd, L. N., & Walker, K. F. (1986). Distribution and conservation status of small freshwater fish in the River Murray, South Australia. *Transactions of the Royal Society of South Australia*, *110*, 49–57.

Lytle, D. A., & Poff, N. L. (2004). Adaptation to natural flow regimes. *Trends in Ecology & Evolution*, *19*(2), 94–100.

Mackay, N., & Eastburn, D. (1990). *The Murray*. Canberra, Australia: Murray Darling Basin Commission.

Magoulick, D. D., & Kobza, R. M. (2003). The role of refugia for fishes during drought: A review and synthesis. *Freshwater Biology*, *48*(7), 1186–1198. https://doi.org/10.1046/j.1365-2427.2003.01089.x

Maheshwari, B., Walker, K. F., & McMahon, T. (1995). Effects of regulation on the flow regime of the River Murray, Australia. *Regulated Rivers: Research & Management*, *10*(1), 15–38.

Mallen-Cooper, M. (1999). Developing fishways for non-salmonid fishes: A case study from the Murray River in Australia. In M. Odeh (Ed.), *Innovations in fish passage technology* (pp. 173–195). Bethesda: American Fisheries Society.

Mallen-Cooper, M., & Brand, D. (2007). Non-salmonids in a salmonid fishway: What do 50 years of data tell us about past and future fish passage? *Fisheries Management and Ecology*, *14*(5), 319–332.

Mallen-Cooper, M., & Stuart, I. (2003). Age, growth and non-flood recruitment of two potamodromous fishes in a large semi-arid/temperate river system. *River Research and Applications*, *19*(7), 697–719.

Marohasy, J. (2012). Plugging the Murray River's mouth: The interrupted evolution of a barrier estuary. Australian Environment Foundation, Canberra. Report No: 001/12. 21 pp.

McJannet, D., Webster, I., Stenson, M., & Sherman, B. (2008). Estimating open water evaporation for the Murray Darling Basin. A report to the Australian Government from the CSIRO Murray-Darling Basin Sustainable Yields Project: CSIRO, Australia, pp. 50.

McKay, R. T. (1903). *The Murray River: Irrigation and navigation*. Sydney: Sydney University Engineering Society.

McMahon, T. A., & Finlayson, B. L. (2003). Droughts and anti-droughts: The low flow hydrology of Australian rivers. *Freshwater Biology*, *48*(7), 1147–1160.

McMaster, D., & Bond, N. (2008). A field and experimental study on the tolerances of fish to Eucalyptus camaldulensis leachate and low dissolved oxygen concentrations. *Marine and Freshwater Research*, *59*(2), 177–185. https://doi.org/10.1071/MF07140

McNeil, D. G. (2004). Ecophysiology and behaviour of Ovens River floodplain fish: Hypoxia tolerance and the role of the physicochemical environment in structuring Australian billabong communities. *Unpublished Ph.D. thesis, Department of Environmental Management & Ecology, La Trobe University, Bundoora, Australia*.

McNeil, D. G., & Closs, G. P. (2007). Behavioural responses of a south-east Australian floodplain fish community to gradual hypoxia. *Freshwater Biology*, *52*(3), 412–420.

Murray, S. (1892). *River Gauging*. Melbourne: Victorian Institute of Surveyors.

Murray-Darling Basin Commission (2005). The living Murray Foundation report on the significant ecological assets targeted in the first step decision. Canberra, ACT: Murray-Darling Basin Commission.

Murray-Darling Basin Commission. (2012). Basin Plan. *Prepared for the Commonwealth of Australia under subparagraph 44(2)(c)(ii) of the Water Act 2007*: http://www.comlaw.gov.au/Details/F2012L02240/Download Accessed 28 November 2013.

New South Wales Royal Commission Conservation of Water (1886). Second report of the commissioners of the Royal Commission Conservation of water. Sydney: Thomas Richards, Government Printer.

Nielsen, D., Smith, F., Hillman, T., & Shiel, R. (2000). Impact of water regime and fish predation on zooplankton resting egg production and emergence. *Journal of Plankton Research*, *22*(3), 433–446.

Oberdorff, T., Pont, D., Hugueny, B., & Porcher, J. P. (2002). Development and validation of a fish-based index for the assessment of 'river health' in France. *Freshwater Biology*, *47*(9), 1720–1734.

Overton, I., Pollino, C., Roberts, J., Reid, J., Bond, N., McGinness H., … Doody T. (2014). Development of the Murray-Darling Basin plan SDL adjustment ecological elements method. *Report prepared by CSIRO for the Murray-Darling Basin Authority. Licensed from the Murray–Darling Basin Authority under a Creative Commons Attribution 3.0 Australia Licence. 190 p.*

Papworth, S., Rist, J., Coad, L., & Milner-Gulland, E. (2009). Evidence for shifting baseline syndrome in conservation. *Conservation Letters*, *2*(2), 93–100.

Passy, S. I. (2001). Spatial paradigms of lotic diatom distribution: A landscape ecology perspective. *Journal of Phycology*, *37*(3), 370–378.

Pauly, D. (1995). Anecdotes and the shifting baseline syndrome of fisheries. *Trends in Ecology & Evolution*, *10*(10), 430.

Pauly, D., Watson, R., & Alder, J. (2005). Global trends in world fisheries: Impacts on marine ecosystems and food security. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *360*(1453), 5–12.

Pelicice, F. M., & Agostinho, A. A. (2008). Fish-passage facilities as ecological traps in large Neotropical rivers. *Conservation Biology*, *22*(1), 180–188.

Pelicice, F. M., Pompeu, P. S., & Agostinho, A. A. (2015). Large reservoirs as ecological barriers to downstream movements of Neotropical migratory fish. *Fish and Fisheries*, *16*(4), 697–715. https://doi.org/10.1111/faf.12089

Pittock, J., Finlayson, C. M., & Howitt, J. (2013). Beguiling and risky: 'Environmental works and measures' for wetland conservation under a changing climate. *Hydrobiologia*, *708*(1), 111–131. https://doi.org/10.1007/s10750-012-1292-9

Poff, N. L., Allan, J. D., Bain, M. B., Karr, J. R., Prestegaard, K. L., Richter, B. D., … Stromberg, J. C. (1997). The natural flow regime. *BioScience*, *47*(11), 769–784.

Poff, N. L., Olden, J. D., Merritt, D. M., & Pepin, D. M. (2007). Homogenization of regional river dynamics by dams and global biodiversity implications. *Proceedings of the National Academy of Sciences*, *104*(14), 5732–5737.

Poff, N. L., Richter, B. D., Arthington, A. H., Bunn, S. E., Naiman, R. J., Kendy, E., … Henriksen, J. (2010). The ecological limits of hydrologic alteration (ELOHA): A new framework for developing regional environmental flow standards. *Freshwater Biology*, *55*(1), 147–170.

Poff, N. L., & Ward, J. V. (1989). Implications of streamflow variability and predictability for lotic community structure: A regional analysis of streamflow patterns. *Canadian Journal of Fisheries and Aquatic Sciences*, *46*(10), 1805–1818.

Poff, N. L., & Ward, J. V. (1990). Physical habitat template of lotic systems: Recovery in the context of historical pattern of spatiotemporal heterogeneity. *Environmental Management*, *14*(5), 629–645.

Poff, N. L., & Zimmerman, J. K. H. (2010). Ecological responses to altered flow regimes: A literature review to inform the science and management of environmental flows. *Freshwater Biology*, *55*(1), 194–205. https://doi.org/10.1111/j.1365-2427.2009.02272.x

Pressey, R. L. (1986). *Wetlands of the River Murray below Lake Hume*. Canberra: River Murray Commission.

Puckridge, J., Sheldon, F., Walker, K. F., & Boulton, A. (1998). Flow variability and the ecology of large rivers. *Marine and Freshwater Research*, *49*(1), 55–72.

Puckridge, J., & Walker, K. (1990). Reproductive biology and larval development of a gizzard shad, *Nematalosa erebi* (Gunther)(Dorosomatinae: Teleostei), in the River Murray, South Australia. *Marine and Freshwater Research*, *41*(6), 695–712.

Reeves, J. M., Haynes, D., García, A., & Gell, P. A. (2015). Hydrological change in the Coorong Estuary, Australia, past and present: Evidence from fossil invertebrate and algal assemblages. *Estuaries and Coasts*, *38*(6), 2101–2116.

Reich, P., McMaster, D., Bond, N., Metzeling, L., & Lake, P. S. (2010). Examining the ecological consequences of restoring flow intermittency to artificially perennial lowland streams: Patterns and predictions from the Broken—Boosey creek system in northern Victoria, Australia. *River Research and Applications*, *26*(5), 529–545.

Reid, M., & Brooks, J. (2000). Detecting effects of environmental water allocations in wetlands of the Murray–Darling Basin, Australia. *Regulated Rivers: Research & Management*, *16*(5), 479–496.

Reid, M., Sayer, C., Kershaw, A., & Heijnis, H. (2007). Palaeolimnological evidence for submerged plant loss in a floodplain lake associated with accelerated catchment soil erosion (Murray River, Australia). *Journal of Paleolimnology*, *38*(2), 191–208.

Richardson, A. J., & Cook, R. A. (2006). Habitat use by caridean shrimps in lowland rivers. *Marine and Freshwater Research*, *57*(7), 695–701. https://doi.org/10.1071/MF05160

Richter, B., & Postel, S. (2004). Saving earth's rivers. *Issues in Science and Technology*, *20*(3), 31–36.

Richter, B. D., Baumgartner, J. V., Powell, J., & Braun, D. P. (1996). A method for assessing hydrologic alteration within ecosystems. *Conservation Biology*, *10*(4), 1163–1174.

Richter, B. D., Mathews, R., Harrison, D. L., & Wigington, R. (2003). Ecologically sustainable water management: Managing river flows for ecological integrity. *Ecological Applications*, *13*(1), 206–224.

Robinson, S. J., Souter, N. J., Bean, N. G., Ross, J. V., Thompson, R. M., & Bjornsson, K. T. (2015). Statistical description of wetland hydrological connectivity to the River Murray in South Australia under both natural and regulated conditions. *Journal of Hydrology*, *531*, 929–939.

Rowland, S. (1998). Aspects of the reproductive biology of Murray cod, *Maccullochella peelii peelii*. *Proceedings of the Linnean Society of New South Wales*, *120*, 147–162.

Schlosser, I. J., & Angermeier, P. L. (1995). Spatial variation in dynamic processes in lotic fishes: Conceptual models, empirical evidence, and implications for conservation. *American Fisheries Society Symposium*, *17*, 360–370.

Schneider, C., Laizé, C., Acreman, M., & Florke, M. (2013). How will climate change modify river flow regimes in Europe? *Hydrology and Earth System Sciences*, *17*(1), 325–339.

Select Committee on the Navigation of the Murray & c (1858). Report from the select committee on the navigation of the Murray, & c.; together with the proceedings of the committee, minutes of evidence, and appendix. *New South Wales Legislative Assembly* Philip Street, Sydney: Government Printer.

Sheldon, F., Bunn, S. E., Hughes, J. M., Arthington, A. H., Balcombe, S. R., & Fellows, C. S. (2010). Ecological roles and threats to aquatic refugia in arid landscapes: Dryland river waterholes. *Marine and Freshwater Research*, *61*(8), 885–895.

Sheldon, F., & Thoms, M. C. (2006). Relationships between flow variability and macroinvertebrate assemblage composition: Data from four Australian dryland rivers. *River Research and Applications*, *22*(2), 219–238.

Sheldon, F., & Walker, K. F. (1989). Effects of hypoxia on oxygen consumption by two species of freshwater mussel (Unionacea: Hyriidae) from the River Murray. *Marine and Freshwater Research*, *40*(5), 491–499.

Sheldon, F., & Walker, K. F. (1997). Changes in biofilms induced by flow regulation could explain extinctions of aquatic snails in the lower River Murray, Australia. *Hydrobiologia*, *347*(1–3), 97–108. https://doi.org/10.1023/A:1003019302094

Sheldon, F., & Walker, K. F. (1998). Spatial distribution of littoral invertebrates in the lower Murray-Darling River system, Australia. *Marine and Freshwater Research*, *49*(2), 171–182. https://doi.org/10.1071/MF96062

Shiel, R. J., Walker, K. F., & Williams, W. D. (1982). Plankton of the Lower River Murray, South Australia. *Australian Journal of Marine and Freshwater Research*, *33*, 301–327.

Silberstein, R., Best, A., Hickel, K., Gargett, T., & Adhitya, A. (2004). The effect of clearing of native forest on flow regime. *CRC for Catchment Hydrology Technical Report*, *4*(4), 59.

Silvertown, J., Tallowin, J., Stevens, C., Power, S. A., Morgan, V., Emmett, B., … Buxton, R. (2010). Environmental myopia: A diagnosis and a remedy. *Trends in Ecology & Evolution*, *25*(10), 556–561.

Siriwardena, L., Finlayson, B. L., & McMahon, T. A. (2006). The impact of land use change on catchment hydrology in large catchments: The Comet River, Central Queensland, Australia. *Journal of Hydrology*, *326*(1), 199–214.

South Australia Royal Commission (1891). *Second report of the commission on the utilisation of the River Murray waters*. North Terrace, Adelaide: Government Printer.

Southwood, T. (1977). Habitat, the templet for ecological strategies? *Journal of Animal Ecology*, *46*(2), 337–365.

Stanley, S., & De Deckker, P. (2002). A Holocene record of allochthonous, aeolian mineral grains in an Australian alpine lake; implications for the history of climate change in southeastern Australia. *Journal of Paleolimnology*, *27*(2), 207–219.

State Rivers and Water Supply Commission (1908–1923). Annual Report of State Rivers and Water Supply Commission. [15 separate reports for each financial year] Melbourne: Government Printer.

Stephens, S. C. (1974). *River Murray Gaugings to June 1973*. Adelaide, South Australia: South Australian Engineering and Water Supply Department.

Sturt, C. (1833). *Two expeditions into the interior of southern Australia, during the years 1828, 1829, 1830 and 1831: With observations on the soil, climate and general resources of the colony of New South Wales*. London: Smith, Elder & Co. [Facsimile edition, Doubleday Australia: Sydney, 1982]

Swetnam, T. W., Allen, C. D., & Betancourt, J. L. (1999). Applied historical ecology: Using the past to manage for the future. *Ecological Applications*, *9*(4), 1189–1206.

Swirepik, J. L., Burns, I. C., Dyer, F. J., Neave, I. A., O'Brien, M. G., Pryde, G. M., & Thompson, R. M. (2016). Establishing environmental water requirements for the Murray–Darling Basin, Australia's largest developed river system. *River Research and Applications*, *32*, 1153–1165. https://doi.org/10.1002/rra.2975

Tennant, D. L. (1976). Instream flow regimens for fish, wildlife, recreation and related environmental resources. *Fisheries*, *1*(4), 6–10. https://doi.org/10.1577/1548-8446(1976)001%3C0006:ifrffw%3E2.0.co;2

Thoms, M. C., Rayburg, S. C., & Neave, M. R. (2008). The physical diversity and assessment of a large river system: The Murray-Darling Basin, Australia. In A. Gupta (Ed.), *Large Rivers: Geomorphology and Management* (pp. 587–607). West Sussex, England: John Wiley & Sons.

Thoms, M. C., & Walker, K. F. (1993). Channel changes associated with two adjacent weirs on a regulated lowland alluvial river. *Regulated Rivers: Research & Management*, *8*(3), 271–284.

Thomson, M. B. (1986). *River Murray Wetlands: Their characteristics, significance and management*. Adelaide: The University of Adelaide, Department of Environment and Planning and the Nature Conservation Society of South Australia.

Tiffan, K. F., Kock, T. J., Haskell, C. A., Connor, W. P., & Steinhorst, R. K. (2009). Water velocity, turbulence, and migration rate of subyearling fall Chinook salmon in the free-flowing and impounded Snake River. *Transactions of the American Fisheries Society*, *138*(2), 373–384.

Traunspurger, W. (2000). The biology and ecology of lotic nematodes. *Freshwater Biology*, *44*(1), 29–45. https://doi.org/10.1046/j.1365-2427.2000.00585.x

Vardakas, L., Kalogianni, E., Papadaki, C., Vavalidis, T., Mentzafou, A., & Koutsoubas, D. (2017). Defining critical habitat conditions for the conservation of three endemic and endangered cyprinids in a Mediterranean intermittent river before the onset of drought. *Aquatic Conservation: Marine and Freshwater Ecosystems.*, *2017*, 1–11. https://doi.org/10.1002/aqc.2735

Verdon, D. C., Wyatt, A. M., Kiem, A. S., & Franks, S. W. (2004). Multidecadal variability of rainfall and streamflow: Eastern Australia. *Water Resources Research*, *40*(10), W10201.

Verdon-Kidd, D. C., & Kiem, A. S. (2009). Nature and causes of protracted droughts in southeast Australia: Comparison between the Federation, WWII, and Big Dry droughts. *Geophysical Research Letters*, *36*(22), L22707. https://doi.org/10.1029/2009GL041067

Vilizzi, L. (2012). Abundance trends in floodplain fish larvae: The role of annual flow characteristics in the absence of overbank flooding. *Fundamental and Applied Limnology / Archiv fűr Hydrobiologie*, *181*(3), 215–227. https://doi.org/10.1127/1863-9135/2012/0394

Vörösmarty, C. J., McIntyre, P., Gessner, M. O., Dudgeon, D., Prusevich, A., Green, P., … Liermann, C. R. (2010). Global threats to human water security and river biodiversity. *Nature*, *467*(7315), 555–561.

Walker, K. F. (1985). A review of the ecological effects of river regulation in Australia. In B. R. Davies & R. D. Walmsley (Eds.), *Perspectives in Southern Hemisphere Limnology* (pp. 111–129). Dordrecht: Springer.

Walker, K. F. (1992). The River Murray, Australia: A semi-arid lowland river. In P. Calow, & G. E. Petts (Eds.), *Rivers Handbook* (Vol. 1) (pp. 472–492). Oxford: Blackwell Scientific Publications.

Walker, K. F. (2006). Serial weirs, cumulative effects: The lower River Murray, Australia. In R. Kingsford (Ed.), *Ecology of Desert Rivers* (pp. 248–279). Cambridge, UK: Cambridge University Press.

Walker, K. F., Sheldon, F., & Puckridge, J. T. (1995). A perspective on dryland river ecosystems. *Regulated Rivers: Research & Management*, *11*(1), 85–104.

Walker, K. F., & Thoms, M. C. (1993). Environmental effects of flow regulation on the lower River Murray, Australia. *Regulated Rivers: Research & Management*, *8*(1–2), 103–119.

Ward, J., Tockner, K., Uehlinger, U., & Malard, F. (2001). Understanding natural patterns and processes in river corridors as the basis for effective river restoration. *Regulated Rivers: Research & Management*, *17*(4–5), 311–323.

Water Conservation and Irrigation Commission (1924). Report of the Water Conservation and Irrigation Commission for the year ended 30th June, 1923. Sydney: NSW Government Printer.

Webb, M., Thoms, M., & Reid, M. (2012). Determining the ecohydrological character of aquatic refugia in a dryland river system: The importance of temporal scale. *Ecohydrology & Hydrobiology*, *12*(1), 21–33. https://doi.org/10.2478/v10104-011-0005-8

Wedderburn, S. D., Hammer, M. P., Bice, C. M., Lloyd, L. N., Whiterod, N. S., & Zampatti, B. P. (2017). Flow regulation simplifies a lowland fish assemblage in the Lower River Murray, South Australia. *Transactions of the Royal Society of South Australia*, *141*(2), 169–192.

Welcomme, R. L. (1979). *Fisheries ecology of floodplain rivers*. London: Longman.

Wikipedia (2013). Murray River. (http://en.wikipedia.org/) Retrieved from (http://en.wikipedia.org/) Viewed 26 November 2013

Wilde, G. R., & Urbanczyk, A. C. (2013). Relationship between river fragment length and persistence of two imperiled great plains cyprinids. *Journal of Freshwater Ecology*, *28*(3), 445–451. https://doi.org/10.1080/02705060.2013.785984

Winemiller, K., McIntyre, P., Castello, L., Fluet-Chouinard, E., Giarrizzo, T., Nam, S., … Harrison, I. (2016). Balancing hydropower and biodiversity in the Amazon, Congo, and Mekong. *Science*, *351*(6269), 128–129.

Young, W. J., Schiller, C. B., Harris, J. H., Roberts, J., & Hillman, T. J. (2001). River flow, processes, habitats, and river life. In W. J. Young (Ed.), *Rivers as ecological systems: The Murray-Darling Basin*. Murray Darling Basin Commission: Canberra, Australia.

Zampatti, B. P., Bice, C. M., & Jennings, P. R. (2010). Temporal variability in fish assemblage structure and recruitment in a freshwater-deprived estuary: The Coorong, Australia. *Marine and Freshwater Research*, *61*(11), 1298–1312.

Zampatti, B. P., & Leigh, S. J. (2013). Within-channel flows promote spawning and recruitment of golden perch, Macquaria ambigua ambigua–implications for environmental flow management in the River Murray, Australia. *Marine and Freshwater Research*, *64*, 618–630.

Zampatti, B. P., Wilson, P. J., Baumgartner, L., Koster, W., Livore, J. P., McCasker, N., … Ye, Q. (2015). Reproduction and recruitment of golden perch (*Macquaria ambigua ambigua*) in the southern Murray–Darling Basin in 2013–2014: An exploration of river-scale response, connectivity and population dynamics. South Australian Research and Development Institute (Aquatic Sciences), Adelaide. SARDI Publication No. F2014/000756–1. SARDI Research Report Series No. 820. 61pp.

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Background Paper: Use of life history conceptual models of fish in flow management in the Murray-Darling Basin

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Executive Summary

Conceptual life history models can form the basis of natural resource management but often the practical link between models and on-ground actions is unclear. For fish, conceptual models that link spawning and recruitment (survival of young), to broad hydrological categories such as floods, in-channel flows, or low-flows, provide little quantitative guidance for management. Significantly, fish do not respond to flow (i.e. discharge) *per se* but to the hydraulic characteristics of flow at a range of spatial scales and these features are the basis for the *ecohydraulic recruitment guilds* developed in this paper. The guilds distinguish between fish that spawn and recruit in lotic (flowing water) and lentic (still-water) habitats, over micro (< 100 m), meso (100s m to 10s km) and macro (100s km) spatial scales.

The guilds readily identify groups of threatened fish species that share ecohydraulic characteristics. All species that require lotic habitats (e.g. Murray cod) and all species that are lentic (wetland) specialists (e.g. southern pygmy perch) have declined and these two groups contain almost all threatened species in the MDB. Conversely, almost all species that are habitat generalists and spawn and recruit in lentic and lotic habitats over a micro or meso-scale (e.g. carp gudgeons) remain relatively abundant. This group also includes most of the non-native fish species.

The immediate implication for flow management is that the high priority rehabilitation actions in the MDB are: i) creating or maintaining lotic habitats at the meso- and macro-scale, and ii) providing flows to create or maintain specialised lentic habitats for wetland specialists. Examples are provided in Mallen-Cooper and Zampatti (2015)[1] .

Ecohydraulic recruitment guilds enable qualitative and quantitative environmental outcomes to be developed directly for flow recommendations, and the use of spatial scale and hydraulics readily lends itself to SMART (Specific, Measurable, Attainable, Realistic, Tim-Related) flow targets. For example, fish in the *macro-lotic guild* with a Qualitative Environmental Outcome of 'enhance spawning and recruitment' would have a Quantitative Environmental Outcome of 'provide lotic conditions for sufficient uninterrupted longitudinal distance', and SMART flow targets of: distance >500 km; mean channel velocity >0.2 m/s and Reynolds number > 2500.

Using hydraulics and spatial scale in *ecohydraulic recruitment guilds* helps identify where flow can be used for the most effective ecological outcome and areas that have high potential for rehabilitation.

[1] Background Paper: The Natural Flow Paradigm and managing flows in the Murray-Darling Basin.

Contents

1 INTRODUCTION

Conceptual models are representations of complex systems that use available data and contemporary understanding of causal factors to describe ecological processes and patterns and interactions between these. They can be simple or complex and are usually pictorial or diagrammatic, but can also be a concise description in text. The strength of conceptual models is that, in addition to being predictive, they link components of a system together to present a holistic view. The model, and the process of constructing the model, can highlight knowledge gaps, identify research and monitoring priorities, and clarify and synthesise thinking.

Conceptual models of life history and ecology are fundamental to natural resource management. They represent contemporary understanding of available data and are used to inform management decisions. For example, investment in fishways is based on data of fish migration that forms a conceptual model about the whole life history of fish (e.g. adults migrate upstream; spawning occurs; larvae drift downstream) and the role that migration plays in sustaining populations. Various elements of the model (e.g. distance of downstream larval drift) remain as knowledge gaps but this does not restrain using the model to inform management and investment.

In this paper we briefly examine a broad conceptual model of fish and flows to highlight the differences in the management of fish and aquatic biota compared to terrestrial floodplain flora and fauna. We then propose a series of *recruitment guilds* that can be used to develop flow management objectives for fish and could further lead to qualitative and quantifiable environmental outcomes. Using these guilds we show how hydrologic change in the Murray River has led to declines of fish populations and where to target rehabilitation.

2 CONCEPTUAL MODELS

2.1. Flow-habitat-connectivity; a universal model for freshwater fish

At a high level, a fundamental ecological model for riverine fish is that "*flow*, *habitat* and *connectivity* are all required for sustainable fish populations". Any one aspect can affect fish populations but the extent varies between species depending on life history flexibility. *Flow* here incorporates hydrology, hydraulics (hydrodynamics) and water physico-chemistry, which are all particularly relevant to the management of floodplain rivers. These characteristics, plus *habitat* and *connectivity*, differentiate fish and aquatic biota from floodplain flora and fauna, where water depth, inundation area and duration are more important. *Connectivity* is often considered in terms of the movement of biota but it also includes hydrological connectivity, where the river and floodplain hydrographs are in phase and transport of carbon and propagules occurs freely, and hydrodynamics, where a mosaic of interconnected lotic and lentic habitats are maintained.

Implications for flow management

Delivery of flow for aquatic ecosystems needs to consider *connectivity* and *habitat* to optimise benefits. For example, flows that are delivered to river reaches that are less fragmented by weirs and have more diverse habitat, including hydrodynamic diversity, are likely to result in greater ecological outcomes.

2.2. General Models of Recruitment

There are seven general models of recruitment that apply to fish in the Murray-Darling Basin. Recruitment is defined here as the survival of young (eggs and larvae) in the first year of life, which overcomes the period of highest mortality.

Flood recruitment (Lake 1967)

Recruitment occurs when floodplains are inundated, increasing productivity and larval survival. Likely applies to all lowland and arid species to some degree.

Implications for flow management

Hydrological and hydrodynamic connections between the river and floodplain are important in managing flows for the environment, to enable carbon transport between the river and floodplain and to enable fish to use multiple habitats.

In-channel flow recruitment (Mallen-Cooper and Stuart 2003)

Recruitment occurs when there is variation in within-channel flows in spring and summer. Applies to golden perch, silver perch, and possibly Murray cod and trout cod. Potentially applies to the Southern and Northern Basin, including arid rivers.

Implications for flow management

In-channel flow pulses are a part of the hydrograph that has been severely impacted by river regulation in the Murray-Darling Basin, particularly in the Murray and Darling rivers (Maheshwari *et al.* 1995; Thoms 2003; Zampatti and Leigh 2013).

Low-flow channel recruitment (Humphries *et al.* 1999)

Recruitment occurs within channel habitats of lowland slow-flowing rivers at low stable flows. Applies to generalist species which, apart from freshwater catfish and dwarf flat-headed gudgeon, remain common in regulated rivers in the Murray-Darling Basin.

Implications for flow management

Downstream of irrigation areas low flows are common throughout the Basin and in many cases accentuated. Between storage dams and irrigation areas, however, low flows are often impacted by the spring/summer delivery of water for consumptive use, hence flows are unseasonally high. The impact of artificially high flows in these reaches is difficult to mitigate as they are primary conduits to deliver irrigation flows. Nevertheless, increasing the structural complexity of these reaches (e.g. reinstatement of snags) may provide greater hydrodynamic diversity.

Off-channel (lentic) recruitment

Survival of young to maturity occurs entirely within off-channel habitats, such as wetlands, billabongs, lakes, and isolated anabranches. Includes wetland specialists such as southern pygmy perch and flat-headed galaxias, and generalists such as carp gudgeons and freshwater catfish. Applies to rivers with well-developed floodplains, usually with permanent off-channel habitats, although suitable lentic habitats can occur in the river channels with zero or very low flows.

Implications for flow management

Flows are required to maintain off-channel refugia as the full life cycle is completed in habitats that can be disconnected from the river and are susceptible to dessication.

Arid refugia recruitment

Spawning and recruitment occurs in zero flows in channel refugia in arid rivers (Balcombe *et al.* 2006; Kerezsy *et al.* 2011). (For some species recruitment is enhanced by pulses of flow, conforming more to in-channel flow recruitment).

Implications for flow management

Abstraction of low flow needs to consider the maintenance of channel refugia, especially since their volume and permanency may have been reduced by sedimentation.

Estuarine recruitment

Spawning and recruitment occurs in the estuary, either by estuarine residents (e.g. black bream) or freshwater species after migration from upstream (e.g. *Galaxias maculatus*).

Implications for flow management

Flow is required to connect freshwater habitats with the estuary and create a gradient of salinities. Estuarine recruitment is dependent on productivity created by influxes of freshwater.

Marine recruitment

Spawning occurs in the sea after migration from freshwater (e.g. shortfinned eels and congolli).

Implications for flow management

Flow is required to connect freshwater habitats with the estuary, stimulate downstream migration of adults and upstream migration of juveniles. Recruitment of these species is probably not dependent on productivity in the estuary.

For the fish that recruit in freshwater (the first five groups above) these models provide broad principles for flow management, particularly with regards to hydrology. Nevertheless, they generally lack reference to scale and a hydraulic perspective. These two factors, which incorporate principles of connectivity, habitat and hydrodynamics, are integral to understanding the life history processes (and hence population dynamics) of freshwater fishes and provide new opportunities for flow management.

2.3. Fish Guilds

2.3.1. Background

Guilds have been used for Murray-Darling fishes to understand the broad relationships between recruitment (survival of young) and floods (Lloyd *et al.* 1991), and to group fishes based on reproductive characteristics such as fecundity (number of eggs), size of embryo and parental care (Humphries *et al.* 1999; Growns 2004). "The implicit assumption for the use of guilds for management . . . is that species with the same traits . . . respond in the same manner to the same ecological conditions" (Growns 2004). In the regulated rivers of the Murray Darling Basin, however, there are species within the same reproductive guild that have severely declined while others thrive. Examples are carp gudgeons (thriving) and southern pygmy perch (declined) in Humphries *et al*.'s (1999) Mode 3b (long spawning period, low fecundity, small eggs, short period to first feed), or flat-headed gudgeon (thriving) and trout cod (declined) in Grown's (2004) Guild C2 (parental care, no spawning migration, adhesive demersal eggs). Hence, under the same environmental conditions, fish within the same guild are responding very differently.

More recently Murray–Darling fishes have been grouped using reproductive characteristics, longevity, and partly habitat, trophic level, and response to flow; to develop four flow guilds (long-lived apex predators, flow-dependent specialists, foraging generalists, and floodplain specialists) (Baumgartner *et al.* 2013). These guilds enabled the development of hydrographs and frequency of application.

Rather than reproductive characteristics, we propose a model of *recruitment guilds* based on the primary characteristics of the river to which fish respond i.e. hydrodynamics, spatial scale and habitat. These *ecohydraulic* characteristics correspond to the major changes in river systems in the MDB – flow, fragmentation by dams and weirs, and habitat - and to the key management tools available for rehabilitation. We use hydrodynamics rather than flow (i.e. discharge) because this not only incorporates volumes of water and rates of movement but includes hydraulic complexity (depth, width, velocity, vector [direction] and turbulence) over time and space; it thus makes the important ecological distinction between *lentic* and *lotic* habitats, and it is these features which have a fundamental influence on life history processes such as migration, dispersal, feeding, spawning and recruitment. Changes to these hydraulic parameters are not described by discharge metrics.

2.3.2. Ecohydraulic Recruitment Guilds

To develop ecohydraulic recruitment guilds of freshwater fish species in the MDB we examined two key characteristics (Table 1):

i) *Hydrodynamics of habitats where recruitment occurs*: *lotic* or *lentic*, applying to spawning and recruitment (i.e. nursery areas). Lotic habitats include flowing streams with a pool-riffle structure and large flowing rivers. Lotic recruitment was differentiated if it: i) occurred wholly in lotic habitats, ii) occurred in large lentic habitats downstream of lotic habitats, or iii) was enhanced by increasing discharge within–channel, or overbank flooding.

ii) *Minimum spatial scale of spawning and recruitment*: the minimum scale over which spawning movements occur and over which recruitment occurs. Scales comprise micro (< 100 m), meso (100s m to 10s km) and macro (100s km). Fish that recruit at small-scales can recruit at larger scales, given the appropriate environmental conditions, but larger-scale species cannot recruit at smaller scales.

The broad habitat type (channel, off-channel or intermittent arid river) in which the life cycle is completed (i.e. not only recruitment) - determined by the presence of larvae and adults in a habitat - was then examined to review correlation of ecohydraulic recruitment guilds with habitat guilds and align these with flow management. Short-lived species that were present only in isolated off-channel habitats, preferably including adult and early life stages, were considered lentic.

We included species found presently or historically in the lowlands (<400m[1]) of the Murray-Darling Basin but excluded diadromous species in the lower lakes because they are not riverine. Short-headed lamprey is the only diadromous species included because it utilises and spawns in riverine habitats.

For context, Table 1 includes characteristics that were not used in the classification, including population trend (based on threatened species status and SRA data), body size, longevity, and conservation status. The biological information is from books on Australian fish biology (Merrick and Schmida 1984; McDowall 1996; Pusey *et al.* 2004; Lintermans 2007) or peer reviewed literature as referenced in Table 1.

Based on hydrodynamics and spatial scale there are three specific recruitment guilds of *macro lotic*, *meso lotic,* and *micro lentic;* and two combined guilds *of meso lotic-lentic, micro-lotic-lentic* which have species with flexible recruitment strategies (Figure 1).

A few species do not clearly fit the guilds. The spatial scale of the lotic-lentic guilds is uncertain for four species and is shown as overlapping in Figure 1. The non-native species, carp, is considered a lotic-lentic generalist and completes its life cycle in a range of habitats, but it requires specific spawning habitats that most frequently occur in wetlands. The spatial scale of small-bodied fish movements is also poorly known, but it is assumed that if they

[1] Only one species is found exclusively above 400 m elevation: barred galaxias.

Table 1. Freshwater fish in the lowlands (< 400m elev.) in the Murray-Darling Basin, with habitat and hydrodynamic recruitment characteristics. Diadromous species in the lower lakes are excluded. Threatened species (state or federal) are shaded in grey.

	CRITERIA USED IN CLASSIFICATION											
	HABITATS (completes life cycle)			SCALE	LOTIC			LENTIC				
	Channel habitats	Off-channel habitats (wetlands)	Intermittent arid rivers	Minimum spatial scale of spawning and recruitment • micro (< 100 m) ● meso (100s m–10s km) ⬤ macro (100s km)	Spawning and recruitment in lotic habitats	Recruitment in large lentic habitats downstream of lotic habitats	Recruitment enhanced by increasing discharge within-channel and/or floodplain inundation	Spawning and recruitment in lentic habitats	Specific substrate required for spawning	Pop^{n}. trend ↓↓ severe decline ↓ decline – stable ↑ increasing	Bodysize • Small ● Medium ⬤ Large	Longevity • Short ● Moderate ⬤ Long
Golden perch	✓[xx]		✓	⬤	✓[xx, i]	✓[ii]	✓[iii]	?[iv]		↓	●	⬤
Silver perch	✓[xx]		✓	⬤	✓[xx]		✓[v]			↓	●	⬤
Shortheaded lamprey	✓			⬤ [vi]	✓[vii]					↓	●	●
Murray cod	✓[xx]			●[viii, ix, x]	✓[xx, xi]		✓[xii]			↓	⬤	⬤
Trout cod	✓[xx]			●[xiii]	✓[xx]		?		?	↓↓	⬤	⬤
Macquarie perch	✓			●	✓[xiv]				✓	↓↓	●	⬤
River blackfish	✓			●	✓[i, xv]				✓	↓	●	●
Two-spined blackfish	✓			●	✓				✓	↓	●	●
Broad-finned galaxias (T[xvi])	✓[xx, i]			●	✓[xx, i]	✓				↑	•	?
Spotted galaxias (T?)	✓			●	✓	✓				↑	•	?
Mountain galaxias	✓[xx]			●[xvii]	✓[xx]					↓	•	?
Darling River hardyhead	✓			?	?		?	?		?	•	•
Dwarf flat-headed gudgeon	✓	✓		?	?			?		↓	•	•
Freshwater catfish	✓	✓	✓[iv]	●[xviii, xix]	✓		?	✓		↓	●	●
Bony herring	✓	✓	✓	●	✓		✓	✓		–	●	●
Spangled perch	✓	✓	✓	●	✓		✓	✓		–	●	●
Flat-headed gudgeon	✓[i, xx, xi]	✓[xx]		•	✓[i, xx]		✓[xi]	✓[xx]		–	•	•
Un-specked hardyhead	✓[xi]	✓[xx]		•	✓[xi]		✓[xi]	✓[xx]		–	•	•
Murray–Darling rainbowfish	✓[i, xi]	✓	✓	•	✓[i]			✓?		–	•	•
Carp gudgeons	✓[xx, i, xi]	✓[xx, xxvi]	✓	•	✓[i, xx]		✓[xi, xxi]	✓[xx, xxvi]		–	•	•
Australian smelt	✓[i, xx, xi]	✓[xx, xxvi]	✓	•	✓[i, xx]		✓[xxii]	✓[xx, xxvi]		–	•	•
Southern pygmy perch		✓		•	?[xx]		✓[xxiii]	✓[xxiii]	?	↓↓	•	•
Yarra pygmy perch		✓		•				✓	?	↓↓	•	•
Southern purple-spotted gudgeon		✓		•				✓	?	↓↓	•	•
Flat-headed galaxias		✓		•				✓		↓	•	•
Murray hardyhead		✓		•				✓		↓↓	•	•
Olive perchlet		✓	✓	•	?			✓	?	↓↓	•	•
Desert rainbowfish			✓	?				✓		?	•	•
Rendahl's tandan			✓	?				✓		?	⬤	?
Hyrtl's tandan			✓	?			✓	✓		?	⬤	?

	CRITERIA USED IN CLASSIFICATION											
	HABITATS (completes life cycle)			SCALE	LOTIC			LENTIC				
	Channel habitats	Off-channel habitats (wetlands)	Intermittent arid rivers	Minimum spatial scale of spawning and recruitment • micro (< 100 m) ● meso (100s m–10s km) ⬤ macro (100s km)	Spawning and recruitment in lotic habitats	Recruitment in large lentic habitats downstream of lotic habitats	Recruitment enhanced by increasing discharge within-channel and/or floodplain inundation	Spawning and recruitment in lentic habitats	Specific substrate required for spawning	Pop[n]. trend ↓↓ severe decline ↓ decline – stable ↑ increasing	Bodysize • Small ● Medium ⬤ Large	Longevity • Short ● Moderate ⬤ Long
Non-Native Species												
Carp	✓[i,xx]	(✓)[xxiv,xx]	✓	⬤	?[i]	✓	✓[xxv]	✓[xxv]		–	●	⬤
Goldfish	✓[xx]	✓[xx]	✓	●				✓		–	•	?
Eastern gambusia	✓[xx]	✓[xx, xxvi]	✓	●		✓	✓	✓[xxvi]		–	•	•
Redfin perch	✓[xx]	✓[xx]		●	?[i]	?[i]		✓		–	●	●
Tench	✓	✓		⬤?				✓		–	●	⬤
Oriental weatherloach		✓[xx]		•?			✓	✓		↑	•	•

[i] Humphries, P., and Lake, P. (2000) Fish larvae and the management of regulated rivers. *Regulated Rivers: Research & Management* **16**(5), 421-432.
[ii] Recruitment occurs in terminal systems or large floodplain lakes that fill from lotic riverine habitats (e.g. Menindee Lakes, Lake Cowal)
[iii] Zampatti, B.P., and Leigh, S.J. (2013) Within-channel flows promote spawning and recruitment of golden perch, Macquaria ambigua ambigua–implications for environmental flow management in the River Murray, Australia. *Marine and Freshwater Research* **64**, 618-630.
[iv] Balcombe, S.R., Arthington, A.H., Foster, N.D., Thoms, M.C., Wilson, G.G., and Bunn, S.E. (2006) Fish assemblages of an Australian dryland river: abundance, assemblage structure and recruitment patterns in the Warrego River, Murray–Darling Basin. Ibid. **57**(6), 619-633.
[v] Mallen-Cooper, M., and Stuart, I. (2003) Age, growth and non-flood recruitment of two potamodromous fishes in a large semi-arid/temperate river system. *River Research and Applications* **19**(7), 697-719.
[vi] Migration of adults is macro-scale, while spawning and survival of young dependent on meso-scale habitat.
[vii] McDowall, R. (1996) 'Freshwater fishes of south-eastern Australia.' (Reed)
[viii] Koehn, J., McKenzie, J., O'Mahony, D., Nicol, S., O'Connor, J., and O'Connor, W. (2009) Movements of Murray cod (*Maccullochella peelii peelii*) in a large Australian lowland river. *Ecology of Freshwater Fish* **18**(4), 594-602.
[ix] Leigh, S.J., and Zampatti, B.P. (2013) Movement and mortality of Murray cod, Maccullochella peelii, during overbank flows in the lower River Murray, Australia. *Australian Journal of Zoology* **61**(2), 160-169.
[x] Zampatti, B.P., Bice, C.M., Wilson, P.J., and Ye, Q. (2014) Population dynamics of Murray cod (*Maccullochella peeli*) in the South Australian reaches of the River Murray: a synthesis of data from 2002-2013. Report to PIRSA Fisheries and Aquaculture. South Australian Research and Development Institute (Aquatic Sciences), Adelaide. SARDI Puiblication No. F2014/000089-1. SARDI Reseach Report Series No. 761. 42 pp.
[xi] Vilizzi, L. (2012) Abundance trends in floodplain fish larvae: the role of annual flow characteristics in the absence of overbank flooding. *Fundamental and Applied Limnology / Archiv fűr Hydrobiologie* **181**(3), 215-227.
[xii] Rowland, S. (1998) Aspects of the reproductive biology of Murray cod, *Maccullochella peelii peelii*. *Proceedings of the Linnean Society of New South Wales* **120**, 147-162.
[xiii] Koehn, J.D., Nicol, S.J., McKenzie, J.A., Lieschke, J.A., Lyon, J.P., and Pomorin, K. (2008) Spatial ecology of an endangered native Australian Percichthyid fish, the trout cod Maccullochella macquariensis. *Endangered Species Research* **4**(1-2), 219-225.10.
[xiv] Lintermans, M. (2007) 'Fishes of the Murray-Darling Basin: an introductory guide.' (Murray-Darling Basin Commission Canberra, ACT)
[xv] Very low level of current required (McDowall, R. (1996) 'Freshwater fishes of south-eastern Australia.' (Reed))
[xvi] T = translocated
[xvii] Recolonisation by juveniles at meso-scale:
Lintermans, M. (2000) Recolonization by the mountain galaxias *Galaxias olidus* of a montane stream after the eradication of rainbow trout *Oncorhynchus mykiss*. *Marine and Freshwater Research* **51**(8), 799-804.
, Bond, N.R., and Lake, P.S. (2005) Ecological Restoration and Large-Scale Ecological Disturbance: The Effects of Drought on the Response by Fish to a Habitat Restoration Experiment. *Restoration Ecology* **13**(1), 39-48.
[xviii] Koster, W.M., Dawson, D.R., Clunie, P., Hames, F., McKenzie, J., Moloney, P.D., and Crook, D.A. (2014) Movement and habitat use of the freshwater catfish (*Tandanus tandanus*) in a remnant floodplain wetland. *Ecology of Freshwater Fish*, Published online 26 June 2014. DOI: 10.1111/eff.12159.
[xix] Stoffels, R.J., Clarke, K.R., Rehwinkel, R.A., and McCarthy, B.J. (2014) Response of a floodplain fish community to river-floodplain connectivity: natural versus managed reconnection. *Canadian Journal of Fisheries and Aquatic Sciences* **71**(2), 236-245.
[xx] Koehn, J.D., and Harrington, D.J. (2005) Collection and distribution of the early life stages of the Murray cod (*Maccullochella peelii peelii*) in a regulated river. *Australian Journal of Zoology* **53**(3), 137-144.
[xxi] Beesley, L., King, A.J., Amtstaetter, F., Koehn, J.D., Gawne, B., Price, A., Nielsen, D.L., Vilizzi, L., and Meredith, S.N. (2012) Does flooding affect spatiotemporal variation of fish assemblages in temperate floodplain wetlands? *Freshwater Biology* **57**(11), 2230-2246.
[xxii] Tonkin, Z.D., King, A.J., Robertson, A.I., and Ramsey, D.S.L. (2011) Early fish growth varies in response to components of the flow regime in a temperate floodplain river. Ibid. **56**(9), 1769-1782.
[xxiii] Tonkin, Z., King, A.J., and Mahoney, J. (2008) Effects of flooding on recruitment and dispersal of the Southern Pygmy Perch (Nannoperca australis) at a Murray River floodplain wetland. *Ecological Management & Restoration* **9**(3), 196-201.
[xxiv] Use shallow vegetated areas for spawning which can occur near the river channel but are more plentiful on floodplains.
[xxv] Stuart, I., and Jones, M. (2006) Large, regulated forest floodplain is an ideal recruitment zone for non-native common carp (*Cyprinus carpio* L.). *Marine and Freshwater Research* **57**(3), 333-347.
[xxvi] King, A., Humphries, P., and Lake, P. (2003) Fish recruitment on floodplains: the roles of patterns of flooding and life history characteristics. *Canadian Journal of Fisheries and Aquatic Sciences* **60**(7), 773-786.

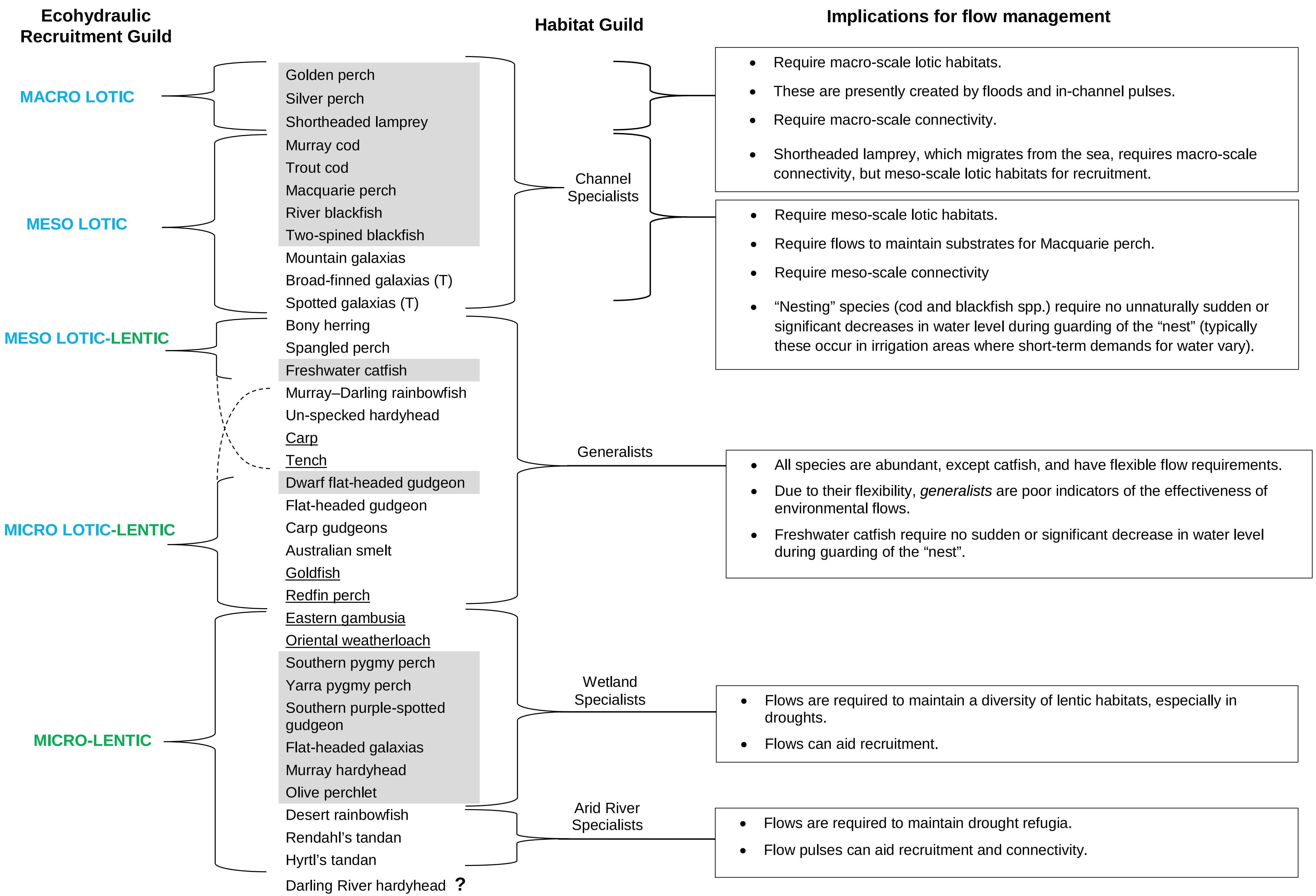

Figure 1. Ecohydraulic Recruitment Guilds and Habitat Guilds for native fish in the Murray-Darling Basin, shown with flow recommendations. Shaded species are threatened or have declined significantly.

complete their life cycle in small lentic habitats that a larger spatial scale is not specifically required in rivers. The life history of the Darling River hardyhead is poorly known in general.

As noted earlier, fish that recruit at small-scales can recruit at larger scales. Murray cod is classified as *meso-lotic*, however, for this species it may be that macro-scale recruitment is more significant for population dynamics and sustaining populations over the long term.

The recruitment guilds are presented in Figure 1 alongside habitat guilds and implications for flow management. All these guilds do not include the parameters of water temperature or water quality. Spawning of all fish is seasonal and related to water temperature and often day length. Water temperature is impacted by low–level offtakes of dams releasing cold water. The recruitment guilds apply to rivers that are not impacted by reduced water temperature or poor water quality, as these factors would override the life history characteristics considered here.

The habitat guilds align well with ecohydraulic recruitment guilds (Figure 1). The *macro-* and *meso-lotic* species are channel specialists while the *micro-lentic* guild has two identifiable habitat guilds of: wetland specialists and arid river specialists.

All species that can spawn and recruit in both lentic and lotic habitats, over a meso- or micro-scale, are generalist species that remain relatively abundant. Four of the six non-native species (carp, goldfish, redfin and tench) are also generalist species, while two (gambusia and oriental weatherloach) are wetland specialists.

The recruitment guilds are independent of reproductive characteristics such as fecundity or size of larvae, but importantly they identify: i) the type and scales of flows that are required for fish recruitment and, ii) the guilds that have declined in regulated rivers of the MDB. Declining species, with the exception of freshwater catfish and dwarf flat-headed gudgeon, either require *lotic* habitats over macro or meso scales, or specific *micro-lentic* (wetland) habitats.

The immediate implication for flow management is that the high priorities are: i) creating or maintaining lotic habitats at the meso- and macro-scale, and ii) providing flows to create or maintain specific lentic habitats for *wetland specialists*. The first can be achieved through: management of weir-pools; water delivery to meet a minimum velocity and hence create lotic conditions; use of irrigation systems based on natural anabranches; and reconnecting anabranches that have been cut off from the river (Mallen-Cooper and Zampatti 2015[1]). The second priority can be achieved through identifying suitable wetlands and maintaining them as a network of permanent drought refugia, which would require small amounts of water but could be achieved independently of large-scale floodplain watering (Mallen-Cooper and Zampatti 2015[1]).

The following discussion of guilds expands on the management implications and uses traffic light symbols that indicate priorities of very high (red), high (orange), and low (green). There is no group that is a moderate or intermediate priority. *Arid river specialists* have been tentatively included as a group that has not declined as they are still regularly collected, but little is known of their natural abundance.

[1] Background Paper: The Natural Flow Paradigm and managing flows in the Murray-Darling Basin.

2.3.2.1. Macro-lotic Guild

Three species are represented in this guild: golden perch, silver perch and short-headed lamprey (Figure 1). These fish spawn and recruit in lotic habitats but golden perch is more flexible, as it recruits in lentic habitats, such as semi-terminal lakes, that are downstream of macro-scale lotic spawning areas in rivers (Rolls and Wilson 2010; Sharpe 2011). Examples of these sites include Menindee Lakes and Lake Cowal (Lachlan River catchment).

Golden perch and silver perch have drifting larvae and are considered to conform to the flood-recruitment model. These two species also have strong year classes associated with in-channel pulses (Mallen-Cooper and Stuart 2003; Zampatti and Leigh 2013). In both these hydrological scenarios, continuous lotic habitats occur over 100's of kilometres of river, presumably with larval drift over this scale.

The life cycle of short-headed lamprey is macro-scale; adults migrate from the estuary up to 2000 km upstream, passing through lentic (weir-pools) and lotic conditions. Recruitment, however, appears to be meso-scale with spawning in lotic habitats with substrates of sand, pebbles or gravels, and juveniles (ammocetes) found in slow-flowing, but not lentic, habitats of sand, silt or mud (Koehn and O'Connor 1990; Lintermans 2007). A diversity of lotic conditions and substrates at the meso-scale is important for this species.

Management Implications

The *macro-lotic guild* is highly susceptible to river regulation due to the fragmentation and loss of connectivity, and loss of lotic habitats. Physical connectivity for species that are moving over large distances is being addressed through fishways across the Basin, most notably the Hume-to-Sea fish passage program, although passage of lampreys through fishways remains unknown.

Flow management needs to consider protection of macro-scale flow events that create suitable hydrodynamic conditions. In the Murray River in particular, large floods (e.g. >100,000 ML/d) remain little impacted by river regulation but the smaller flood events and in-channel pulses, such as flows with a 1 year Annual Recurrence Interval[1] (ARI), have been severely impacted by flow regulation (Maheshwari *et al.* 1995; Thoms 2003; Zampatti and Leigh 2013).

Restoration of the 1 year ARI would be a desirable ecological goal but is unlikely to be practical on a macro-scale. Considering that the species in this guild are long-lived, a productive discussion would be on the merits and practicality of reinstating the 1 year ARI volume and spatial scale, but at a lower frequency, such as 1-in-3 years. Using this temporal scale suggests that management of environmental flows needs to consider decadal hydrological cycles.

[1] A peak flow with a probability of occurring once a year.

2.3.2.2. Meso-lotic Guild

The meso-lotic guild has eight species, five of which are threatened or have declined including Murray cod, two blackfish species, trout cod and Macquarie perch. *Meso-lotic* species move over 100s metres to 10s kilometres and spawn in lotic habitats that are slow-moving (e.g. blackfish) to faster flowing (e.g. Macquarie perch). As noted earlier, the minimum scale of recruitment for Murray cod is meso but the population dynamics may be dependent on macro-scale recruitment events.

These species could also be tentatively grouped into two sub-guilds based on specificity of spawning substrates. Murray cod are known to spawn on rocks, large woody debris and even in earthen ponds. Trout cod are presumed to be similar in reproductive biology to Murray cod, but unlike Murray cod do not spawn in earthen ponds suggesting they have more specific spawning substrate requirements. Trout cod have demersal, adhesive eggs and rocks and logs have been suggested as spawning substrates; both of these habitat features have declined due to desnagging and sedimentation. Compared to Murray cod, trout cod also prefer slightly faster-flowing habitats (Koehn and Nicol 2014), which have been more impacted by weirs. Interestingly, when trout cod were present in the lower Murray (i.e. downstream of the Darling River junction) they were referred to as “rock cod” (Stead 1929), often being collected at sites with rocky substrates and fast flow.

Macquarie perch also appear to require specific substrates for spawning; in this case cobbles or gravel riffles (Lintermans 2007). These habitats have been severely impacted by the creation of weir pools and sedimentation in the lowlands of the MDB. Within the *meso-lotic guild* Macquarie perch and trout cod have had a major reduction in distribution while Murray cod, which use a wider range of spawning substrates, have declined in abundance but retain much more of their original range. The two blackfish species have declined in range and abundance but not to the same extent as Macquarie perch and trout cod.

An interesting unifying feature of the threatened species in this group is that they all have eggs that are either attached to a substrate and guarded by a parent (cod and blackfish species), or spawned in a substrate (Macquarie perch); both strategies have direct implications for flow management that are discussed below.

Management Implications

Fish in the *meso-lotic guild* are less susceptible to the fragmentation of habitats in regulated rivers than the *macro-lotic* guild, if three conditions are met:

i) the spatial scale of the life cycle is not fragmented (i.e. the life cycle can be completed between barriers);

ii) there are sufficient lotic habitats available; and

iii) spawning substrates are available.

The meso-lotic guild is more susceptible to changes in spawning substrates than other guilds, which is likely to be a major contributing factor in the decline of these species.

The spawning strategy of these species, to have attached or placed eggs, also makes them particularly susceptible to rapid and unseasonal changes in water levels, which can occur when water is delivered for consumptive use and is exaggerated near irrigation areas which have short-term demands. Rapid decreases in water level (e.g. 0.5 m over a few days) in the spawning season may cause adult fish to abandon the nest, or eggs to be directly exposed, in both cases causing the eggs to die.

Meso-scale is a highly manageable scale as it frequently fits within present flow management units. Flow recommendations for this guild need to incorporate two key hydrodynamic objectives: 1) maintaining lotic conditions and 2) restricting sudden water level changes in the spawning season.

Lotic conditions appear critical for the survival of larvae of the two cod species and critical for spawning of Macquarie perch and the two blackfish species. To quantify lotic conditions for management, the simplest and most readily applicable measure is mean channel velocity (e.g. 0.4 to 0.9 m/s). Further investigation could also use measures of hydraulic roughness or turbulence, using the extent of rocky substrates, snags and the sinuosity of the stream channel, to reflect hydrodynamic complexity.

Sudden level changes, mainly decreases, are easily measured and need to be avoided during the spawning season. Managing levels can be done through flow management or by topping up irrigation flows with environmental flows to suppress variation. This approach has recently been demonstrated in Gunbower Creek (Sharpe *et al.* 2014).

Meso-lotic conditions need to be protected where they presently occur. Site examples include Mullaroo Creek, near Lock 7, the Chowilla anabranch creeks in the vicinity of Lock 6, and the Murray River downstream of Yarrawonga and Torrumbarry weirs.

Identifying meso-lotic conditions as a feature for spawning and recruitment of a group of fish provides opportunities for investigating habitats where these conditions could be created or enhanced. Examples include optimising flow in anabranch creeks that are presently used for irrigation, lowering weir-pools, and managing flows in the lower Darling River (downstream of Menindee). Most of these can be achieved without additional flow (Mallen-Cooper and Zampatti 2015).

The effects of floods, which are macro-scale, are variable in this guild. Murray cod recruitment is enhanced by floods (Rowland 1998; Ye and Zampatti 2007) and it is possible that trout cod follow the same pattern. Macquarie perch and blackfish are now restricted to upland streams that have little floodplain development and high flows in these streams post-spawning may cause displacement and mortalities of eggs and larvae (Mark Lintermans, pers. comm.).

Using the term *meso-scale* in these guilds refers to the minimum spatial scale of recruitment within one season or year, and to the spatial scale of the flow regime. *Macro-scale* movements are still required to maintain genetic heterogeneity of metapopulations[1] and to repopulate areas following large-scale perturbations such as drought and blackwater events.

2.3.2.3. Lotic-lentic guilds

There are two combined lotic–lentic guilds, at the micro and meso scale. Although the minimum scale of recruitment of some species is uncertain, all species in these guilds are *habitat generalists*, spawning and recruiting in a wide range of lentic and lotic habitats including river channels, weir-pools, and wetlands of varying sizes (Koehn and Harrington 2005; Smith *et al.* 2009). With the exception of dwarf flat-headed gudgeon and freshwater catfish, these fish appear not to have declined in the Murray-Darling Basin, and in the artificial lentic habitats of weir-pools, are arguably more abundant.

Management Implications

Since the *habitat generalists* have declined little and, in a regulated, modified river system, they have extensive habitat for spawning and recruitment, specific environmental flows are not required for this group. These species are also inappropriate indicators of the effectiveness of environmental flows as they are likely to recruit under most conditions. Large natural floods appear to be the only conditions where recruitment of this group is reduced in the main channel (Bice *et al.* 2013), but they remain abundant in wetlands.

2.3.2.4. Micro-lentic Guild

Native fish in the *micro-lentic guild* can be divided into two sub-guilds based on habitat use. The first are the *wetland specialists*, which spawn and recruit in lentic habitats and have specific requirements for wetland size, aquatic vegetation, turbidity and connectivity. These are generally off-channel habitats but rivers and streams that cease to flow can develop suitable lentic characteristics. The species in this group are all threatened and have suffered major reductions in range and abundance.

The second sub-guild is the *arid river specialists*. These spawn and recruit in arid rivers with intermittent flow and frequent periods of zero flow with lentic conditions, but also in flow pulses or floods (Balcombe *et al.* 2006; Kerezsy *et al.* 2011).

Management Implications

The *wetland specialists* are a management priority and consideration of habitat quality as well as flow is integral. At the most basic level flow is required to maintain these habitats, which are susceptible to desiccation in droughts due to storage and diversion of flow (Hammer *et al.* 2013). Two modes of flow management are applicable to this group: 1) localised application of flow to maintain specific refugia and 2) managing large events to establish a mosaic of habitats.

For the second sub-guild of *arid river specialists* two major processes structure the fish assemblage: 1) refugia shape and size (Balcombe et al. 2006) and 2) flow pulses

[1] A population with physically separated, but genetically linked groups, where gene flow between the groups maintains heterogeneity.

or floods (Balcombe and Arthington 2009; Puckridge et al. 2010). Under natural conditions, permanent refugia are prevented from desiccation by small flow pulses which compensate for evaporation (Hamilton et al. 2005). An essential flow management objective for this sub-guild and for these ecosystems is to prevent desiccation and protect small flow pulses from abstraction. It is worth noting that historical flows may not provide accurate indicators of the required flow, or an acceptable level of abstraction, as land use and sedimentation may have affected the depth of these refugia, as it has elsewhere in the MDB (Bond and Lake 2005), making them more prone to evaporation. The connectivity of arid rivers in the Basin has also been affected by weirs, reducing the opportunities for recolonisation from 100% during periods of flow to less than 5% of the time (Nichols *et al.* 2012).

2.4. Floods, in-channel pulses and ecohydraulic recruitment guilds

Floods and in-channel pulses have specific ecological roles in river-floodplain ecosystems and these directly relate to the proposed ecohydraulic recruitment guilds (Figure 2). Large floods are major ecological events that inundate the floodplain and release carbon leading to large increases in productivity. This is a fundamental part of the Flood Pulse concept (Junk *et al.* 1989) and leads to the Flood Recruitment Model for fish (Lake 1967) where high productivity produces high densities of plankton and high survival of fish larvae. All species in the *macro-lotic guild*, except short-headed lamprey, appear to conform to the Flood Recruitment Model and, since they are also long-lived, it may be the fundamental process of recruitment that structures these populations and provides resilience in the long-term.

In-channel pulses are known to increase recruitment of two *macro-lotic* species, golden perch (Zampatti and Leigh 2013) and silver perch (Mallen-Cooper and Stuart 2003), and arid river species that also recruit in zero flows and meso-lentic habitats (Balcombe *et al.* 2006; Kerezsy *et al.* 2011). Although the productivity of in-channel pulses is not documented, benches within the river channel and dry anabranches are terrestrial sources of carbon that would provide a productivity pulse from these flows (Francis and Sheldon 2002; Sheldon and Thoms 2006; McGinness and Arthur 2011). Equally, a pulse of flow between arid river refugia would likely pick up carbon and transport it with associated productivity to waterholes.

In addition to increasing recruitment of *macro-lotic* species and arid river species; floods and in-channel pulses directly affect the *meso-lotic guild* by maintaining substrates for species such as Macquarie perch. The *wetland specialists* in the *meso-lentic guild* are also dependent on floods for maintaining a diversity of off-channel lentic habitats and to pulses of flow that prevent desiccation of low-lying refugia in droughts.

3 USING RECRUITMENT GUILDS FOR FLOW MANAGEMENT

3.1. Guilds, Flow Targets and Quantitative Environmental Outcomes

Ecohydraulic recruitment guilds can be directly used for flow management. Knowing the spatial scale over which fish are likely to respond, and the hydrodynamics in which spawning and recruitment occurs, enables flow to be targeted to meet these criteria.

Table 2 provides examples of two guilds and their application to flow management. The guilds enable qualitative and quantitative environmental outcomes to be developed and the use of spatial scale and hydraulics readily lends itself to SMART (Specific, Measurable, Attainable, Realistic, Time-Related) flow targets. The suggestions for SMART targets in Table 2 are not comprehensive for the guilds shown and are examples only. If this approach was considered appropriate, further work and peer review would be needed to provide sufficient detail for application. Two temporal hydrological parameters of timing and duration are included for context. Some key structural habitat features are also included as these determine hydraulic complexity.

SMART flow targets based on ecohydraulic recruitment guilds would help identify where flow can be used for the most effective ecological outcomes and help identify areas that have high potential for rehabilitation. In one scenario for example, existing rating curves could be used to determine whether a particular discharge or volume is sufficient to develop threshold channel velocities and create lotic habitats in the spawning season. If the volume was insufficient it could be saved until additional water became available.

For rehabilitation, hydrodynamic modelling can be used to assess areas with potential for different guilds. In some cases the spatial scale may be fragmented and flow may already be present; hence, providing connectivity would expand the spatial scale and more guilds would benefit. SMART flow targets can also be used to identify areas to protect (e.g. *meso-lotic* examples discussed in section 2.3.2.2).

Table 2. Example of using two *ecohydraulic recruitment guilds* to develop measurable flow targets. Items shaded in blue are key hydrological attributes, while areas in green are habitat attributes that are independent of flow but enhance the ecological value of flow.

Guild	Qualitative Environmental Outcomes	Quantitative Environmental Outcomes	Examples of SMART Targets for flow management
Macro-lotic	• Enhance spawning and recruitment with in-channel flow pulses	• Provide lotic conditions for sufficient uninterrupted longitudinal distance	• Longitudinal distance >500 km
		• Provide continuous hydrodynamic complexity in–channel	• Mean channel velocity >0.3 m/s (as a surrogate for cross-sectional channel complexity, with slow littoral zones)
			• Reynolds number[1] >2500 (non-laminar flow; also a surrogate for cross-sectional complexity)
			• >50 LWDs[2] per km in channel
		• Inundate instream benches to incorporate terrestrial carbon to initiate a productivity pulse	• 90% of instream benches inundated.
		• Timing	• Southern Basin: spring, early summer. • Northern Basin: spring, summer, autumn.
		• Duration	• 1-3 weeks
	• Enhance spawning and recruitment in floods	• Synchronised river and floodplain hydrographs over large spatial scale	• > 500 km of river, combined with inundation of 50% of floodplain.
		• Provide continuous hydrodynamic complexity in–channel	Achieved in floods and not manageable
		• Provide continuous hydrodynamic complexity in anabranches and flood	• Uninterrupted movement of flow through lateral floodplains (not applicable

[1] Reynolds number is the ratio of inertial forces over viscous forces; in stream ecology it provides a measure of stream turbulence and the change from lentic to lotic conditions.
[2] Large woody debris ("snags")

Guild	Qualitative Environmental Outcomes	Quantitative Environmental Outcomes	Examples of SMART Targets for flow management
		runners	to semi-terminal lakes).
		• Floodplain productivity is transported to and synchronised with the river, especially for *channel specialist* species	• Connectivity, transparency and integrity of flow between river and floodplain
		• Timing	• Southern Basin: spring, early summer. • Northern Basin: spring, summer, autumn.
		• Duration	• >2 weeks
Meso-lotic	• Enhance spawning and recruitment	• Provide lotic conditions for sufficient uninterrupted longitudinal distance	• Longitudinal distance >5 km
		• Provide sufficient continuous hydrodynamic complexity in-channel	• Mean channel velocity >0.3 m/s
			• Reynolds number >2500 (non-laminar flow; also a surrogate for cross-sectional complexity)
		• Ensure parental care of 'nesting' species (e.g. Murray cod)	• From October to early December (Southern Basin), reduction of water level within main channels (not on floodplain) < 0.1 m per day and < 0.5 m over 6 weeks.
		• Provide spawning habitats	Depending on biogeographic zone and species: • LWD: >50 per km in channel • Rocks: D_{50} 300-2000mm; >100m^2 continuous area • Cobbles, gravels: D_{50} 20-300mm; >100m^2 continuous area
		• Timing	• Permanent
		• Duration	• Permanent[1]

[1] Existing populations have permanent habitats, which may be necessary to ensure homing.

3.2. Flows for the whole fish community and complementary benefits

Management of aquatic ecosystems in the MDB needs to provide conditions that promote improvement of the whole fish community and all aquatic biota. The ecohydraulic recruitment guilds are a useful tool to do this as they not only potentially encompass all aquatic species - invertebrates, macroinvertebrates (including mussels and crayfish), and even biofilms differ in lentic and lotic habitats - but also they specifically identify priorities for management. The present background paper, for example, has identified generalist species that, with the exception of two species, are abundant in regulated reaches of rivers. Generalist species use lotic or lentic conditions for recruitment over meso- or micro-scales and require little, if any, specific flow recommendations. This group would be accommodated by any flow recommendations for the other guilds. Importantly, targeting the needs of generalist species would dilute the needs of those species with specific flow requirements.

In many cases flow recommendations for a specific guild will have overlapping and complementary benefits. Flows for the macro-lotic guild are likely to directly overlap with the meso-lotic guild, although the reverse does not apply. Flows for either of these guilds could also be used to provide refugia flows for the meso-lentic specialists, while all flows will aid generalist species.

3.3. Complementary actions

Identifying guilds provides opportunities for complementary actions to support flow management. Those species using lotic habitats for recruitment require hydrodynamic complexity (variation in water velocity and turbulence), which can be enhanced through the additional actions of re-snagging or adding rocky habitats. Lowering weirpools is a complementary action that increases the extent of lotic habitats.

Species in the macro-lotic guild are dependent on connectivity on a broad scale and fish passage becomes an important complementary action. Wetland specialists were severely impacted in the Millennium Drought; to avoid a repeat of those impacts flow management needs to include complementary actions such as nominating a network of refugia where water can be delivered.

3.4. Potential sites

The ecohydraulic recruitment guilds readily group fish species into those that have declined and those that are common. This provides flow priorities that can be addressed using hydrodynamic characteristics and identifies potential sites. For example:

Macro-lotic guild

Hydrodynamic flow target:

> Manage flows that generate mean channel velocities > 0.3 m/s over a longitudinal distance > 500 km.

Potential sites:

- Mid-Murray (Yarrawonga–Darling or Torrumbarry–Darling.
- Lower Murray (downstream of Darling River Junction).
- Middle Darling (Brewarrina to Menindee).
- Lower Darling (downstream of Menindee).
- Murrumbidgee.

Meso-lotic guild

The scale of the meso-lotic guild enables flow to be managed over smaller scales of 10s of kilometres to provide environmental benefits for fish. It also provides a suite of new possibilities where streams and anabranches can be used for regional rehabilitation of fish populations, creating new lotic habitats to compensate for lost lotic habitats in the weirpools of the main channels of rivers.

Hydrodynamic flow target:

> Manage flows that generate mean channel velocities > 0.3 m/s over a longitudinal distance > 5 km.

Potential sites:

i) Managing/protecting flows in existing lotic habitats:

- All macro-lotic sites above.
- Upland streams with Macquarie perch and blackfish species (e.g. Cotter River).
- Anabranches that presently have permanent flow (e.g. Mullaroo Creek and Chowilla).

ii) Creating new lotic habitats

- Lower weirpool elevations of the Murray River. Lotic habitats can be created by lowering weirpools without the addition of flow.
- Irrigation areas based on anabranch systems (e.g. Gunbower Creek, Pyramid Creek, Edwards-Wakool system). These require: i) permanent flow [presently little flow in the irrigation off-season of winter], ii) connectivity [fishways required in some cases], and in a few cases, iii) habitat rehabilitation such as re-snagging. Flow is returned to the Murray, less channel losses.
- Carrs Capitts Bunberoo system (anabranch near Lock 9); requires a higher, permanent baseflow [new inlet regulator] and connectivity [fishway]. Flow is returned to the Murray, less minor channel losses.
- Bookmark Creek (anabranch near Lock 5); requires a higher, permanent baseflow [new inlet regulator] and connectivity [fishway]. Flow is returned to the Murray, less minor channel losses.
- Several creeks in the Katarapko and Pike anabranch systems of the lower Murray.

Micro-lentic guild (wetland specialists)

Hydrodynamic flow target:

Create a network of permanent wetland refugia.

Potential sites:

- Barmah Forest.
- Gunbower Forest.
- Koondrook-Pericoota Forest.
- New floodplain SDL regulators.
- Jury Swamp (downstream of Lock 1).
- Hunters Creek, Hindmarsh Island.

4 CONCLUSION

Key Messages

1. Reproductive guilds or broad models of fish recruitment and flow provide little quantitative guidance for flow management.

2. *Ecohydraulic recruitment guilds* are based on the primary characteristics of the river to which fish respond - hydrodynamics, habitat and spatial scale – and these also correspond to the key tools available for management and rehabilitation.

3. All the fish species in the two guilds that require flowing water (lotic) rather than still-water (lentic) have had major population declines and almost all are threatened.

    - Protecting, rehabilitating and creating flowing water habitats for these lotic species can be achieved, in many cases, through changed management and additional infrastructure with zero or minimal additional water (Mallen-Cooper and Zampatti 2015). In other cases restoration of macro-scale (100s kms) annual in-channel pulses may be needed.

4. The species in the guild that uses specialized still-water (lentic) habitats (e.g. small permanent wetlands with aquatic vegetation) have all had major population declines and are all threatened.

    - Protecting, rehabilitating and creating habitats for these species would use minimal additional water (Mallen-Cooper and Zampatti 2015).

5. The guild that contains habitat generalists that use still-water habitats (e.g. weir-pools, wetlands etc.) includes all the abundant native fish species and these thrive independently of flow. This group seldom requires specific flow recommendations and are also poor indicators of the effectiveness of environmental flows.

6. The proposed guilds can be used to develop SMART flow targets which would help identify where flow can be used for the most effective ecological outcomes and areas that have high potential for rehabilitation.

References

Balcombe, S.R., and Arthington, A.H. (2009) Temporal changes in fish abundance in response to hydrological variability in a dryland floodplain river. *Marine and Freshwater Research* **60**(2), 146-159.

Balcombe, S.R., Arthington, A.H., Foster, N.D., Thoms, M.C., Wilson, G.G., and Bunn, S.E. (2006) Fish assemblages of an Australian dryland river: abundance, assemblage structure and recruitment patterns in the Warrego River, Murray–Darling Basin. *Marine and Freshwater Research* **57**(6), 619-633.

Baumgartner, L.J., Conallin, J., Wooden, I., Campbell, B., Gee, R., Robinson, W.A., and Mallen-Cooper, M. (2013) Using flow guilds of freshwater fish in an adaptive management framework to simplify environmental flow delivery for semi-arid riverine systems. *Fish and Fisheries*, n/a-n/a.

Beesley, L., King, A.J., Amtstaetter, F., Koehn, J.D., Gawne, B., Price, A., Nielsen, D.L., Vilizzi, L., and Meredith, S.N. (2012) Does flooding affect spatiotemporal variation of fish assemblages in temperate floodplain wetlands? *Freshwater Biology* **57**(11), 2230-2246.

Bice, C., Gehrig, S., Zampatti, B., Nicol, J., Wilson, P., Leigh, S., and Marsland, K. (2013) Flow-induced alterations to fish assemblages, habitat and fish–habitat associations in a regulated lowland river. *Hydrobiologia*, 1-18.

Bond, N.R., and Lake, P.S. (2005) Ecological Restoration and Large-Scale Ecological Disturbance: The Effects of Drought on the Response by Fish to a Habitat Restoration Experiment. *Restoration Ecology* **13**(1), 39-48.

Francis, C., and Sheldon, F. (2002) River Red Gum (*Eucalyptus camaldulensis* Dehnh.) organic matter as a carbon source in the lower Darling River, Australia. *Hydrobiologia* **481**(1-3), 113-124. [In English]

Growns, I. (2004) A numerical classification of reproductive guilds of the freshwater fishes of south-eastern Australia and their application to river management. *Fisheries management and Ecology* **11**(6), 369-377.

Hamilton, S.K., Bunn, S.E., Thoms, M.C., and Marshall, J.C. (2005) Persistence of aquatic refugia between flow pulses in a dryland river system(Cooper Creek, Australia). *Limnology and Oceanography* **50**(3), 743-754.

Hammer, M.P., Bice, C.M., Hall, A., Frears, A., Watt, A., Whiterod, N.S., Beheregaray, L.B., Harris, J.O., and Zampatti, B.P. (2013) Freshwater fish conservation in the face of critical water shortages in the southern Murray–Darling Basin, Australia. *Marine and Freshwater Research* **64**(9), 807-821.

Humphries, P., King, A., and Koehn, J. (1999) Fish, flows and flood plains: links between freshwater fishes and their environment in the Murray-Darling River system, Australia. *Environmental Biology of Fishes* **56**(1), 129-151.

Humphries, P., and Lake, P. (2000) Fish larvae and the management of regulated rivers. *Regulated Rivers: Research & Management* **16**(5), 421-432.

Junk, W.J., Bayley, P.B., and Sparks, R.E. (1989) The flood pulse concept in river-floodplain systems. *Canadian special publication of fisheries and aquatic sciences* **106**(1), 110-127.

Kerezsy, A., Balcombe, S.R., Arthington, A.H., and Bunn, S.E. (2011) Continuous recruitment underpins fish persistence in the arid rivers of far-western Queensland, Australia. *Marine and Freshwater Research* **62**(10), 1178-1190.

King, A., Humphries, P., and Lake, P. (2003) Fish recruitment on floodplains: the roles of patterns of flooding and life history characteristics. *Canadian Journal of Fisheries and Aquatic Sciences* **60**(7), 773-786.

Koehn, J., McKenzie, J., O'Mahony, D., Nicol, S., O'Connor, J., and O'Connor, W. (2009) Movements of Murray cod (*Maccullochella peelii peelii*) in a large Australian lowland river. *Ecology of Freshwater Fish* **18**(4), 594-602.

Koehn, J., and O'Connor, W. (1990) 'Biological information for management of native freshwater fish in Victoria.' (Department of Conservation and Environment, Freshwater Fish Management Branch, Arthur Rylah Institute for Environmental Research)

Koehn, J.D., and Harrington, D.J. (2005) Collection and distribution of the early life stages of the Murray cod (*Maccullochella peelii peelii*) in a regulated river. *Australian Journal of Zoology* **53**(3), 137-144.

Koehn, J.D., and Nicol, S.J. (2014) Comparative habitat use by large riverine fishes. *Marine and Freshwater Research* **65**(2), 164-174.

Koehn, J.D., Nicol, S.J., McKenzie, J.A., Lieschke, J.A., Lyon, J.P., and Pomorin, K. (2008) Spatial ecology of an endangered native Australian Percichthyid fish, the trout cod Maccullochella macquariensis. *Endangered Species Research* **4**(1-2), 219-225.10.

Koster, W.M., Dawson, D.R., Clunie, P., Hames, F., McKenzie, J., Moloney, P.D., and Crook, D.A. (2014) Movement and habitat use of the freshwater catfish (*Tandanus tandanus*) in a remnant floodplain wetland. *Ecology of Freshwater Fish*, Published online 26 June 2014. DOI: 10.1111/eff.12159.

Lake, J.S. (1967) Rearing experiments with five species of Australian freshwater fishes. I. Inducement to spawning. *Marine and Freshwater Research* **18**(2), 137-154.

Leigh, S.J., and Zampatti, B.P. (2013) Movement and mortality of Murray cod, Maccullochella peelii, during overbank flows in the lower River Murray, Australia. *Australian Journal of Zoology* **61**(2), 160-169.

Lintermans, M. (2000) Recolonization by the mountain galaxias *Galaxias olidus* of a montane stream after the eradication of rainbow trout *Oncorhynchus mykiss*. *Marine and Freshwater Research* **51**(8), 799-804.

Lintermans, M. (2007) 'Fishes of the Murray-Darling Basin: an introductory guide.' (Murray-Darling Basin Commission Canberra, ACT)

Lloyd, L., Puckridge, J., and Walker, K. (1991) The significance of fish populations in the Murray-Darling system and their requirements for survival. In Conservation and Management of the River Murray System – Making Conservation Count. (Eds. T Dendy and M Coombe). (South Australian Department of Environment and Planning: Adelaide)

Maheshwari, B., Walker, K.F., and McMahon, T. (1995) Effects of regulation on the flow regime of the River Murray, Australia. *Regulated Rivers: Research & Management* **10**(1), 15-38.

Mallen-Cooper, M., and Stuart, I. (2003) Age, growth and non-flood recruitment of two potamodromous fishes in a large semi-arid/temperate river system. *River Research and Applications* **19**(7), 697-719.

Mallen-Cooper, M., and Zampatti, B.P. (2015) Background Paper: The Natural Flow Paradigm and managing flows in the Murray-Darling Basin. Report prepared for the Murray-Darling Basin Authority. 37 p.

McDowall, R. (1996) 'Freshwater fishes of south-eastern Australia.' (Reed)

McGinness, H.M., and Arthur, A.D. (2011) Carbon dynamics during flood events in a lowland river: the importance of anabranches. *Freshwater Biology* **56**(8), 1593-1605.

Merrick, J.R., and Schmida, G.E. (1984) 'Australian freshwater fishes.' (Griffin Press: Netley, South Australia)

Nichols, S., Berghuis, A., Lay, C., and Mallen-Cooper, M. (2012) Fishway options for weirs of the Northern Murray Darling Basin. Report prepared for the Murray-Darling Basin Authority. 29 p.

Padmore, C.L. (1997) Biotopes and their hydraulics: a method for defining the physical component of freshwater quality. In Freshwater Quality: defining the indefinable? (Eds. PJ Boon and DL Howell) pp. 251-257. (SNH: Edinburgh)

Passy, S.I. (2001) Spatial paradigms of lotic diatom distribution: a landscape ecology perspective. *Journal of Phycology* **37**(3), 370-378.

Puckridge, J.T., Costelloe, J.F., and Reid, J.R.W. (2010) Ecological responses to variable water regimes in arid-zone wetlands: Coongie Lakes, Australia*. *Marine and Freshwater Research* **61**(8), 832-841.

Pusey, B., Kennard, M.J., and Arthington, A.H. (2004) 'Freshwater fishes of north-eastern Australia.' (CSIRO publishing: Collingwood, Australia)

Ramírez, A., and Pringle, C. (1998) Invertebrate drift and benthic community dynamics in a lowland neotropical stream, Costa Rica. *Hydrobiologia* **386**(1-3), 19-26. [In English]

Rolls, R., and Wilson, G.G. (2010) Spatial and Temporal Patterns in Fish Assemblages Following an Artificially Extended Floodplain Inundation Event, Northern Murray-Darling Basin, Australia. *Environmental Management* **45**(4), 822-833. [In English]

Rowland, S. (1998) Aspects of the reproductive biology of Murray cod, *Maccullochella peelii peelii*. *Proceedings of the Linnean Society of New South Wales* **120**, 147-162.

Sharpe, C. (2011) Spawning and recruiment ecology of golden perch (*Macquaria ambigua* Richardson 1845) in the Murray and Darling Rivers. PhD Thesis, Griffith University,

Sharpe, C., Stuart, I., and Mallen-Cooper, M. (2014) Optimising eflows in Gunbower Creek to enhance spawning opportunities for large bodied fish. Summary of Findings. Draft report for North Central Catchment Management Authority.

Sheldon, F., and Thoms, M. (2006) In-channel geomorphic complexity: The key to the dynamics of organic matter in large dryland rivers? *Geomorphology* **77**(3), 270-285.

Smith, B., Conallin, A., and Vilizzi, L. (2009) Regional patterns in the distribution, diversity and relative abundance of wetland fishes of the River Murray, South Australia. *Transactions of the Royal Society of South Australia* **133**(2), 339-360.

Stead, D.G. (1929) Murray cod and Trout cod. In The Sydney Mail. (John Fairfax and Sons: Sydney)

Stoffels, R.J., Clarke, K.R., Rehwinkel, R.A., and McCarthy, B.J. (2014) Response of a floodplain fish community to river-floodplain connectivity: natural versus managed reconnection. *Canadian Journal of Fisheries and Aquatic Sciences* **71**(2), 236-245.

Stuart, I., and Jones, M. (2006) Large, regulated forest floodplain is an ideal recruitment zone for non-native common carp (*Cyprinus carpio* L.). *Marine and Freshwater Research* **57**(3), 333-347.

Thoms, M.C. (2003) Floodplain–river ecosystems: lateral connections and the implications of human interference. *Geomorphology* **56**(3), 335-349.

Tonkin, Z., King, A.J., and Mahoney, J. (2008) Effects of flooding on recruitment and dispersal of the Southern Pygmy Perch (Nannoperca australis) at a Murray River floodplain wetland. *Ecological Management & Restoration* **9**(3), 196-201.

Tonkin, Z.D., King, A.J., Robertson, A.I., and Ramsey, D.S.L. (2011) Early fish growth varies in response to components of the flow regime in a temperate floodplain river. *Freshwater Biology* **56**(9), 1769-1782.

Vilizzi, L. (2012) Abundance trends in floodplain fish larvae: the role of annual flow characteristics in the absence of overbank flooding. *Fundamental and Applied Limnology / Archiv fűr Hydrobiologie* **181**(3), 215-227.

Wetzel, R.G. (2001) 'Limnology: lake and river ecosystems.' (Gulf Professional Publishing)

Ye, Q., and Zampatti, B. (2007) Murray cod stock status – the Lower River Murray, South Australia. Stock Status Report to PIRSA Fisheries. South Australian Research and Development Institute (Aquatic Sciences), Adelaide, 32pp. SARDI Publication Number F2007-000211-1.

Zampatti, B.P., Bice, C.M., Wilson, P.J., and Ye, Q. (2014) Population dynamics of Murray cod (*Macullochella peeli*) in the South Australian reaches of the River Murray: a synthesis of data from 2002-2013. Report to PIRSA Fisheries and Aquaculture. South Australian Research and Development Institute (Aquatic Sciences), Adelaide. SARDI Puiblication No. F2014/000089-1. SARDI Reseach Report Series No. 761. 42 pp.

Zampatti, B.P., and Leigh, S.J. (2013) Within-channel flows promote spawning and recruitment of golden perch, Macquaria ambigua ambigua–implications for environmental flow management in the River Murray, Australia. *Marine and Freshwater Research* **64**, 618-630.

Background Paper: Rethinking the Natural Flow Paradigm in the Murray-Darling Basin

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Executive Summary

Contemporary flow restoration in the MDB primarily considers the impact of river regulation on flow volume and rate (i.e. discharge) and, following the tenets of the Natural Flow Paradigm (NFP), aims to reinstate ecologically significant components of the flow regime. Such approaches, however, seldom consider the hydraulic and hydrodynamic impacts of river regulation and catchment degradation (e.g. sedimentation).

Although flow is the key parameter used to manage rivers, volumes of water and rates of discharge are not abiotic factors to which aquatic biota (including fish) respond. Instead organisms are influenced by the hydraulic elements that constitute flow (i.e. velocity, depth, wetted perimeter and turbulence) and their distribution at a range of spatial and temporal scales (i.e. hydrodynamics).

Consequently the application of the NFP must consider alteration to hydrodynamics.

We advocate that hydrodynamic restoration, at a range of spatial and temporal scales, is paramount to restoring essential habitats and life history processes for native fish, and for broader riverine ecosystem function in the MDB. Hydrodynamic objectives should form an integral component of objectives for environmental flow management and river health assessment. In concert there needs to be explicit consideration of connectivity, habitat, and the longitudinal and lateral integrity of flow.

Contents

Distribution and variation in hydraulic complexity over a range of spatial (e.g., cm, m, km, 100s km) and temporal scales.

Hydrology

Study of streamflow and the various characteristics associated with discharge (e.g. magnitude, duration, rate of rise and fall, seasonality, etc.).

1 INTRODUCTION

In regulated rivers managing flows for consumptive use whilst considering ecological requirements is a balancing act. Seldom can natural hydrological patterns be restored so the perennial questions are *how much*, *where* and *what* flows provide the greatest ecological benefits? In this arena the *natural flow paradigm* (Poff *et al.* 1997) dominates thinking. The paradigm considers that restoring aspects of the natural flow regime is integral to restoring ecosystem processes, habitats and biodiversity; and that this should serve as the template for river rehabilitation.

Restoring the natural hydrology, or aspects of it, has an intuitive logic and appeal. From a practical viewpoint, modelling of natural flows is well established and there are often long-term quantitative datasets of streamflow (some over 100 years), which are beyond any comparable ecological datasets.

The impact of flow regulation on aquatic biota is well documented, but rivers with highly regulated flows also often have intensive land clearing, agriculture and infrastructure for water storage and diversion, which confound this relationship. Water quality, notably temperature, is well acknowledged as an impact that can be independent of flow, as are barriers to movement of biota. Less recognised is the impact of river regulation on the hydraulic characteristics of flow, which hydrological measures such as discharge do not account for.

Hydrodynamics is the distribution and change in hydraulic complexity (velocity, depth, wetted area, turbulence) over a range of spatial (e.g. cm, m, km, 100s km) and temporal (e.g. hourly, daily, monthly, seasonally) scales. The importance of hydrodynamics in ecology is reflected in the primary dichotomy of still-water (lentic[1]) and flowing water (lotic[2]) habitats.

In this paper we discuss the role of hydrodynamics in riverine ecology and the use of the natural flow paradigm (NFP) in hydrological and ecological restoration in the Murray-Darling Basin (MDB). We outline significant changes to hydrodynamics in the Murray-Darling Basin, principally in the Murray River, and suggest that contemporary application of the NFP in the Murray River overlooks hydrodynamic change. To support this argument we examine case studies of three threatened fish species where we suggest that altered hydrodynamics rather than altered hydrology is the primary cause of population decline. Finally, we propose novel approaches to the restoration of hydrodynamics and to the rehabilitation of native fish populations in the MDB.

[1] *Lentic*
[2]

2 THE ROLE OF HYDRODYNAMICS

2.1. Hydrology and Hydrodynamics

The term 'flow' is often used as a synonym for discharge i.e. the rate that a volume of water passes a specific point over a unit of time (e.g. m^3/s, ML/d, GL/month). Nevertheless, volumes of water and rates of discharge are not abiotic factors to which aquatic biota (including fish) respond. Instead organisms are influenced by the hydraulic elements that constitute flow (i.e. velocity, depth, and turbulence) and their distribution at a range of spatial and temporal scales.

The hydraulic characteristics of flow (i.e. hydrodynamics) are determined by the *physical template* (Southwood 1977; Poff and Ward 1990) of the river which comprises the geomorphology of the river channel and various sources of hydraulic roughness such as substrate, large woody debris and littoral vegetation (Figure 1). Dams and weirs change the physical template in their immediate vicinity, but their impact on hydrodynamics is extensive because impounded water extends upstream creating a still-water habitat (Figure 1). This impact is particularly exaggerated in low gradient rivers, such as those in the lowlands of the Murray-Darling Basin, where extensive weir-pools are created.

Hydrodynamics are also determined by discharge but can be independent. For example, the same discharge will produce very different hydraulic characteristics in a stream channel that is wide, straight, smooth sided and with no roughness such as large woody habitat, compared with a channel on the same gradient that is sinuous, narrow, with extensive woody habitat; the latter will have greater hydraulic complexity which will produce a greater diversity of habitats. The corollary of this is that hydrodynamics can be modified independently of flow; large woody debris (snags) can be added to increase roughness and turbulence, and weirs can be lowered or removed to create flowing-water habitats.

In highly regulated rivers, such as the Murray River, the physical template of the river channel has been significantly modified through the construction of weirs, desnagging and sedimentation. In the Murray River, applying the natural flow paradigm does not necessarily promote the same hydrodynamic diversity and hence ecological processes that occurred naturally.

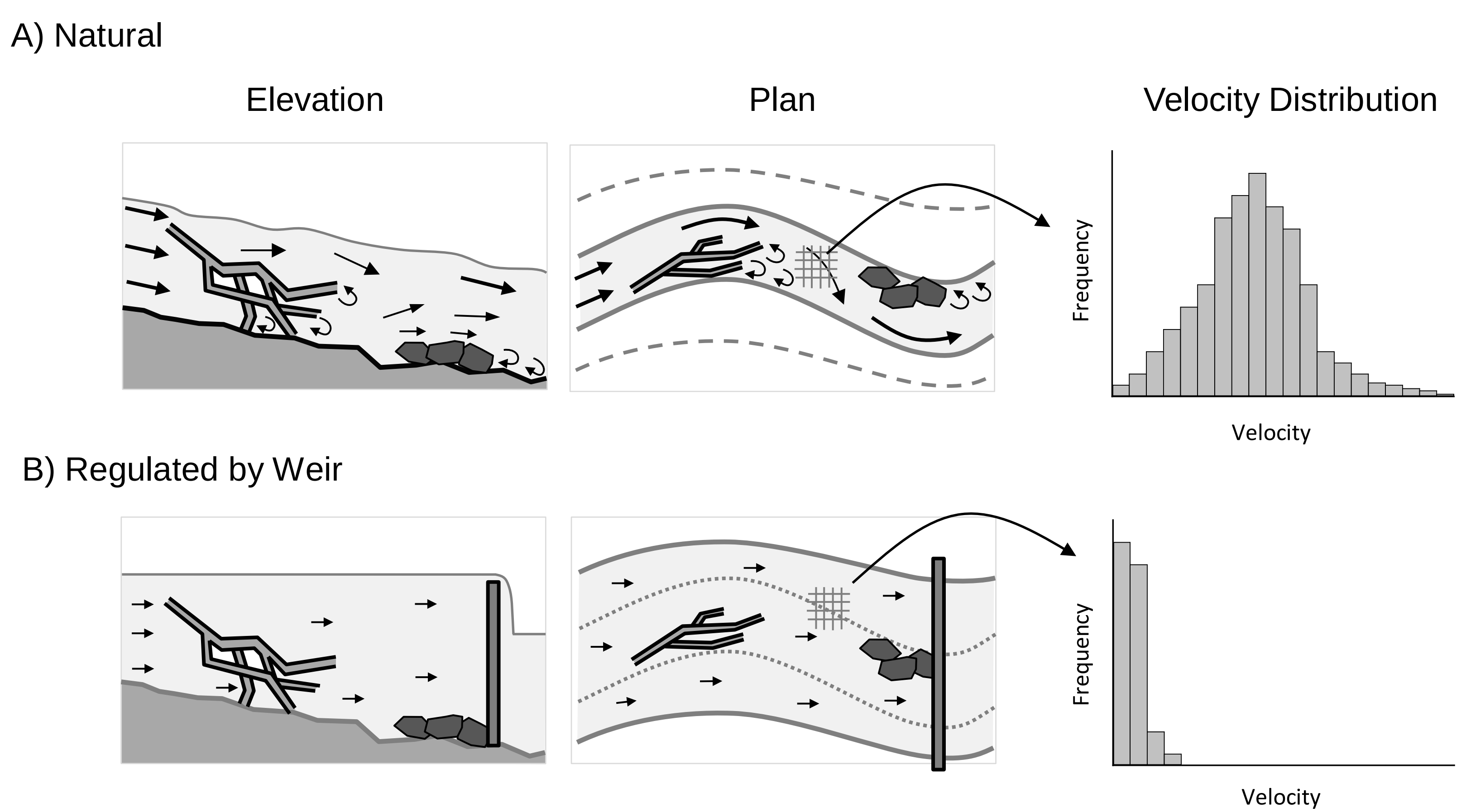

Figure 1. Conceptual diagram of a river illustrating hydrodynamic diversity and the impact of a weirpool. Elevation and plan sections of a stream are shown with vectors (flow direction and water velocity magnitude) as arrows, and a histogram of water velocities.

The natural stream (a) has complex changes in flow direction, higher mean velocities, a greater diversity of velocity with roughness such as large woody debris and rocks creating eddies.

The river regulated by a weir (b) has comparatively uniform flow direction, low mean velocity, a narrow range of velocities and the woody debris and rocks create very little hydrodynamic complexity due to the slow flow.

2.2. Hydrodynamics and fish ecology: the importance of scale

The hydrodynamic division between still-water and flowing water habitats is fundamental in riverine ecology and provides the basis for four fish life cycle guilds (groups with similar traits) related to flow and habitat in the Murray-Darling Basin (Mallen-Cooper and Zampatti 2014):

i) *Channel specialists*, which complete their life cycle within flowing water channel habitats, but may also temporarily use still-water channel and inundated floodplain habitats (e.g. flood runners). Examples include Murray cod, trout cod and silver perch.

ii) *Generalists*, which can complete their life cycle in still-water or flowing water habitats, including river channels and wetlands. Examples include carp gudgeons and Australian smelt.

iii) *Wetland specialists*, specifically complete their life cycle in wetland habitats that are generally isolated from the main channel. These habitats include some intermittently-flowing upland streams, which become a series of still-water pool habitats in zero flow. Examples include southern pygmy perch and Murray hardyhead.

iv) Arid river specialists, which compete their life cycle only in intermittently-flowing arid rivers. Examples include desert rainbowfish, Hyrtl's tandan and Rendahl's tandan.

Hydrodynamics influences the ecology of these guilds at micro (<100 m), meso (100s of m to 10s of km), and macro-scales (100s of km). Hence, river management also needs to be at local, river reach, and system scales.

Micro-scale

At the micro-scale, key hydrodynamic differences between flowing water and still-water habitats can be seen in Figure 2. The flowing water habitat exhibits substantial velocity differentials – that is, hydrodynamic complexity - with slow-flowing edges adjacent to a fast-flowing central current, and a velocity refuge, or slackwater, on the left-hand side. The slow-flowing edges and slackwaters collect and concentrate plankton, providing a feeding and nursery area for fish larvae. The implication for flow management is that allocating flow to river reaches where structural and channel complexity are present, may be a higher priority than sites with less complexity. Equally, habitat rehabilitation projects, such as re-snagging, may be more effectively sited where flow can be managed.

Six species of native fish are specifically known to spawn in flowing water habitats: Murray cod, trout cod, golden perch, silver perch, Macquarie perch, and shortheaded lamprey. The larvae of the first four species are often collected in drift samples in flowing water habitats (Koehn and Harrington 2006; King *et al.* 2009; Zampatti and Leigh 2013) and silver perch larvae have been shown to concentrate along the edges and bottoms of streams (i.e. littoral and epibenthic zones) (Tonkin *et al.* 2007). Murray cod will spawn in still-water habitats but commonly they migrate to flowing water habitats in the spawning season (Saddlier *et al.* 2008; Koehn *et al.* 2009). Furthermore, recruitment (survival of larvae and young fish) of Murray cod consistently occurs in flowing water habitats and is poor in still-water habitats of the lower Murray River (Zampatti *et al.* 2014). Consequently, hydrodynamic complexity of flowing water habitats at the micro-scale is significant for the larval ecology and survival of these native species. Indeed, with the exception of golden perch, these species are now extinct or rare in the regulated, hydrodynamically simple, weir-pools of the lower Murray River.

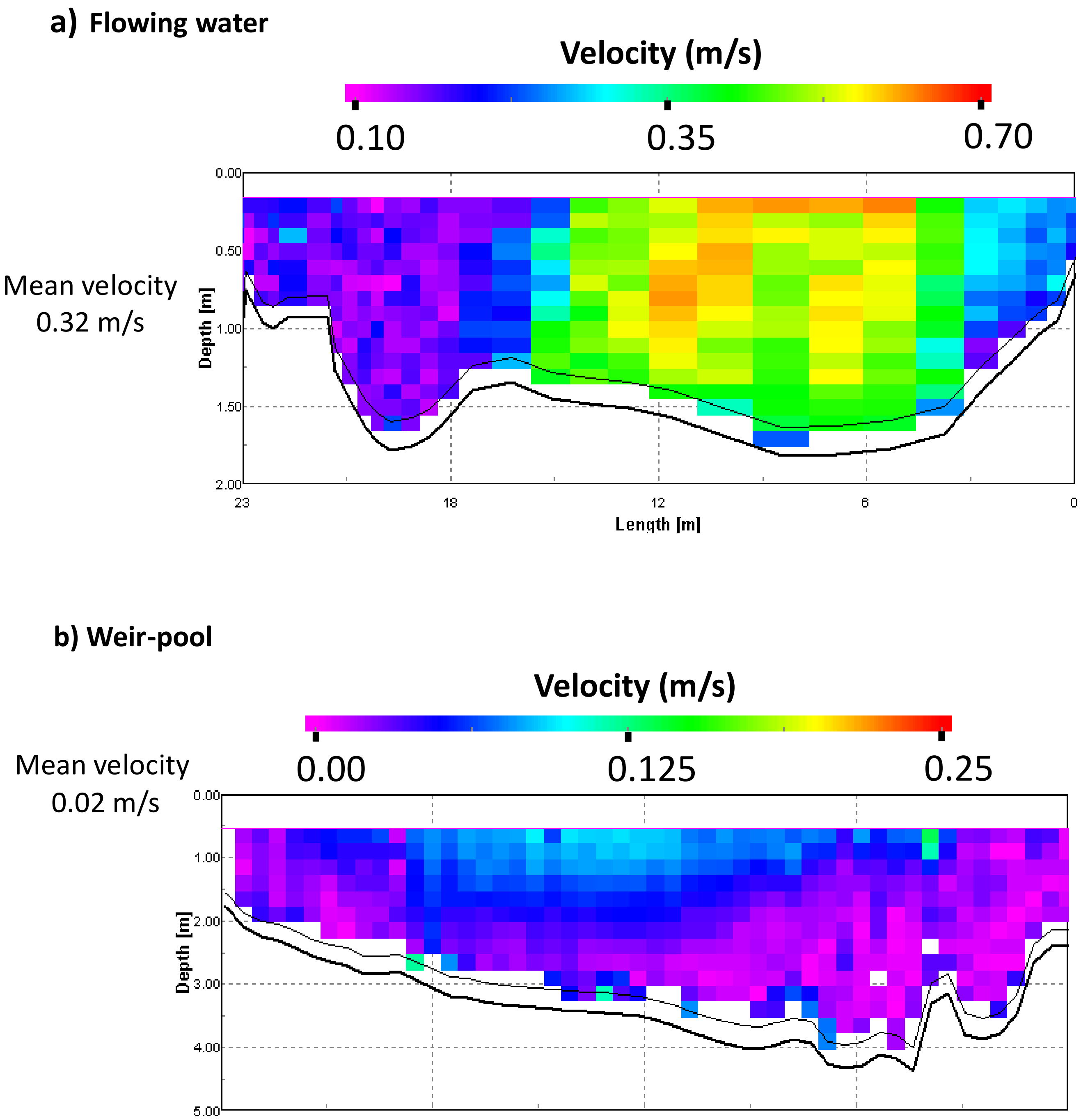

Figure 2. ADCP (Acoustic Doppler Current Profiler) outputs showing velocity profiles of cross-sections of: a) an anabranch stream with flowing water and b) a weir-pool. Both sites in the Lower Murray River, near Lock 6. Note that the scales vary between each figure.

Substrate also influences micro-scale hydrodynamics. Sand, gravels, cobbles and rocks impart roughness and provide a diversity of hydraulic habitats which are exploited by various fish species and life stages. Macquarie perch, for example, spawn in flowing water habitats with gravel, pebble and cobble substrates (Cadwallader and Rogan 1977). In regions of the MDB where these habitats have been impacted by river regulation and siltation (e.g. the middle reaches of the Murray River and the lower reaches of the Murrumbidgee River) Macquarie perch is now extinct (Lintermans 2007; Mallen-Cooper and Brand 2007).

Compared to the flowing anabranch in Figure 2 the micro-scale hydrodynamics of weir-pools during low flows (Figure 2) are relatively uniform. These habitats provide suitable spawning and nursery areas for *generalist species* (e.g. carp gudgeons and Australian smelt), particularly at low flows when there are abundant aquatic macrophytes (Bice *et al.* 2014). Most of the *generalist species* in the lowlands of the Murray-Darling Basin remain common or abundant, probably reflecting the increase in still-water habitats caused by numerous weir-pools in the Basin. This highlights the importance of maintaining flowing water habitats, particularly in droughts, and investigating weirpool management to increase flowing water habitats.

Meso-scale

Meso-scale hydrodynamics reflect the heterogeneity of habitats within a river reach, including pools, runs, riffles and associated off-channel habitats. Seasonal meso-scale movement of Murray cod between reaches with differing hydrodynamics is well-known. Murray cod in Lake Mulwala, in the mid-upper reaches of the Murray River, move to flowing water reaches of the Ovens River in spring and back to the lake; a cyclic movement of up to 130 km (Koehn *et al.* 2009). Murray cod in the Lindsay River-Mullaroo Creek system (Saddlier *et al.* 2008) and in the Chowilla anabranch system (Leigh and Zampatti 2013) use a range of still-water and flowing water mesohabitats within a year, typically moving tens of kilometres, and often occupying flowing water habitats in spring.

Macquarie perch also migrate over meso-scales in spring to spawn in specific flowing water riffle habitats (Tonkin *et al.* 2010). Some meso-scale movements occur over short-time frames, related to feeding or flow variability. For example, river blackfish move between slow and fast-flowing habitats, including riffles, within a diel period and move onto flooded riparian zones in high flows (Khan *et al.* 2004; Koster and Crook 2008).

These meso-scale movements between habitats with differing hydrodynamics are usually related to seasonal changes in water temperature and are frequently independent of discharge, although changes in discharge can influence movement in some species.

An integral part of hydrodynamic diversity at the meso-scale is micro-scale diversity. For those species with larval drift, micro-scale diversity (e.g. low water velocities along stream edges) over a meso-scale (up to 10s kilometres) is important. Preservation of hydrodynamically diverse habitats over a meso-scale and connectivity between these habitats appears essential for the completion of the life cycle of numerous species of native fish.

Macro-scale

Macro-scale hydrodynamics, which occur over 100s of kilometres, directly influence numerous aspects of fish ecology including spawning, dispersal (migration and larval drift) and metapopulation dynamics. Two notable species, golden perch and silver perch, regularly move over 100s of kilometres and both have drifting larval stages. Both migrate in spring in association with increasing discharge, likely responding to changing hydrodynamic characteristics of increased velocity and turbulence. Chemical cues may also be a stimulus for migration, such as tannins from inundated ground upstream (Lake 1967). Both species spawn in flowing water channel habitats and larvae have been collected drifting downstream (King *et al.* 2009).

For migration, spawning and drift to occur for these two species there needs to be continuity of flowing water habitats over a macro-scale. Eggs and drifting larvae of both species are semi-buoyant and require a minimum water velocity to facilitate drift. A change in hydrodynamics, such as a long deep weir-pool with low water velocity would likely prevent further drift and the larvae would settle in areas with poor micro-scale diversity.

Golden perch larvae and juveniles are also found in large, shallow, still-water habitats, such as terminal or semi-terminal lakes (e.g. Lake Cowal, Menindee Lakes) or ephemeral floodplain lakes that are inundated in floods and are downstream of flowing water spawning habitats. These habitats may be more productive than weir-pools, providing a plankton assemblage develops that is the appropriate type and size for golden perch larvae (Tonkin *et al.* 2006). Food resources may also be more dense and accessible in these shallow habitats compared to weir-pools.

The flexible use of fundamentally different hydrodynamic habitats by golden perch larvae over a macro-scale does not appear to apply to silver perch or Murray cod. Despite extensive studies, juveniles of these two species are not collected in substantial numbers in large still-water habitats or inundated ephemeral floodplain habitats; continuity and integrity of flowing water habitats appears more important. A notable example is the silver perch population between Torrumbarry and Euston weirs on the Murray River. This is likely the most robust silver perch population in abundance and age structure in the Basin (Mallen-Cooper and Stuart 2003) and it is in the longest (427 km) continuous flowing water habitat in the Basin (Figure 3) (Mallen-Cooper 1996).

Another significant macro-scale process that is directly related to hydrodynamics is dispersal. Dispersal is an important process for all animal populations, enabling distributions to contract and expand as resources and habitats vary among seasons and years. For fish in the Murray-Darling Basin this particularly applies to drought and catastrophic events such as blackwater events and fish kills (Hladyz *et al.* 2011; Whitworth *et al.* 2012). These events can occur over macro-scales and so too does dispersal, which may be of larvae or small proportions of adult populations that are commonly seen moving long distances in most migration and movement studies (Reynolds 1983; Leigh *et al.* 2011) .

Independently of major perturbations, dispersal is also essential for the maintenance of metapopulations - these are genetically linked but spatially separated sub-populations. Low numbers of fish disperse between sub-populations and maintain genetic heterogeneity and fitness of the larger metapopulation.

A specific case of dispersal is the upstream migration of immature golden perch and silver perch, yearlings and older (Mallen-Cooper and Stuart 2003), which is to counter their downstream drift as larvae. These fish migrate upstream, like the adults, potentially in response to increase in water velocity, turbulence and depth caused by increasing discharge. Juvenile golden and silver perch respond to small pulses of flow and maintaining these flows over a macro-scale enables these fish to redistribute along the river, resulting in less competition and greater growth and survival.

The scale of migration in these species and the mechanism of larval drift emphasizes the need to consider macro- or riverscape scale hydrodynamic patterns and to ensure connectivity and continuity of these hydraulic features.

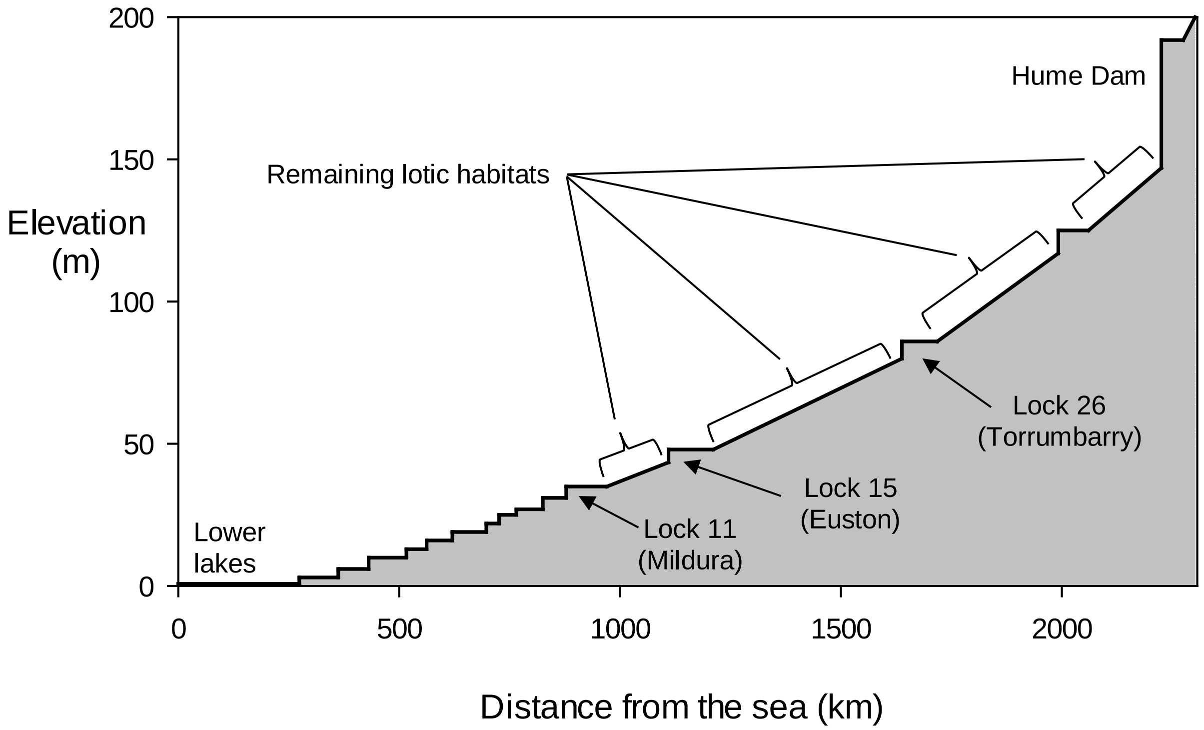

Figure 3. Profile of the Murray River showing weir-pools and remaining flowing water habitats in the main channel at low and regulated flows (<10,000 ML d^{-1}). At high flows (>50,000 ML d^{-1}) the weirs from Lock 26 downstream are removed and the channel becomes an entirely flowing-water habitat downstream to the lower lakes.

3 IMPACTS ON HYDRODYNAMICS

3.1. The natural river channel

As hydrodynamics are determined by discharge and the physical template of the river any changes to these has impacts on hydraulic complexity. Weirs provide the most profound impact as these transform the habitat of a river from flowing water to still-water. Hydrodynamic modelling (1D) of the Murray River channel between Lock 5 and Lock 7 shows that under natural conditions the river channel was hydrodynamically complex, with high channel velocities (0.4 to 0.8 m/s) and meso-scale variation, even at relatively low flows (e.g. <10,000 ML/d) (Figure 4). Under present conditions with the weirs and locks, the river is a slow-flowing (0.05 to ≤0.3 m/s) generally still-water habitat (Figure 4) and needs a discharge greater than 15,000 ML/d to achieve hydrodynamic complexity similar to 7,000 ML/d under natural conditions.

Prior to regulation of flows in the Murray River there was pulse of increased flow every spring. In drought conditions in the lower Murray the pulse was at least 8500 ML/d every year and 25,000 ML/d in any two years (e.g. Figure 5), creating increased hydrodynamic diversity and flowing water conditions along the entire river channel. This was a regular, seasonal ecohydraulic feature of the Murray River that occurred over a riverscape scale, and to which fish and other aquatic biota are adapted.

Research on golden perch in the lower Murray River has shown that spawning and recruitment (survival of young) occurs in spring/summer when there are riverscape scale flows greater than 15,000 ML/d (Zampatti and Leigh 2013). The flow directly correlates with the weir-pools in the lower Murray becoming flowing water (> 0.17 m/s) for their entire length (Figure 6).

In addition to the seasonal pulse of increased hydrodynamic complexity, under natural conditions there were also flowing water refugia at low flows. Hydrodynamic modelling suggests that 20% of the river channel was flowing water (> 0.17 m/s mean channel velocity) under ‘natural’ flows of 1,000 ML/d (exceeded 99.9% of time). These results are consistent with early descriptions of the lower Murray River including those of the explorer Charles Sturt who described pools and “rapids” at low flows (Sturt 1833). Under natural conditions the lower Murray River provided permanent flowing water spawning, recruitment and refuge habitats.

There is no hydrodynamic complexity without flow and intuitively reduced flows due to river regulation should have reduced hydrodynamic complexity. This is certainly true where naturally low flows have been reduced creating more pool habitats, but if these flows have not been affected the impacts on hydrodynamics in a natural channel are much less than expected. The modelling of the Murray River channel without weirs at various flows shows that hydrodynamics remain complex with predominantly flowing water habitats from 5000 ML/d upwards, including at bank full and flood flows. This is because it is the river gradient and channel morphology that determine meso-scale hydrodynamics; increasing discharge increases mean channel velocity slightly but it mainly increases depth while maintaining the

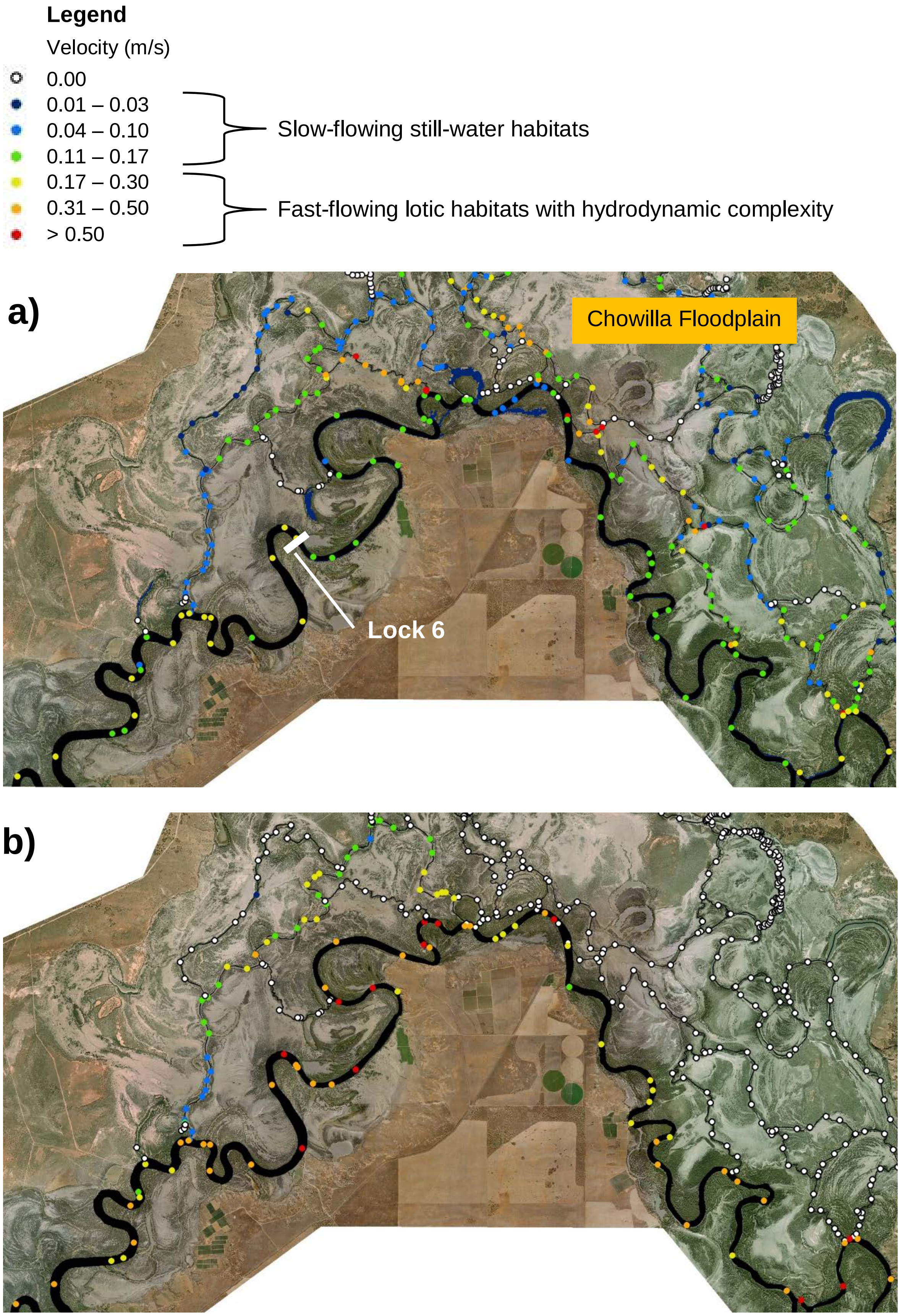

Figure 4. Hydrodynamic modelling (1D) of the Murray River and Chowilla anabranch at 7000 ML/d with a) Lock 6 present and b) with no locks and weirs.

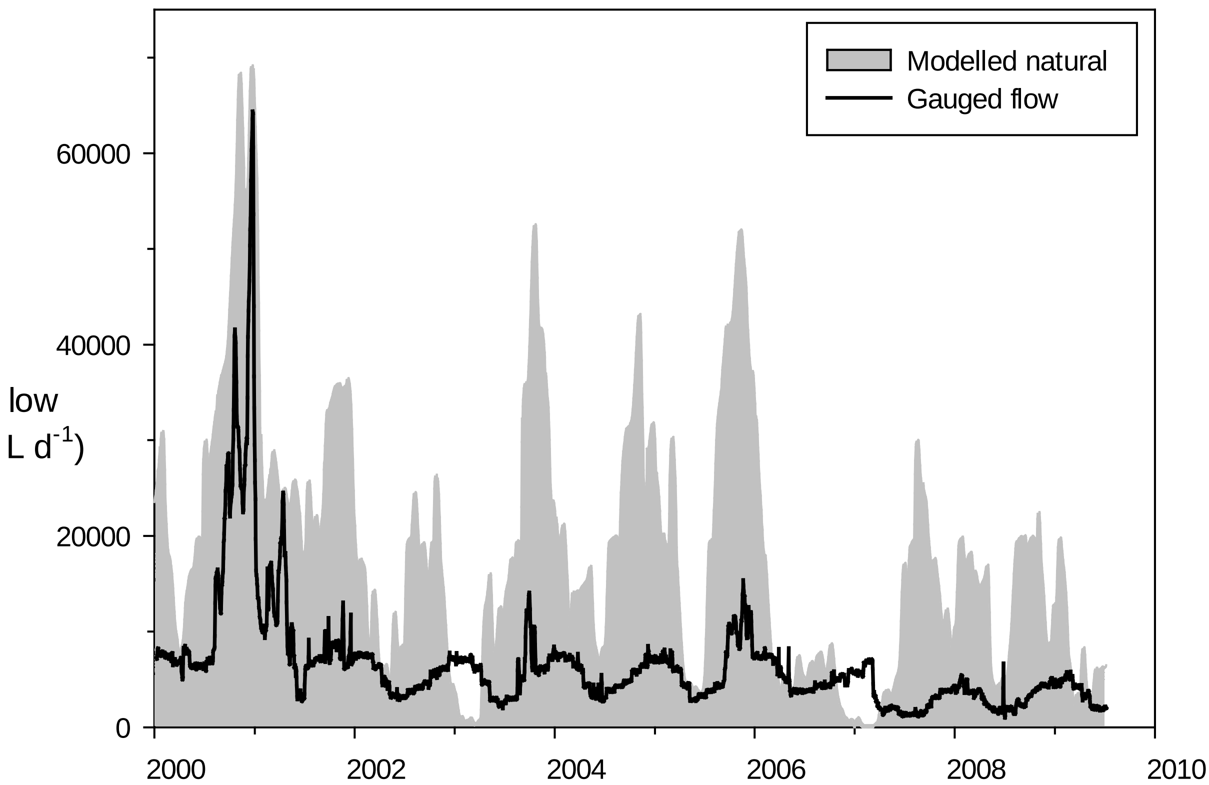

Figure 5. Comparison of gauged and natural daily flow in the lower Murray River (SA border) in the recent Millenium Drought (Zampatti and Leigh 2013).

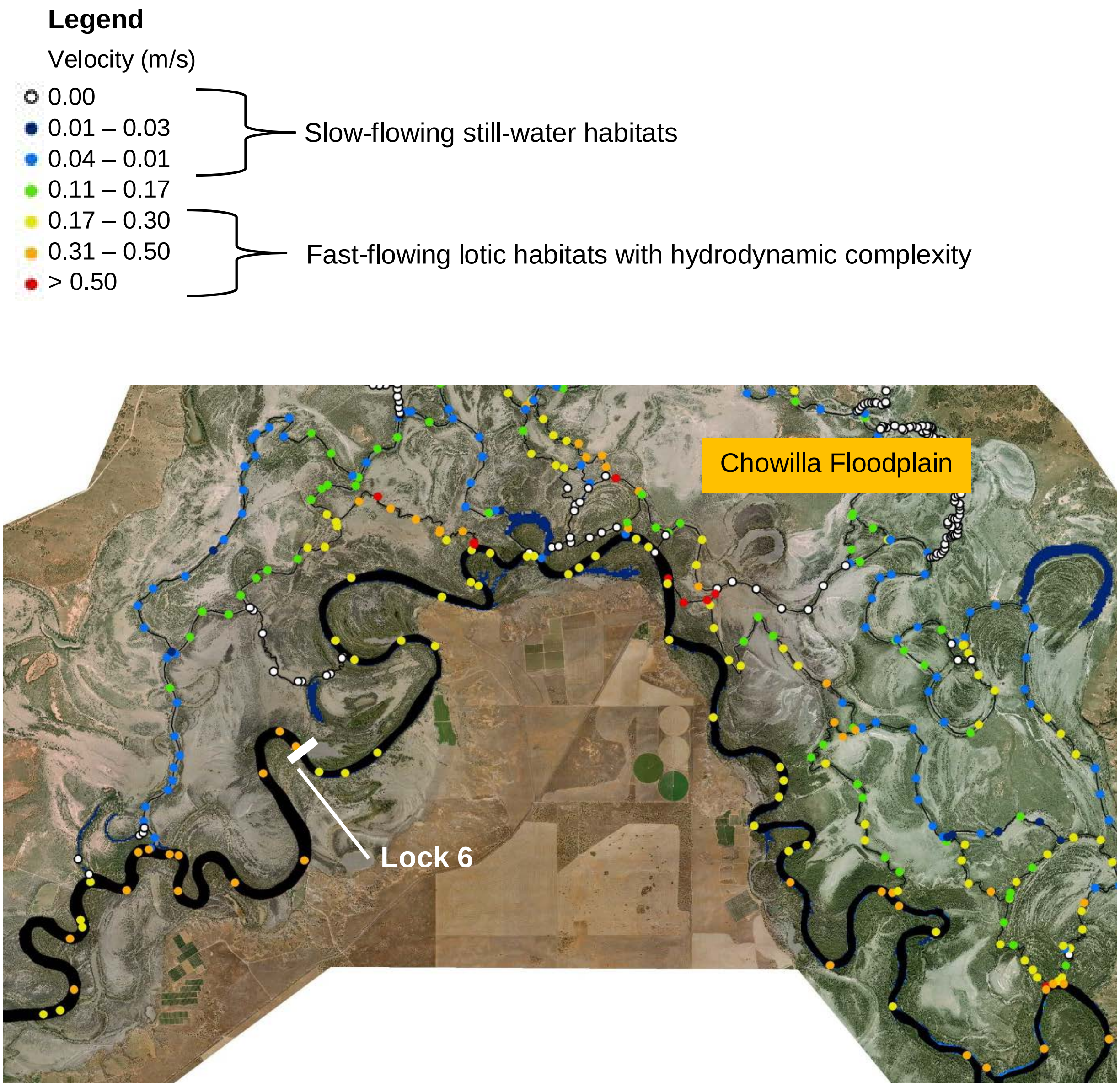

Figure 6. Hydrodynamic modelling (1D) of the Murray River with 15,000 ML/d under present conditions with the weirs and locks. Note that the entire river channel is flowing water (>0.17 m/s).

hydraulic characteristics. Hence, within the very broad range of flows impacted by river regulation, hydrodynamics would be little affected if the weirs were not present.

While acknowledging that floodplains have degraded due to reduced flooding frequency, the impact of weirs on river ecology is probably underestimated. The radical impact on hydrodynamics of the lower river, rather than the change in discharge, is much more likely to be the major cause of the extinctions from the lower Murray River of trout cod, Macquarie perch, Murray crayfish and river snail (Walker 1985; Reid *et al.* 1997).

In reaches that have increased summer flow due to regulation, such as downstream of Yarrawonga Weir and downstream of major dams in NSW and Queensland, the hydrodynamics also change. Mean channel velocities are higher in a season when they would naturally be lower and consequently low velocity zones associated with littoral margins are compressed. There is little hydrodynamic data on this or the impacts on fish ecology but these reaches may need higher than natural roughness (e.g. more large woody debris) and more slackwaters to compensate for the loss of low velocity areas (Humphries *et al.* 2006.

Sedimentation of rivers has a direct impact on hydrodynamics, smothering complex substrates (e.g. gravels, cobbles and rocks), and reducing the depth and frequency of refuge pools (Bond and Lake 2005; Lintermans 2005). In the Murray-Darling Basin, "60% of river length has sediment and nutrient loads in excess of 20 times the natural load, and 20% have deposits of sand that degrade bed habitat" (Prosser *et al.* 2003). Early navigation charts (1897-1908) for paddle steamers on the Murray River had extensive areas of rocky habitats and variation in channel width, (Figure 7), which are features that produce complex flowing water habitats. The rocks have either been submerged by sediment or are permanently inundated by weir-pools; in both cases losing their value in maintaining flowing water complexity. Desnagging has also had a major impact, reducing hydraulic roughness and complexity.

Altered discharge has changed channel morphology influencing not only hydrodynamics but other ecosystem processes. In the Darling River, within-channel benches are a common geomorphic feature, shaped by regular flow variation (Sheldon and Thoms 2006). These serve as terrestrial carbon stores (mainly *Eucalyptus* leaves) and each spring or summer an increase in flow promotes a pulse of carbon with a corresponding increase in productivity (Francis and Sheldon 2002). These within-channel benches in the Darling River have become less diverse through flow regulation (Sheldon and Thoms 2006) and similar benches in the pre-regulation lower Murray River have been lost due to the weir-pools (Thoms and Walker 1993).

Connectivity of hydrodynamics at the meso- and macro-scale directly affects the life cycle of fish. For example, adult Murray cod readily utilise weir-pool habitats but need access to flowing water habitats for optimum spawning sites which provide a greater chance of larvae survival. At low and moderate flows the still-water habitat created by weirs fragments flowing water continuity along the river and potentially impacts on larval drift. This impact is particularly significant in low gradient rivers, such as the Murray and Darling rivers where weir-pools typically extend for 20-100 km (Thoms and Walker 1993). Indeed the lower Murray is characterised by a contiguous series of weir pools that extend for over 800 km.

Lateral connectivity between channel and off-channel habitats is also affected by regulating structures, and contemporary approaches to artificial floodplain inundation (e.g. ‘environmental’ regulators and associated blocking banks) may fundamentally alter the hydraulics of overbank flows These reduce flowing water habitats and hydrodynamic complexity of these habitats in high flows, thereby desynchronising river-floodplain hydrodynamics. To explain further, in natural floods there are flowing water habitats both in the channel and in floodplain anabranches and flood-runners, but wetland/floodplain regulators control flow and reduce flowing water habitats on the floodplain while flowing water habitats remain in the river channel (Mallen-Cooper *et al.* 2011).

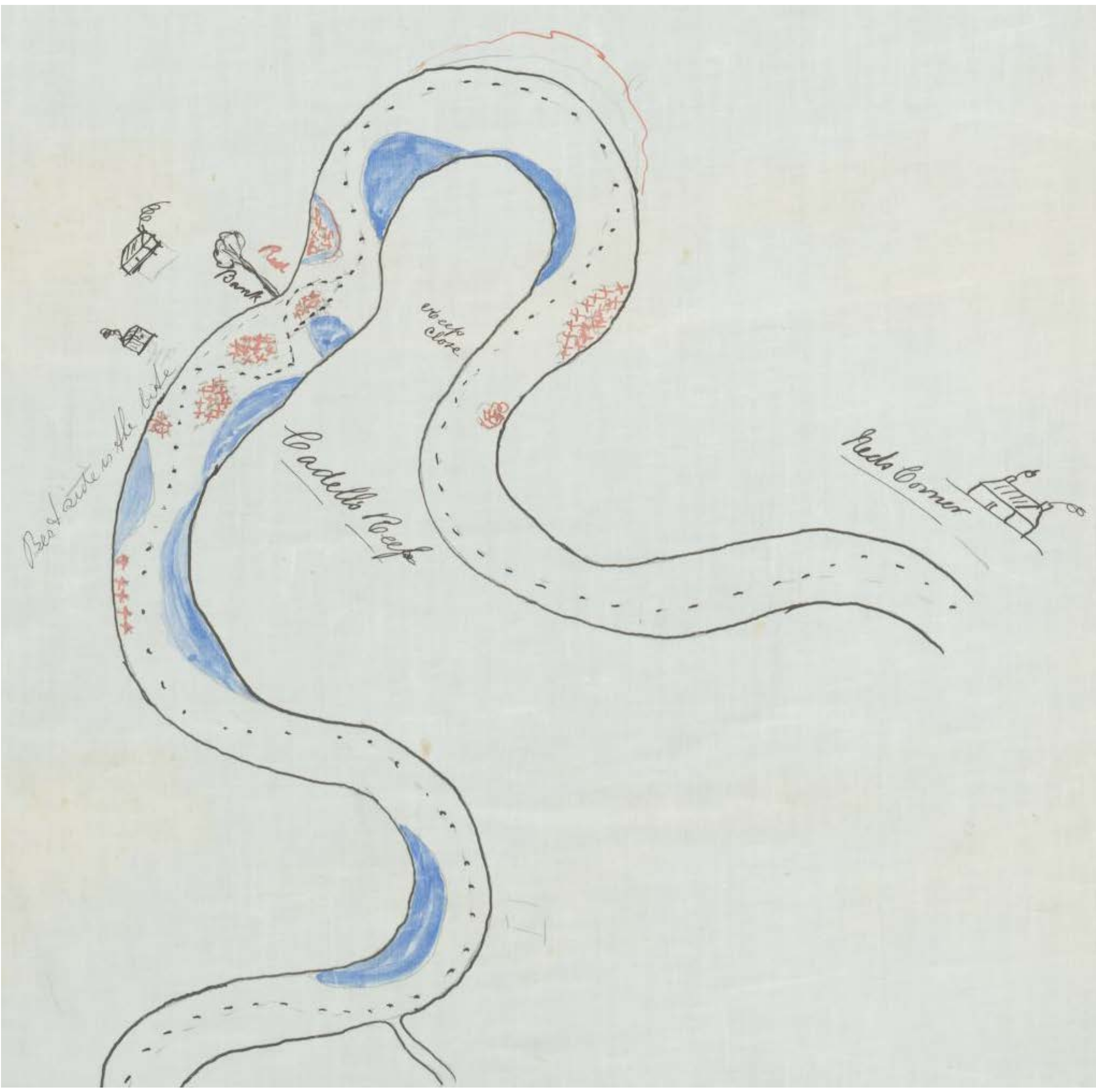

Figure 7. Navigation chart of the Murray River from 1897-1908, prior to the advent of locks and weirs (Anon. 2003), in the region now constrained by Locks 8 and Lock 9, showing rocks, a “reef” and variation in channel width, which would all contribute to flowing water habitat with hydraulic complexity.

3.2. Permanent wetlands

Regulation of the Murray River by dams and weirs has had two significant impacts on the ecohydrology of floodplains. Firstly, storage and regulation of flows has reduced the frequency and duration of floodplain inundation. This is well-documented and contemporary mitigation strategies aim to restore large-scale inundation using infrastructure and environmental flows, which is the basis for most of the Living Murray (TLM) floodplain regulator projects. Secondly, weirs in the lower Murray have caused wetlands that were once of variable size, permanency, and connectivity to the main channel; to become large, permanent and connected to the main river. The management response to artificial perennial inundation has been to use regulators to wet and dry these wetlands (Jensen 2002).

These two mitigation strategies generally overlook a specific ecological niche of diverse permanent wetlands not connected to the river in low flows. Under natural conditions a regular spring pulse (Figure 5) would top up low-lying wetlands as well as ephemeral anabranches which had permanent pools that became wetlands when flow ceased. The anabranches are now either permanently flowing or dry due to block banks at their inlets.

Permanent wetlands, with variable water levels, are key habitats of at least three *wetland specialist* species in the southern Basin: southern pygmy perch, southern purple-spotted gudgeon and flat-headed galaxias. In some cases the small size of the wetland likely excludes large predators such as golden perch and Murray cod and reduces competition with other species.

Contemporary floodplain and wetland rehabilitation strategies in the Murray-Darling Basin broadly consider the natural flow paradigm, often with a large emphasis on ephemerality and minimal consideration of connectivity. Management of wetland and floodplains needs to further consider the spectrum of permanency, variation in size and connectivity with the river. Nevertheless, due to the extent of regulation of overbank flows in the Murray River, application of the natural flow regime where possible on a site-by-site basis is unlikely to reinstate these lost habitats and their ecological role as refugia for metapopulations. There are, however, opportunities to create these habitats within the present river system and these are discussed in Section 5.

3.3. Refugia in intermittently-flowing rivers

Many rivers in the Murray-Darling Basin have naturally intermittent flow regimes. These include rivers in the southern Basin, such as the Campaspe, Avoca and Lachlan and numerous northern Basin rivers. The extent of intermittency varies from a small proportion of the time (e.g. 5% of the time in the Darling River) to being a regular and dominant ecohydrological feature (e.g. 50% of the time in the Warrego River); the latter are arid zones rivers and have fish species that are *intermittently–flowing arid river specialists*.

One of the major impacts in rivers across the Basin is sedimentation from land clearing (Olley and Scott 2002; Prosser *et al.* 2003). Sedimentation can completely fill refuge pools and across a catchment the frequency and depth of these pools is reduced. In the absence of adequate refuge habitats, applying a natural flow regime that includes very low or zero flows may prove detrimental to aquatic biota thus reducing the ecological values of the stream..

3.4. Short-term variations in depth

Short-term (daily or hourly) variations in depth is a very specific hydraulic and hydrodynamic characteristic, which is directly related to discharge. Under natural conditions the low-gradient lowland rivers of the Murray-Darling were buffered from short-term variations in discharge and depth. Under regulated conditions any part of the river system that has actively regulated flow can have widely varying short-term fluctuations in flow as river operators release water to meet downstream demands. In the Murray system this includes the Darling River between Menindee and the Murray junction, the Murray downstream of Yarrawonga and Torrumbarry weirs, and the tail waters of weirs in the lower Murray River (i.e. downstream of Lock 11). In the broader Basin, it includes all rivers downstream of major dams and most low level regulating weirs in irrigation regions.

Short-term variations in depth and discharge are usually contained within the river channel and occur over hours or days. They can cause species that have parental care of eggs, which includes freshwater catfish, Murray cod, trout cod and river blackfish, to abandon their spawning sites or nests (Rowland 1998). As these fish spawn only once a year, the impact is for the entire spawning season. Short-term variations in depth and discharge may also occur under natural conditions with local rain but river regulation has greatly increased the frequency of these events. Significantly, most measures of the impacts on hydrology, including the Sustainable Rivers Audit (Davies *et al.* 2010), use monthly flows or rarely examine changes to daily fluctuations, thereby underestimating this impact on hydrodynamics and fish populations.

4 CASE STUDIES OF SPECIES

The following three case studies of threatened fish species demonstrate how the interactions of discharge, hydrodynamics, habitat and connectivity determine sustainable populations; and how this does not always conform to the Natural Flow Paradigm.

4.1. Trout cod

Trout cod (*Maccullochella macquariensis*) is a large-bodied (850 mm max.) threatened species. Its distribution originally extended into the lower reaches of the Murray River in South Australia (Stead 1929) where it is now extinct. The natural range has contracted from approximately 1500 km of the Murray River to a 350 km reach from Yarrawonga Weir to downstream of Torrumbarry Weir (Koehn *et al.* 2008; Douglas *et al.* 2012).

Surprisingly, for the habitat of a threatened species, this reach has highly regulated flows with reversed seasonality; winter and spring flows are suppressed because they are captured in dams upstream, and summer flows are higher than natural because of releases for irrigation downstream (Close 1990; McMahon and Finlayson 2003). Despite these unfavourable hydrological conditions the reach has 270 km of permanent, continuous, flowing water habitat downstream of Yarrawonga Weir which includes hydrodynamic diversity and extensive large woody debris (Koehn *et al.* 2004).

In the lower Murray River, where the species is extinct, the natural seasonality of flow is retained and the impact of river regulation on summer flows is much less (Maheshwari *et al*. 1995). Regulated flows are higher than natural flows for the very low flows (<1200 ML/d; 99.5% exceedance, natural) but similar for other low flows (1200-3500 ML/d; 99.5 – 95.0% exceedance, natural) and less than natural for higher flows. The far greater impact has been the complete loss of main channel flowing water habitats and hydrodynamic diversity at low to moderate flows, caused by contiguous weirs (Figure 3). Hence, hydrodynamic diversity rather than flow, per se, appears to be the most likely cause of the loss of this species from a large part of its original habitat.

4.2. Murray cod

Murray cod (*Maccullochella peelii*) is a large-bodied (1500 mm max.) threatened species with a wide distribution in the Murray-Darling Basin. Recruitment and strong year classes are associated with riverscape scale flooding (Rowland 1998; Ye and Zampatti 2007). Interestingly, spawning and recruitment have also been recorded at the meso-scale in the Mullaroo Creek-Lindsay River system and the Chowilla Creek system in the lower Murray River. Both sites are anabranches that were originally ephemeral channels and now have permanent flow due to weir-pools in the main river channel. The key characteristics of both sites are they have permanent flowing water habitats with complex channel morphology and large woody debris which produces hydrodynamic complexity including slow-flowing slackwaters and littoral zones. These features are combined with physical connectivity so that fish can move relatively freely between the anabranches and river, although the

Chowilla system has weirs on some creeks which are presently being addressed with fish passage. Importantly, consistent recruitment of Murray cod was evident in the flowing water habitats of the Chowilla system during the Millennium Drought (2001–2010) when recruitment was minimal in the predominantly still-water main channel habitats of the lower River Murray (Zampatti *et al*., 2014).

Another anabranch system, Gunbower Creek, which is used for irrigation has some hydrodynamic diversity but the flow is reduced in winter so there are no permanent flowing water habitats and several weirs fragment physical and hydraulic connectivity (i.e. lotic continuity broken by weir-pools). As a result, it has very poor Murray cod populations as well as poor populations of other large-bodied native fishes.

The habitat features of the Mullaroo and Chowilla systems, especially the hydrodynamic complexity, reflect the habitats of the main channel of the Murray River prior to the advent of locks and weirs. These anabranches now serve a critical role as flowing water refugia in droughts. Applying the Natural Flow Regime – by drying these habitats out in summer – would result in the loss of this ecosystem function which was previously provided by the main river channel. This example also demonstrates the flexibility of native fish in that they will colonise new habitats if their life cycle requirements are met.

4.3. Southern pygmy perch

Southern pygmy perch (*Nannoperca australis*) is a small-bodied fish (< 80 mm) that in the lower Murray River is only known from populations in Lake Alexandrina and its immediate catchment. The population of southern pygmy perch on Hindmarsh Island is located in permanent slow-flowing creek habitats that receive water from Lake Alexandrina and drain to the estuary. Flow through the creeks have been kept artificially consistent since the barrages stabilized lake levels in the 1940s - although in the Millennium Drought lake levels fell below sea level and these fish were rescued from drying habitats (Hammer *et al.* 2013).

The creeks have high densities of aquatic vegetation and low discharge so that suspended solids tend to settle and the water is clear in contrast to the turbid water of the lake and Murray River. Fluctuations in lake levels due to wind seiching varies flow through the creeks and promotes aquatic macrophyte diversity and growth. Southern pygmy perch is found in creeks and off-channel habitats (small wetlands) in northern Victoria that have unregulated flow and hence, follow the Natural Flow Paradigm. The creek habitats on Hindmarsh Island, under natural conditions, would likely have flowed intermittently as fluctuating lake levels would have exposed creek inlets. The changes to the flow regime appear not to have affected this population because key habitat attributes remain, including the predominantly still-water hydrodynamics.

The closely related Yarra pygmy perch (*Nannoperca australis*) provides another useful example of flow and habitat. It was also rescued from drying habitats in the last drought and placed in artificial refugia, which were well vegetated farm dams. In one case the species spawned and expanded in population size 20 times (Hammer *et al.* 2013), demonstrating that fish are flexible about location if their habitat requirements are met and for some species this may be unrelated to the historical flow regime at the site.

4.4. Summary

Each of the case studies above can be summarised thus: fish are flexible about location but demanding about habitat and hydrodynamics. As scientists and managers we tend to view the present distribution of native fish as a relic or contraction of their original distribution. At a catchment scale that is true but at a meso-scale it is also a function of changes to the riverscape and in some cases fish are present and thriving in locations where they were potentially absent prior to regulation. Essentially this emphasizes: i) the flexibility of native fish, in that they can colonise new habitats, and ii) that, in some situations, directly applying the natural flow regime may be detrimental to the present river ecology. These case studies also highlight that hydrodynamics, integrity of flow, connectivity and habitat are interrelated features essential for sustainable fish populations.

The case studies do not preclude that regulated hydrology has impacted these species, or other fishes, but they broaden the perspective that discharge alone may not be the greatest impact on fish and aquatic habitats; and environmental flows (i.e. hydrological restoration) alone may not deliver the intended benefits without considering broader life history requirements.

5 DISCUSSION – IMPLICATIONS FOR FLOW MANAGEMENT

5.1. Themes

From reviewing the applicability of the Natural Flow Paradigm to aquatic ecosystem restoration in the MDB several themes emerge that are directly applicable to flow management:

1. Fish life cycles are directly linked to hydrodynamic complexity, particularly still-water and flowing water habitats, which can be independent of discharge.

2. Many fishes in the MDB are flexible about location and will thrive given the appropriate habitat and hydrodynamics.

3. Hydrodynamic complexity has been grossly reduced in the Murray River and other rivers in the MDB, through weirs creating still-water habitats, removal of large wood, sedimentation reducing depth and covering substrate, and wetland management adopting broad wetting/drying regimes.

4. Flows need to be managed at spatial scales that match the life cycles of fish. Hence, flows specifically need to be managed at the meso- (100s m to 10s km), and macro or river-scale (100s of km).

5. The temporal scale of flows at a monthly or seasonal scale is well understood but flow also needs to be managed to minimise daily variation, particularly in reaches that are used as conduits for irrigation supply.

6. In highly modified catchments and river systems, restoring the natural flow regime or aspects of it, may not always be conducive to positive ecological outcomes and can, in some cases impact negatively on conservation values.

7. Viewing flow in terms of discharge and hydrodynamics provides a range of new opportunities for river rehabilitation.

5.2. Opportunities

Rehabilitation of natural flow regimes on a local and regional scale is often a common goal of river rehabilitation and divergence from pre-regulation hydrology is used as a measure of impact. The comprehensive Sustainable Rivers Audit which included assessments of flow, macroinvertebrates and fish, assessed the hydrological impacts of regulation on rivers in the Murray-Darling Basin by various measures of deviation from a modelled natural condition (Davies *et al*. 2008). These measures are useful to broadly assess and compare rivers, and they have a direct bearing on impacts to fish populations. Holistic methods of estimating environmental flows are also underpinned by the Natural Flow Paradigm (Arthington *et al.* 2004). From a management perspective, the logical interpretation of these assessments of hydrological data is that *incrementally changing flows, or parts of the flow regime, to be closer to natural will improve the health of aquatic ecosystems*; this has become a dominant rehabilitation paradigm for aquatic ecosystems of the Murray-Darling Basin.

The paradigm, however, has constraints. Firstly, flow regimes in rivers regulated for consumptive use can seldom be returned to natural - except for the application of zero and very low flows - because of competing demands for a finite resource. This then raises the issue whether the incremental restoration of aspects of the flow regime are actually enough to achieve a threshold to improve the ecosystem health. Secondly, in many cases geomorphology and hydrodynamics have been fundamentally altered due to changes in discharge, sediment, weirs and desnagging. Restoring a more natural hydrological regime in these conditions may not necessarily make any ecological improvements. For example, restoring ‘natural’ low flow periods in ephemeral rivers may be harmful to fish populations if deep refugia pools are absent due to sediment, whilst increasing discharge in the contiguous weir-pool environments of the lower Murray may be insufficient to create flowing water and associated hydrodynamic complexity.

Overlaid on these constraints of hydrological restoration are habitats and connectivity. Rehabilitation of riverine habitats often involves re-snagging and riparian re-vegetation but there has been less emphasis on the substrates of littoral and benthic zones (e.g. cobble substrates and riffles). The issue of connectivity for fish is well-known and is being addressed through fishway construction in the MDB (Barrett and Mallen-Cooper 2006) but broader ecosystem connectivity, such as macro-scale hydrodynamics and carbon transport, are often overlooked.

We suggest these factors can be integrated into an expanded view of river rehabilitation in the MDB, which presents new opportunities for optimising ecological values at a regional scale.

Rather than seek to recreate natural flows on a site or reach scale, we suggest pooling the hydrodynamic features that occurred under natural conditions at different scales (micro, meso and macro) within a region; and recreate/optimise the features that have declined. Significantly, this approach would not be based on recreating past hydrodynamic features of particular sites or locations but recreating the habitat at an appropriate scale where possible within the whole river, independent of past hydrological or hydrodynamic history, acknowledging that fish are flexible about location and will thrive under appropriate habitat conditions. In many cases this does not require additional discharge.

Such an approach would also pool ecological values (e.g. spawning habitat and fish nursery areas) and examine the optimum potential outcome for the whole regulated reach or system while integrating the spatial scales of fish life cycles This accepts that some changes to the river system are permanent if there are shared users of the river, and that some areas can serve a more productive ecosystem role by adopting a new function (e.g. spawning area) rather than returning to a previous more-natural state.

The philosophy differs from the more traditional approach of returning locations within the ecosystem to as close to perceived natural conditions as possible. The rationale is that more can be achieved on a regional scale by utilising the potential of the creeks, wetlands, floodplains and irrigation systems to serve various ecosystem roles that have declined or been compromised.

The example that illustrates this most effectively are the permanent flowing water habitats created in anabranches of the lower Murray River as a result of the construction of weirs; these habitats presently support significant regional populations of Murray cod in an area where main-channel populations of Murray cod continue to decline.

5.3. Applications

5.3.1. Integrate hydrodynamic objectives into flow management

Management of flow for the environment and consumptive use, by necessity, concerns volumes and discharge. Incorporating hydrodynamic objectives into flow management would enable interpretation of the direct effect of flow on habitat for aquatic biota. For example, reaching a mean channel velocity for a given flow would to some extent describe flowing water habitats. Importantly, real-time data on velocity is potentially available through all stream gauges. Hydrologists use stream cross-sections of velocity to produce a stage (river height) and discharge relationship; hence, as gauge height is used to estimate discharge in real time it can also be used to estimate current velocity.

Inundation of instream riverine benches would also be a useful hydrodynamic objective (e.g. depth, inundation and duration) if a carbon and productivity pulse was the ecological objective. Providing hydrodynamic objectives regarding short-term (e.g. hourly and daily) fluctuations in depth would aid the management of species such as Murray cod that exhibit parental care of eggs and larvae..

Environmental flows are overlaid on the existing physical template of the river. Although it is often acknowledged that changes to the physical template of the river have occurred, integrating explicit hydrodynamic objectives would: i) re-emphasize the value of physical habitat, and ii) provide the opportunity to assess the potential to rehabilitate the physical template (e.g. rock, cobbles, large woody debris, snags, deep holes, lowered weir-pools) to achieve greater hydraulic complexity and potentially improved biodiversity with an equivalent discharge.

5.3.2. Integrate changes in hydrodynamics into river health assessment

Hydrodynamics determine ecosystem process (e.g. the transport of nutrients and propagules) and habitat for a range of aquatic biota including fish, crustacea, mussels, snails, other macroinvertebrates, and biofilms (Walker 1985; Sheldon and Walker 1989; Sheldon and Walker 1997; Sheldon and Walker 1998). The impacts of changes in hydrodynamics, such as weir-pools, sedimentation and short-term fluctuations in discharge and depth constitute significant aspects of river health. The SRA had planned a *Physical Form* theme which would have examined sediment and channel changes (Davies *et al.* 2010). We suggest that river health assessments could be expanded to include some of these aspects with existing data. The impact of weirs (>3,000 in MDB) and loss of flowing water habitats can be assessed using existing physical data on weir heights and river gradients while short-term fluctuations in depth can be assessed using existing hourly or daily hydrological data.

5.3.3. Incorporate 'integrity of flow' as a value in flow management

Hydrologic connectivity is the water mediated transfer of material, energy and organisms within and among components (e.g. channel, floodplain and aquifer) of an aquatic ecosystem, and is fundamental to ecosystem function. We use '*integrity of flow*' here to refer to the continuity and connectivity of flow both *longitudinally* and *laterally*.

Longitudinal integrity of flow is the maintenance of connectivity along river channels, yet in rivers with highly variable flow regimes, such as the Murray River, regulation for consumptive use disrupts longitudinal integrity to the detriment of ecosystem function. We propose that the maintenance of longitudinal integrity of flow is crucial to optimise ecological benefits in the rivers in the MDB. For example, stream flows that originate from rainfall and are allowed to pass unregulated downstream have greater ecological value than flows from storages or flows that are re-regulated en route. The greater the river length of uninterrupted flow the greater the *longitudinal integrity* and the ecological value.

Lateral integrity of flow is the extent that flow in the floodplain is synchronised with flow in the river and with other regional floodplains. Wetlands in the MDB are commonly managed in a compartmentalised manner with hydrological objectives (e.g. wetting and drying regimes) determined at the site scale and water delivered via regulators independently of the riverine hydrograph. The approach is partly a practical response to reduced discharge but also a reflection of jurisdictional boundaries in natural resource management. This management approach would appear to conform to the tenets of the Natural Flow Paradigm but the aim of restoring ecosystem processes is contradicted by compartmentalising flow objectives that separate the river and floodplain.

Incorporating *lateral integrity of flow* as a value in flow management would place greater value on restoration of ecosystem processes and may encourage more coordinated flow management. An example of applying this concept would be to fluctuate water levels in wetlands in the lower Murray by a coordinated lowering and raising of locks and weirs. *Lateral integrity* would best be integrated with *longitudinal integrity* by coordinating lowering with low river flows and raising with higher river flows (Figure 8).

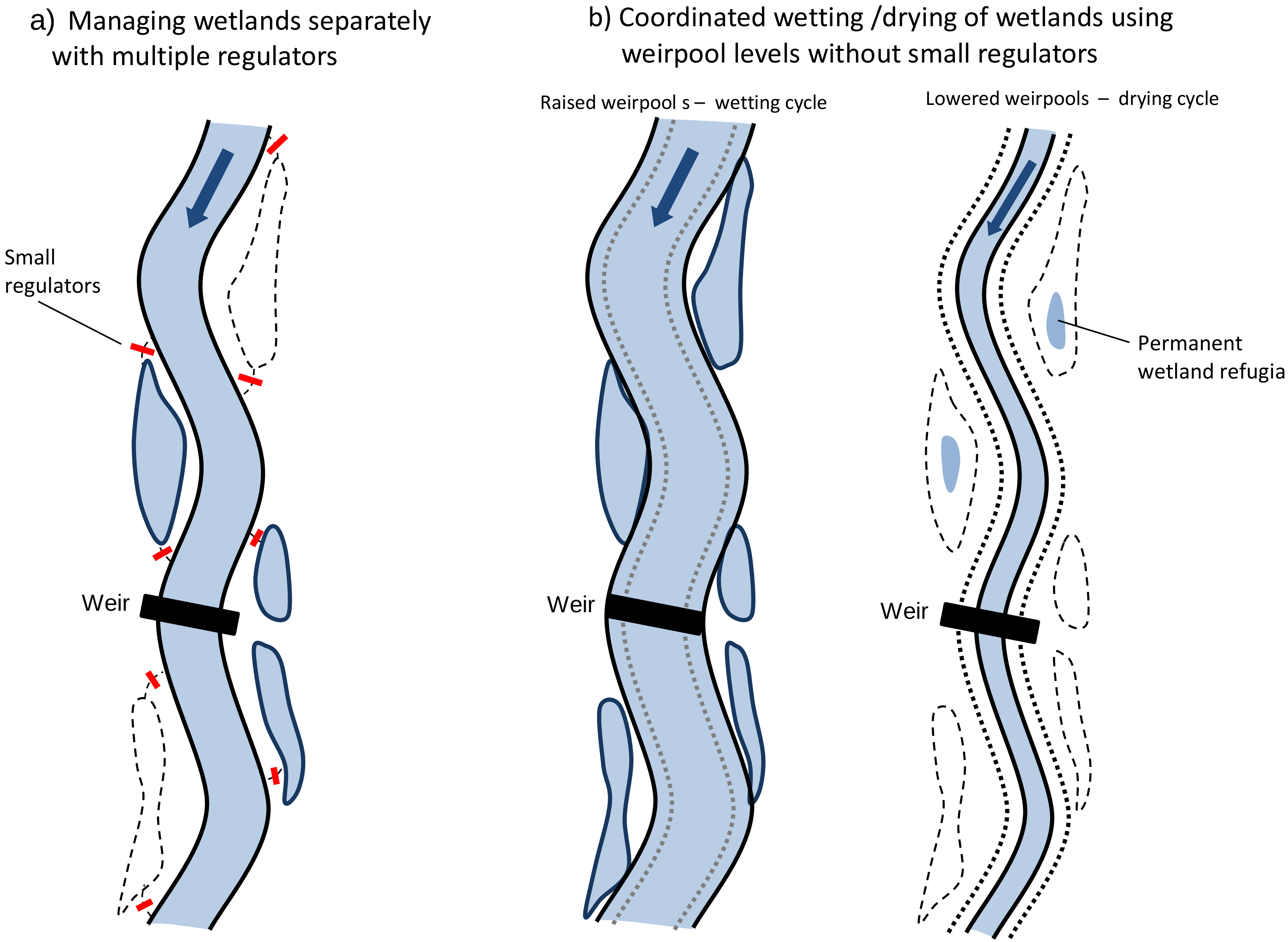

Figure 8. Conceptual diagram of the lower River Murray wetlands: a) under present management using multiple regulators, and b) applying *lateral integrity of flow* by coordinating lowering and raising of locks and weirs to wet and dry wetlands.

5.3.4. Incorporate irrigation areas and storages as functional components of the river ecosystem

Irrigation areas and lowland off-stream storages (e.g. Kow Swamp, Lake Victoria, Lake Cargellico, Lake Brewster and the Menindee Lakes) have traditionally been seen as having lesser conservation value than less regulated floodplain lakes (e.g. Paroo floodplain, Narran Lakes). These storages typically receive a large proportion (>50%) of riverine flow during periods of regulated in-channel flow. Given that almost all riverine fish in the MDB (e.g. *channel specialists* and *generalists*) have larvae that drift and that the season of drift overlaps directly with the irrigation season, substantial proportions of drifting larvae would be diverted into irrigation canals and off-stream storages (O'Connor *et al.* 2008).

Irrigation systems and storages potentially represent major 'sinks' for native fish. They often have good structural habitat (e.g. large woody debris, littoral macrophytes), but connectivity is often poor because of water delivery infrastructure (i.e. regulators and weirs). The hydrology and operation of these systems is at odds with the Natural Flow Paradigm; but the opportunities to utilise these artificial systems to enhance native fish populations are extensive. Significantly, they can be operated to improve ecological values with little compromise in water delivery function. Actions include maintaining winter flow, enhancing flowing water habitats, suppressing short-term variations in flow and providing fish passage, either through regulator management or fishways.

These and other actions are presently being investigated for the Gunbower region and Torrumbarry Irrigation District as part of a 'Sustainable Irrigation – Native Fish Recovery Plan' (Mallen-Cooper *et al.* 2014). If the plan is supported and funded the region would not only have improved biodiversity but would have a new ecosystem role as a refuge for threatened species from major perturbations such as droughts, large–scale blackwater events in the main river and climate change. In this case the Natural Flow Paradigm is less relevant than the new habitats that can be created and maintained at the meso-scale, enabling the region to provide critical habitats and support ecological functions that are now absent from the main river channel.

Other similar regions that have high potential as novel meso-habitats through managing existing flows or operating/modifying infrastructure include the Edwards-Wakool system and Lake Victoria.

5.3.5. Assess in-channel refugia in intermittent streams

In-channel refugia in intermittent streams have been impacted by sedimentation and the application of natural low flows and zero flows may negatively impact aquatic biota. Assessing the specific impacts of changes in geomorphology and hydrodynamics when considering flow recommendations in intermittent streams would be prudent.

5.3.6. Management of weir-pools

Weir-pools represent a pervasive impact of river regulation in the MDB and cause a fundamental change to hydrodynamics by converting flowing water habitats to still-water, and disrupting connectivity. At weirs where upstream water level can be managed by gates or stoplogs, however, two particular restoration strategies manifest:

1) Contemporary weir operation (i.e. use the existing physical template).

   At a Basin level, prioritise environmental flows in river reaches where fragmentation by weirs is less and hence, *longitudinal integrity of flow* is greater. At a reach and site level this may mean using environmental flow only when there is sufficient water to alter hydrodynamics. For example, the lower Murray River regains its flowing water nature at flows > 15,000 ML/d. Consequently, environmental flows of lower magnitude are unlikely to change the ecological outcomes for riverine fish and it may be more effective, if the aim of the flow is to enhance fish populations, to "save" the water until an effective volume can be reached.

2) Changed weir operation (i.e. change the physical template).

   For those weirs where the upstream water levels can be managed there is expanded scope for river rehabilitation. Significantly, lowering weir-pool levels creates flowing water habitats at the upstream end of the weir-pool; in low gradient rivers a small lowering can create a large amount of habitat. For example, hydrodynamic modelling of the Lock 5 and 6 weir-pools showed that lowering the weir-pools by 1.0 m creates an additional 20 km of flowing water habitats. This type of management option would also enable targeted habitat rehabilitation, so that large woody debris and rocky substrates would be located in the flowing water zones. Manipulating weir-pool levels can also be used to coordinate watering of wetlands without the need for wetland regulators, thus maintaining longitudinal and lateral integrity of hydrodynamics.

   Many weirs, including those in the lower Murray River are not used for storage but provide pumping pools for irrigation; lowering weir-pools would not lose this function but would add to pumping costs because the river would be lower. We acknowledge that lowering weir-pools also has a range of issues to consider such as navigation, groundwater levels and salt mobilisation. Nevertheless, the ecological benefits for the riverine ecosystem are considerable and importantly this restoration option uses no additional water.

5.3.7. Establish aquatic reserves based on hydrodynamics, scale and connectivity

The last 15 years of research on freshwater fish ecology of the Murray-Darling Basin has highlighted the importance of hydrodynamic diversity, scale and connectivity in maintaining the life cycles of native fish. One outcome of this work has been to highlight the locations where these conditions presently occur and we recommend that aquatic reserves be established at these locations to highlight their value and enable focused management initiatives. Examples include the Murray River from Torrumbarry to Euston Weir, which is the longest (427 km) uninterrupted flowing water habitat in the Basin; Lindsay-Mullaroo and Chowilla anabranches, which represent flowing water refugia in the lower Murray River, where these habitats have largely been lost from the main channel; and the lower Darling River, which in spring, the main fish spawning season, has flowing water habitats due to a narrow channel and delivery of water to the lower River Murray and Lake Victoria. These examples partly reflect the intensity of work in the southern Basin and further work would be needed to identify relevant habitats in the northern Basin.

5.3.8. Create new habitats

The objective of the Natural Flow Paradigm is to reinstate ecosystem processes, habitats and ultimately biodiversity and ecosystem health. By focusing on these outcomes, management options need not be confined by rigorous adherence to site based restoration of natural flow regimes. Instead regional ecological objectives can incorporate appropriate spatial scale, maintenance and restoration of hydrodynamic and habitat features that have declined, but not necessarily at specific historical locations.

Key habitats that have declined and opportunities to re-establish them include:

Permanent wetlands with variable size and water levels

These are for *wetland specialist* species (e.g. southern pygmy perch). Habitats that can be managed with flow and potentially with weir-pool manipulation include: Barmah and Millewa Forest, Gunbower Forest, Koondrook-Perricoota Forest, lower Murray wetlands (numerous sites),

Flowing water habitats over meso- and macro-scales

These are for c*hannel specialist* species (e.g. Murray cod and trout cod) where recruitment is enhanced by flowing water habitats. Sites where these can be created over a meso-scale include Gunbower Ck-Box Ck-lower Loddon River system, Carrs-Capitts-Bunberoo system near Lock 9, Bookmark Creek near Renmark, and possibly streams in the Edwards-Wakool system. Katarapko Creek near Berri is presently being modified to create more flowing water habitats. <u>In all these sites any additional water that is needed to create these habitats is returned to the main stem of the Murray; the only water used are channel losses en route</u>. A complementary action at these sites would be increasing hydraulic complexity by adding rocky and cobble substrates and large woody debris, which are specific structural elements of flowing water habitats that have declined significantly.

As described in section 5.3.6., main channel flowing habitats can also be restored by lowering weir-pools.

Where possible, flowing water habitats should be connected at the macro–scale during natural or manufactured high flow events. Integral to this is the maintenance of longitudinal integrity by minimising diversion, storage and re-regulation.

In-channel refugia

In some rivers that have extensive sand deposits from erosion there may be scope to create in-channel refugia (Bond and Lake 2005; Lintermans 2005).

6 CONCLUSION

Contemporary flow restoration in the MDB primarily considers the impact of river regulation on flow volume and rate (i.e. discharge) and, following the tenets of the natural flow paradigm, aims to reinstate ecologically significant components of the flow regime. Such approaches, however, seldom consider the hydraulic and hydrodynamic impacts of river regulation and catchment degradation (e.g. sedimentation). Consideration of hydrodynamics, at a range of spatial and temporal scales, is paramount to restoring essential habitats and life history processes for native fish, and for broader riverine ecosystem function in the MDB. We advocate that hydrodynamic restoration is fundamental to restoring ecosystem function in the Murray River and that hydrodynamic objectives should form an integral component of objectives for environmental flow management and river health assessment. In concert there needs to be explicit consideration of connectivity and the longitudinal and lateral integrity of flow.

Restoration of meso and macro scale flowing water habitats in river channels and anabranches with appropriate structural complexity (i.e. large woody debris), should constitute a high priority for natural resource managers in the MDB. Importantly these habitats can be created or restored with minimal additional water and may have substantial ecological outcomes for threatened native fish such as Murray cod, and more broadly for aquatic biota adapted to flowing water habitats (e.g. Murray crayfish). In contrast, adding more water to the existing physical template, particularly in the lower Murray River when flows are contained within the river channel, may have limited ecological outcomes especially for native fish species reliant on hydrodynamic complexity.

The ultimate aim of flow restoration should be to reinstate ecosystem processes and habitats to improve ecosystem health and biodiversity. To achieve this in the Murray River, management options need not be confined by rigorous adherence to site based restoration of natural flow regimes. Instead, regional ecological objectives can incorporate the maintenance and restoration of hydrodynamic and habitat features that have declined, but not necessarily at specific historical locations. Considering appropriate longitudinal and lateral connectivity this facilitates a range of innovative restoration initiatives including creation of new flowing water habitats (e.g. in anabranch systems), novel management of irrigation regions and large off-stream storages, introducing variability in weir-pool levels (particularly drawn down) and establishment of aquatic reserves to protect regions that currently retain meso-scale hydrodynamic complexity and associated significant populations of threatened fish (e.g. Murray cod in the Lindsay-Mullaroo and Chowilla anabranches).

REFERENCES

Anon. (2003) River Pilot Charts of the Murray River, 1897-1908. (Canberra : National Library of Australia)

Arthington, A., Tharme, R., Brizga, S., Pusey, B., and Kennard, M. (2004) Environmental flow assessment with emphasis on holistic methodologies. In Proceedings of the second international symposium on the management of large rivers for fisheries. Vol. 2. pp. 37-65.

Barrett, J., and Mallen-Cooper, M. (2006) The Murray River's 'Sea to Hume Dam'fish passage program: progress to date and lessons learned. *Ecological Management & Restoration* **7**(3), 173-183.

Bice, C., Gehrig, S., Zampatti, B., Nicol, J., Wilson, P., Leigh, S., and Marsland, K. (2014) Flow-induced alterations to fish assemblages, habitat and fish–habitat associations in a regulated lowland river. *Hydrobiologia*, 1-18.

Bond, N.R., and Lake, P.S. (2005) Ecological Restoration and Large-Scale Ecological Disturbance: The Effects of Drought on the Response by Fish to a Habitat Restoration Experiment. *Restoration Ecology* **13**(1), 39-48.

Cadwallader, P., and Rogan, P. (1977) The Macquarie perch, Macquria australasica (Pisces: Percichthyidae), of Lake Eildon, Victoria. *Australian Journal of Ecology* **2**(4), 409-418.

Close, A. (1990) The impact of man on the natural flow regime. In The Murray. (Eds. N Mackay and D Eastburn) pp. 60-74. (Murray-Darling Basin Commission: Canberra, Australia)

Davies, P., Harris, J., Hillman, T.J., and Walker, K.F. (2010) The sustainable rivers audit: assessing river ecosystem health in the Murray–Darling Basin, Australia. *Marine and Freshwater Research* **61**(7), 764-777.

Douglas, J., Hunt, T., and Trueman, W. (2012) Confirmed records of the endangered Trout Cod'Maccullochella macquariensis' from the Murray River at Gunbower Island, Victoria. *Victorian Naturalist, The* **129**(4), 152.

Francis, C., and Sheldon, F. (2002) River Red Gum (*Eucalyptus camaldulensis* Dehnh.) organic matter as a carbon source in the lower Darling River, Australia. *Hydrobiologia* **481**(1-3), 113-124. [In English]

Hammer, M., Bice, C., Hall, A., Frears, A., Watt, A., Whiterod, N., and Zampatti, B. (2013) Freshwater fish conservation in the face of critical water shortages in the southern Murrayâ Darling Basin, Australia. *Marine and Freshwater Research*.

Hladyz, S., Watkins, S.C., Whitworth, K.L., and Baldwin, D.S. (2011) Flows and hypoxic blackwater events in managed ephemeral river channels. *Journal of Hydrology* **401**(1), 117-125.

Jensen, A. (2002) Repairing wetlands of the Lower Murray: Learning from restoration practice. *Ecological Management & Restoration* **3**(1), 5-14.

Khan, M., Khan, T., and Wilson, M. (2004) Habitat use and movement of river blackfish (Gadopsis marmoratus R.) in a highly modified Victorian stream, Australia. *Ecology of freshwater fish* **13**(4), 285-293.

King, A.J., Tonkin, Z., and Mahoney, J. (2009) Environmental flow enhances native fish spawning and recruitment in the Murray River, Australia. *River Research and Applications* **25**(10), 1205-1218.

Koehn, J., McKenzie, J., O'Mahony, D., Nicol, S., O'Connor, J., and O'Connor, W. (2009) Movements of Murray cod (*Maccullochella peelii peelii*) in a large Australian lowland river. *Ecology of Freshwater Fish* **18**(4), 594-602.

Koehn, J., Nicol, S., McKenzie, J., Lieschke, J., Lyon, J., and Pomorin, K. (2008) Spatial ecology of an endangered native Australian Percichthyid fish, the trout cod *Maccullochella macquariensis*. *Endangered Species Research* **4**(1-2), 219-225.

Koehn, J.D., and Harrington, D.J. (2006) Environmental conditions and timing for the spawning of Murray cod (*Maccullochella peelii peelii*) and the endangered trout cod (*M. macquariensis*) in southeastern Australian rivers. *River Research and Applications* **22**(3), 327-342.

Koehn, J.D., Nicol, S.J., and Fairbrother, P.S. (2004) Spatial arrangement and physical characteristics of structural woody habitat in a lowland river in south-eastern Australia. *Aquatic Conservation: Marine and Freshwater Ecosystems* **14**(5), 457-464.

Koster, W., and Crook, D. (2008) Diurnal and nocturnal movements of river blackfish (Gadopsis marmoratus) in a south-eastern Australian upland stream. *Ecology of freshwater fish* **17**(1), 146-154.

Lake, J.S. (1967) Rearing experiments with five species of Australian freshwater fishes. I. Inducement to spawning. *Marine and Freshwater Research* **18**(2), 137-154.

Leigh, S., Zampatti, B., and Authority, M.-D.B. (2011) 'Movement and Spawning of Murray Cod (Maccullochella Peelii) and Golden Perch (Macquaria Ambigua Ambigua) in

Reponse to a Small-scale Flow Manipulation in the Chowilla Anabranch System.' (SARDI Aquatic Sciences)

Leigh, S.J., and Zampatti, B.P. (2013) Movement and mortality of Murray cod, Maccullochella peelii, during overbank flows in the lower River Murray, Australia. *Australian Journal of Zoology* **61**(2), 160-169.

Lintermans, M. (2005) Sand slugs and fish movement in the Murrumbidgee River: can you restore and maintain deepwater habitats in sediment-impacted large rivers. In Native fish Rehabilitation and Managment in the Murray-Darling Basin: Statement, Recommendations and Supporting Papers. Proceedings of a workshop held in Albury, NSW, 10-11 February 2004. pp. 10-11. (Murray-Darling Basin Commission: Canberra)

Mallen-Cooper, M. (1996) Fishways and freshwater fish migration on South-Eastern Australia.

Mallen-Cooper, M., and Stuart, I. (2003) Age, growth and non-flood recruitment of two potamodromous fishes in a large semi-arid/temperate river system. *River Research and Applications* **19**(7), 697-719.

Mallen-Cooper, M., Stuart, I.G., and Sharpe, C. (2014) Making Every Drop Count Twice; Sustaining Irrigation and Recovering Native Fish. Report prepared for the North Central Catchment Management Authority. 163 p.

Mallen-Cooper, M., Zampatti, B.P., Hillman, T.J., King, A., Koehn, J., Saddlier, S., Sharpe, C., and Stuart, I. (2011) Managing the Chowilla Creek Environmental Regulator for Fish Species at Risk. Report prepared for the South Australian Murray-Darling Basin Natural Resources Management Board. 128 p.

McMahon, T., and Finlayson, B. (2003) Droughts and anti-droughts: the low flow hydrology of Australian rivers. *Freshwater Biology* **48**(7), 1147-1160.

O'Connor, J., King, A., Tonkin, Z., Morrongiello, J., and Todd, C. (2008) Fish in the Murray Valley and Torrumbarry Irrigation Areas. *Arthur Rylah Institute for Environmental Research Technical Report Series* **176**, 65.

Olley, J.M., and Scott, A. (2002) 'Sediment supply and transport in the Murrumbidgee and Namoi Rivers since European settlement.' (CSIRO Land and Water)

Poff, N.L., Allan, J.D., Bain, M.B., Karr, J.R., Prestegaard, K.L., Richter, B.D., Sparks, R.E., and Stromberg, J.C. (1997) The natural flow regime. *BioScience* **47**(11), 769-784.

Poff, N.L., and Ward, J. (1990) Physical habitat template of lotic systems: recovery in the context of historical pattern of spatiotemporal heterogeneity. *Environmental Management* **14**(5), 629-645.

Prosser, I., Moran, C.J., Lu, H., Olley, J.M., DeRose, R., Cannon, G., B, C., Hughes, A.O., T, J., L, N., A, S., and M, W. (2003) Basin-wide mapping of sediment and nutrient exports in dryland regions of the Murray-Darling Basin. Technical Report 33/03, CSIRO Land and Water.

Reid, D.D., Harris, J.H., and Chapman, D.J. (1997) NSW Inland Commercial Fishery. NSW Fisheries. FRDC Project No. 94/027

Reynolds, L. (1983) Migration patterns of five fish species in the Murray-Darling River system. *Marine and Freshwater Research* **34**(6), 857-871.

Rowland, S. Aspects of the reproductive biology of Murray cod, Maccullochella peelii peelii. In 'PROCEEDINGS-LINNEAN SOCIETY OF NEW SOUTH WALES', 1998, pp. 147-162

Saddlier, S., O'Mahony, J., Ramsey, D., and Murray, L. (2008) 'Protection and enhancement of Murray cod populations.' (Arthur Rylah Institute for Environmental Research, Department of Sustainability and Environment)

Sheldon, F., and Thoms, M. (2006) In-channel geomorphic complexity: The key to the dynamics of organic matter in large dryland rivers? *Geomorphology* **77**(3), 270-285.

Sheldon, F., and Walker, K. (1989) Effects of hypoxia on oxygen consumption by two species of freshwater mussel (Unionacea: Hyriidae) from the River Murray. *Marine and Freshwater Research* **40**(5), 491-499.

Sheldon, F., and Walker, K.F. (1997) Changes in biofilms induced by flow regulation could explain extinctions of aquatic snails in the lower River Murray, Australia. *Hydrobiologia* **347**(1-3), 97-108. [In English]

Sheldon, F., and Walker, K.F. (1998) Spatial distribution of littoral invertebrates in the lower Murray-Darling River system, Australia. *Marine and Freshwater Research* **49**(2), 171-182.

Southwood, T. (1977) Habitat, the templet for ecological strategies? *Journal of Animal Ecology* **46**(2), 337-365.

Stead, D.G. (1929) Murray cod and Trout cod. In The Sydney Mail. (John Fairfax and Sons: Sydney)

Sturt, C. (1833) 'Two expeditions into the interior of southern Australia, during the years 1828, 1829, 1830 and 1831: with observations on the soil, climate and general resources of the colony of New South Wales. .' (Smith, Elder & Co. [Facsimile edition, Doubleday Australia: Sydney, 1982]: London) 271 pp.

Thoms, M., and Walker, K. (1993) Channel changes associated with two adjacent weirs on a regulated lowland alluvial river. *Regulated Rivers: Research & Management* **8**(3), 271-284.

Tonkin, Z., Humphries, P., and Pridmore, P. (2006) Ontogeny of feeding in two native and one alien fish species from the Murray-Darling Basin, Australia. *Environmental Biology of Fishes* **76**(2-4), 303-315. [In English]

Tonkin, Z., King, A., Mahoney, J., and Morrongiello, J. (2007) Diel and spatial drifting patterns of silver perch Bidyanus bidyanus eggs in an Australian lowland river. *Journal of Fish Biology* **70**(1), 313-317.

Tonkin, Z., Lyon, J., and Pickworth, A. (2010) Spawning behaviour of the endangered Macquarie perch Macquaria australasica in an upland Australian river. *Ecological Management & Restoration* **11**(3), 223-226.

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

Whitworth, K.L., Baldwin, D.S., and Kerr, J.L. (2012) Drought, floods and water quality: Drivers of a severe hypoxic blackwater event in a major river system (the southern Murray–Darling Basin, Australia). *Journal of Hydrology* **450–451**(0), 190-198.

Ye, Q., and Zampatti, B. (2007) Murray cod stock status – the Lower River Murray, South Australia. Stock Status Report to PIRSA Fisheries. South Australian Research and Development Institute (Aquatic Sciences), Adelaide, 32pp. SARDI Publication Number F2007-000211-1.

Zampatti, B.P., Bice, C.M., Wilson, P.J., and Ye, Q. (2014) Population dynamics of Murray cod (*Macullochella peeli*) in the South Australian reaches of the River Murray: a synthesis of data from 2002-2013. Report to PIRSA Fisheries and Aquaculture. South Australian Research and Development Institute (Aquatic Sciences), Adelaide. SARDI Puiblication No. F2014/000089-1. SARDI Reseach Report Series No. 761. 42 pp.

Zampatti, B.P., and Leigh, S.J. (2013) Within-channel flows promote spawning and recruitment of golden perch, Macquaria ambigua ambigua–implications for environmental flow management in the River Murray, Australia. *Marine and Freshwater Research* **64**, 618-630.