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

Martin Mallen-Cooper[1,2]   Brenton P. Zampatti[3,4]

[1] Fishway Consulting Services, NSW, Australia
[2] Institute for Land, Water and Society, Charles Sturt University, NSW, Australia
[3] Inland Waters and Catchment Ecology Program, SARDI Aquatic Sciences, SA, Australia
[4] School of Earth and Environmental Sciences, The University of Adelaide, SA, Australia

Correspondence
Martin Mallen-Cooper, Fishway Consulting Services, 8 Tudor Pl, St Ives Chase, 2075, NSW, Australia

Email: mallencooper@optusnet.com.au.

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: i) cease-to-flow events were not natural, and were instead caused by multiple small-scale irrigation diversions; and ii) 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 pre-regulation 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: i) persistence of lotic in-channel and lentic off-channel refugia, even in droughts; and ii) 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.

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, Arthington, Gessner, Kawabata, Knowler, Lévêque, . . . Stiassny, 2006; Vörösmarty, McIntyre, Gessner, Dudgeon, Prusevich, Green, . . . Liermann, 2010). Contemporary approaches to aquatic ecosystem restoration involve the reinstatement of functionally important aspects of the natural (unaltered) flow regime (Poff, Allan, Bain, Karr, Prestegaard, Richter, . . . Stromberg, 1997; Richter, Mathews, Harrison, & Wigington, 2003). Such approaches, however, require a fundamental knowledge of pre-regulation hydrology and river dynamics (Galat & Lipkin, 2000).

In regulated rivers, perceptions of pre-development flow regimes serve as benchmarks that shape conceptual models of biology and ecosystem function, influence research, and guide management and restoration (Kennard, Pusey, Olden, MacKay, Stein, & Marsh, 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 pre-disturbance 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, Tallowin, Stevens, Power, Morgan, Emmett, . . . Buxton, 2010). Multi-decadal 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 i.e. 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 (Figure 1), and has been regulated for consumptive use for 130 years. The Murray River is generally categorised as a semi-arid, dryland river characterised 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 2001–2009, including a four-year period when no flow reached the sea (Dijk, Beck, Crosbie, Jeu, Liu, Podger, . . . Viney, 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

KEY

1 Lake Alexandrina and Lake Albert (320 rkm)
2 Morgan (571 rkm)
3 Renmark (878 rkm)
4 Mildura (1408 rkm)
5 Swan Hill (1638 rkm)
6 Torrumbarry (1724 rkm)
7 Echuca
8 Goulburn River (1934 rkm)
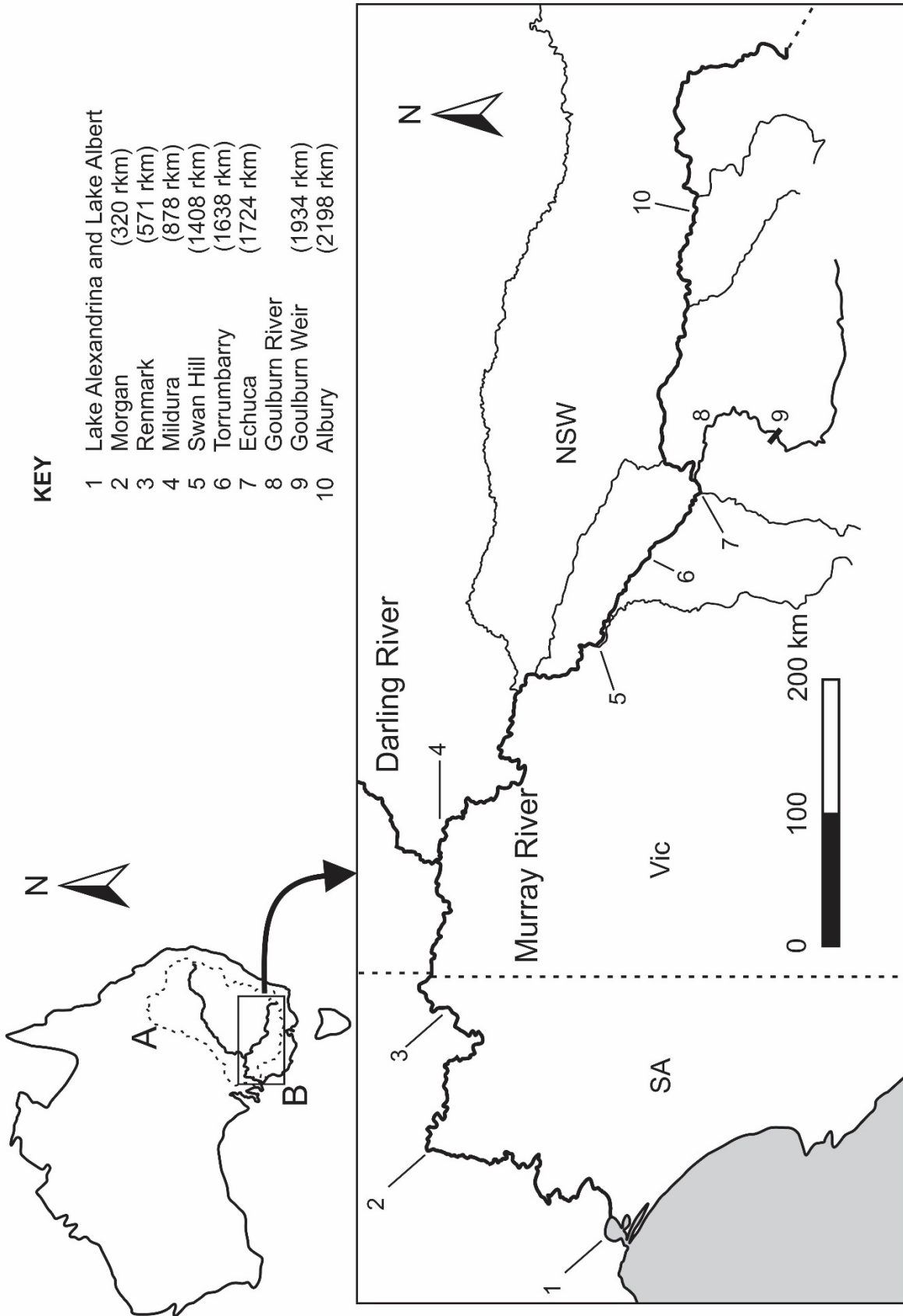9 Goulburn Weir
10 Albury (2198 rkm)

FIGURE 1 The Murray River and sites mentioned in the text

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: i) would cease-to-flow and dry to a "series of pools" during drought, and ii) 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: i) 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 ii) the lower reaches of the river were characterised 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 characterised 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, Johnston, Olley, Prescott, Roberts, Shawcross, & Spooner, 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 ~5500 km. The Murray River rises in the Great Dividing Range in eastern Australia at 2228 m elevation but quickly falls over the first 300 km from its source to an elevation of 150 m at 2225 rkm (river km from the sea), and then gradually decreases in gradient from 0.29 m km^{-1} to 0.03 m 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 1540 GL (3038GL following augmentation in 1961) and 4000 GL, respectively. In addition, a series of 14 downstream weirs were built from 1922-39, 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).

Diversion of flow has reduced mean annual discharge of the Murray River to the sea by 61% from 12,233 GL to 4723 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 chain of water holes". 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 semi-arid or arid, and its grouping with dryland rivers that have extensive periods of low and intermittent flow (Gawne, Merrick, Williams, Rees, Oliver, Bowen, . . . Frankenberg, 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 and the unregulated Murray River is characterised as slow-flowing (Reid & Brooks, 2000; Shiel, Walker, & Williams, 1982; Thoms, Rayburg, & Neave, 2008).

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: 1) the scientific literature (e.g. (Close, 1990; Fluin, Gell, Haynes, Tibby, & Hancock, 2007) which describes a relatively freshwater system in the past 2000 years that was occasionally brackish; and 2) 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 used: i) historical gauging records, and ii) modelled natural daily flows.

Gauging of streamflow commenced in 1865 with sites in the upper Murray River at Albury (2198 rkm) from 1877 (McKay, 1903); the middle Murray at Echuca (1724 rkm) from 1865 to 1905, Torrumbarry (1638 rkm) from 1906, Swan Hill (1415 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, unpubl. data of South Australian Department of Environment, Water and Natural Resources). 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

---

[1] www.nla.gov.au
[2] The Advertiser (Adelaide, SA: 1889-1931), 18 December 1914, page 8.
  The Sydney Morning Herald (Sydney, NSW: 1831-), 7 December 1914, page 7.
  The Argus (Melbourne, Vic.: 1848-1957), 9 December 1914, page 10.

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 are 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, unpubl. data), for five locations, at 320, 887, 1415, 1638, 2198 rkm; corresponding to Morgan, Mildura, Swan Hill, Torrumbarry and Albury.

We use the historical and modelled data to examine the:

i) *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.

ii) *Capacity and diversions of early irrigation*, to show that there was sufficient infrastructure to divert all of the low flows.

iii) *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.

iv) *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.

v) *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: i) historical rating curves (velocity versus river discharge) combined with gauged data for 1886-1913, and ii) 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) (Johnson 1913), Mildura (878 rkm) (Murray 1892) and near Euston (1110 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 (34mm 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 ten flows from 1000 to 80,000 ML d^{-1}. We applied this hydrodynamic model to three scenarios: i) modelled natural flows (MDBA, unpublished data) with no weirs,

ii) gauged flows with existing weirs, and iii) gauged flows with no weirs. We used flow data from 1995 to 2003, which includes three years of drought, and applied mean daily flow for each month, to be comparable with the historical data. Additional hydrodynamic data was 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, 1881-82, 1884-86, 1895-1903 (Federation Drought), 1911-15, 1923 and 1927-29. There were three confirmed occurrences of zero flow, at Morgan in 1901, and at Swan Hill in 1914-15 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 1914-15 has mean flows of 194 to 1036 ML d^{-1} in the dry months of December 1914 to May 1915 and 3333 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 are 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 irrigation areas, which raises two questions: i) did irrigation developments have the capacity to influence low flows in the river and ii) 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 unauthorised diversions, but
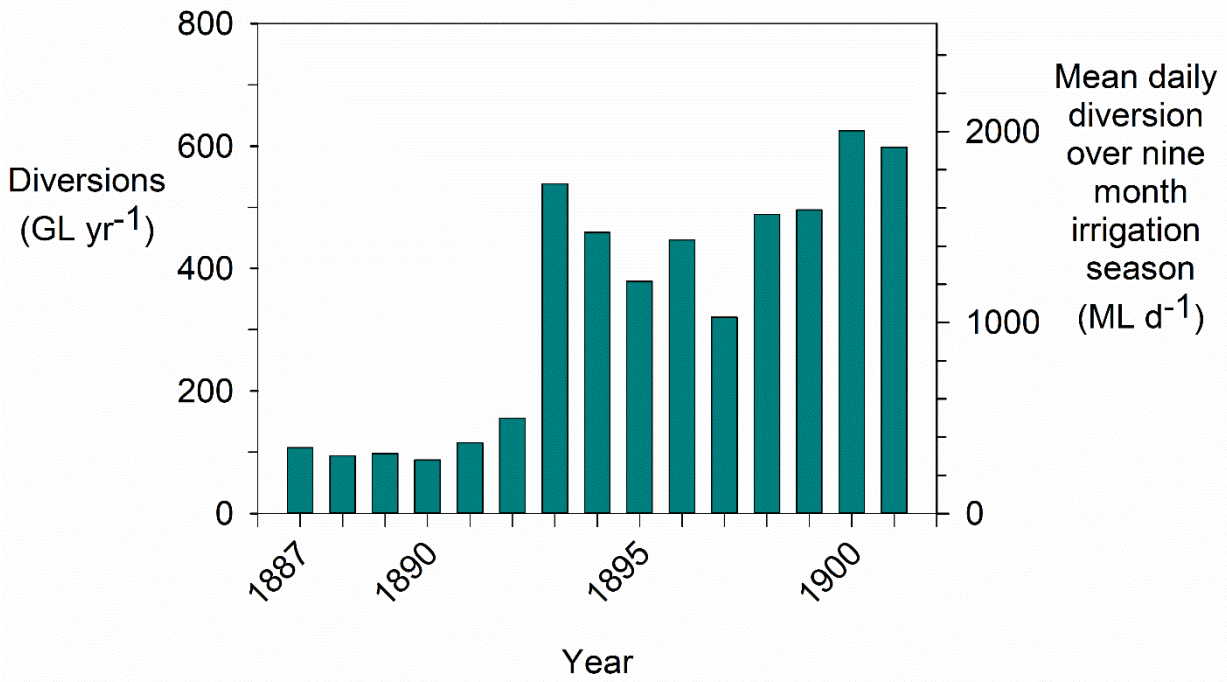
---

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

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

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 (Figure 1) – 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 yr^{-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, 1908-1923). 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 nine months (Davis et al., 1902) the *per annum* figure converts to a daily mean diversion of over 2000 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] (1400 to 1700 rkm), each with a capacity of 10 ML d^{-1} (Ferguson, 1988) potentially diverting 1500 ML d^{-1}; all upstream of the sites with zero flow.
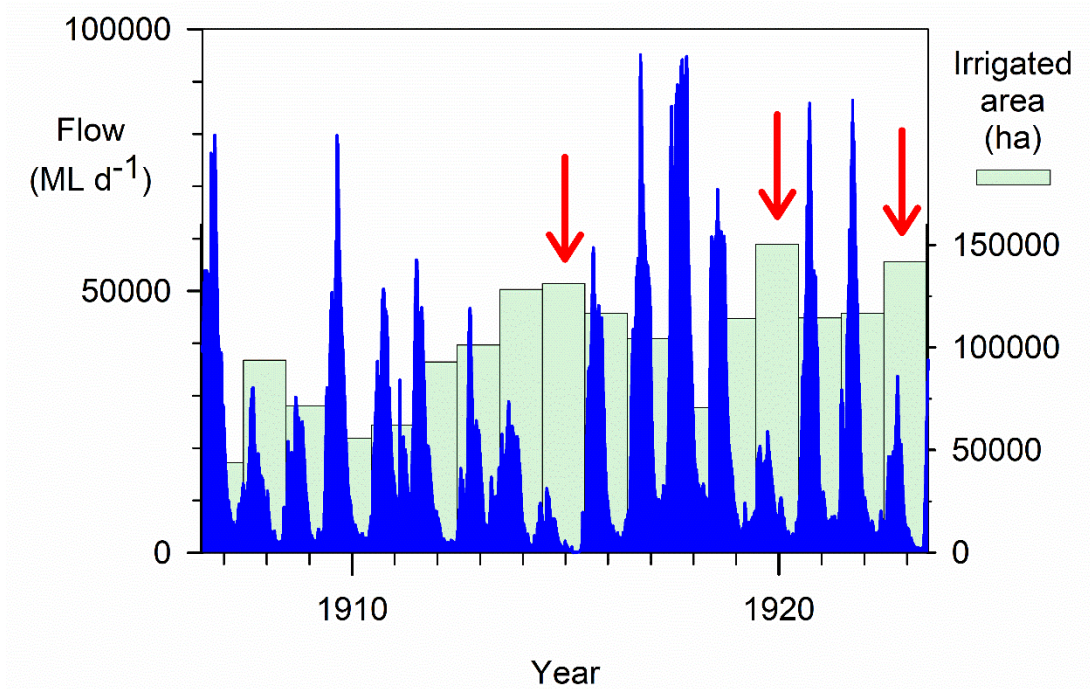

FIGURE 3   Annual irrigated area in Victoria in the catchment of the Murray River from 1907 to 1923 plotted with daily flow. NSW data not available. Arrows show peaks of irrigated area coinciding with low river flow in late summer

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 1199 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 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.

---

[4] The Advertiser (Adelaide, SA : 1889-1931), Tuesday 27 October 1903, page 7.
[5] The Mildura Cultivator (Victoria.: 1888-1920), 20 April 1901, page 7.
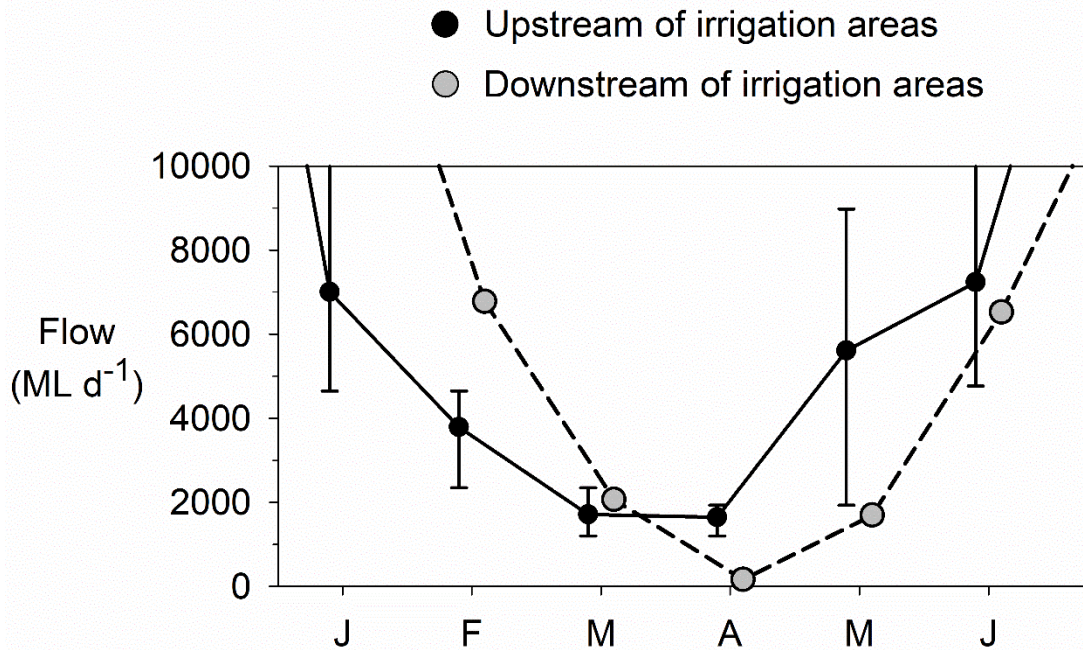   Renmark Pioneer (SA: 1892-1913), 8 March 1901, page 3.

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

The second confirmed zero-flow event occurred at Swan Hill in the 1914-15 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 500–1000 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 1914-15 (State Rivers and Water Supply Commission, 1908-1923).

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 (State Rivers and Water Supply Commission, 1908-1923; Acting Commissioner of Water Conservation and Irrigation, 1915). 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.
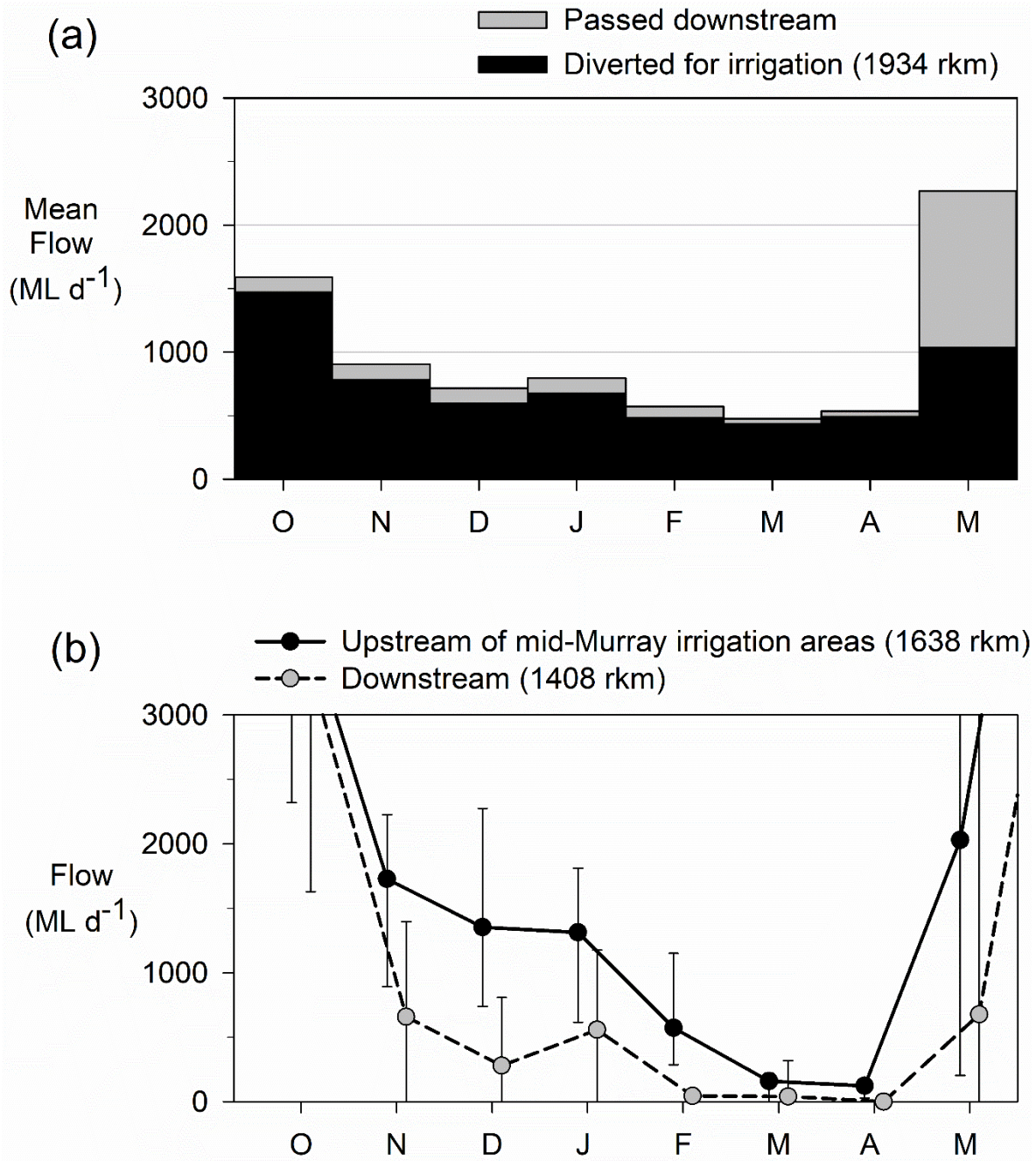
FIGURE 5 Flow in the 1914-15 drought: a) irrigation diversions from a major upstream tributary (Goulburn Weir, Goulburn River, 1934 rkm; mean daily flow); b) Mean daily flow (including maximum and minimum) for each month from October 1914 to May 2015 upstream (Torrumbarry, 1638 rkm, solid symbols) and downstream (Swan Hill, 1408 rkm, grey symbols) of mid-Murray irrigation areas
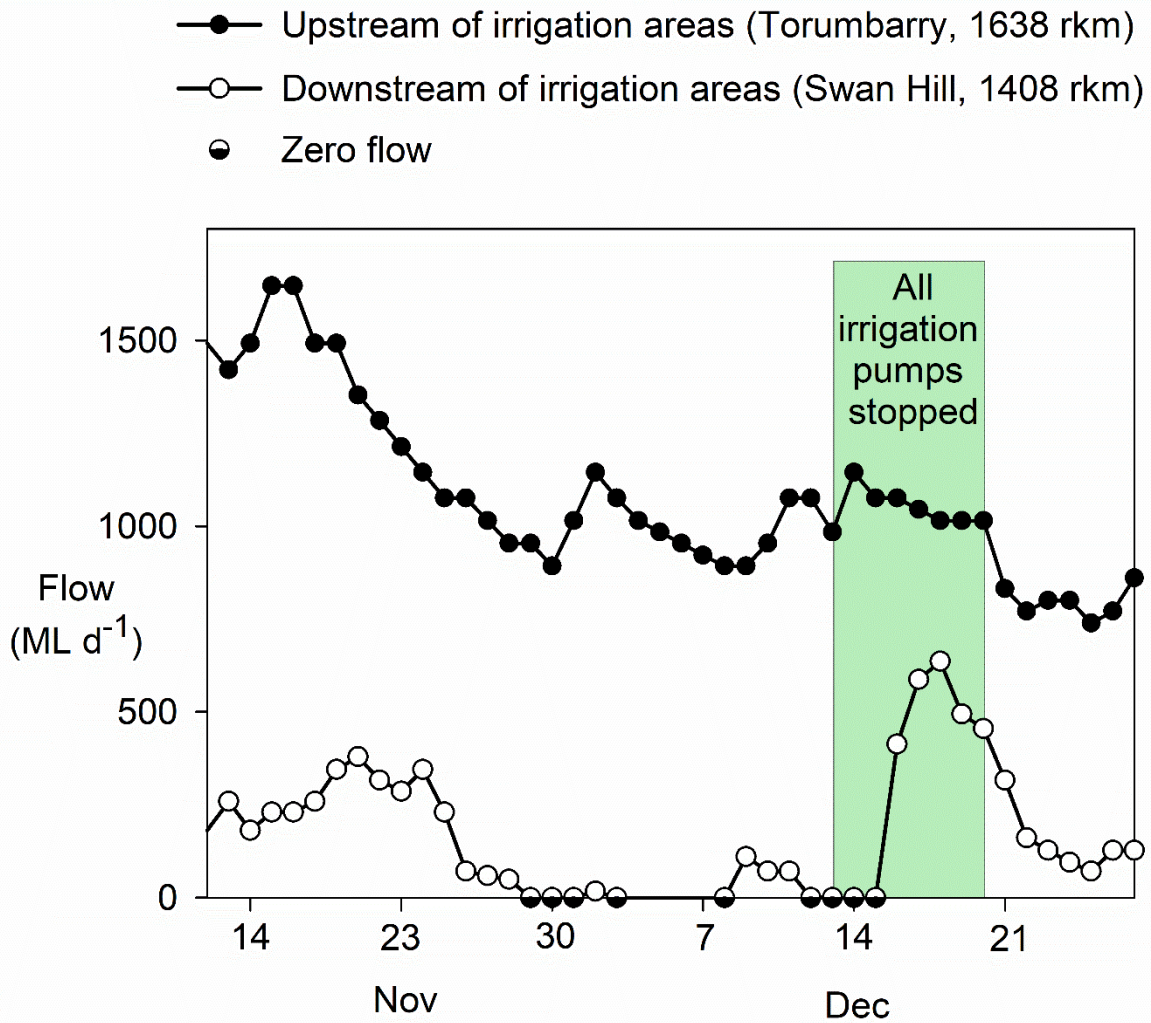
FIGURE 6   Hydrograph of the 1914-15 drought showing daily flow upstream (Torrumbarry, 1638 rkm, solid symbols) and downstream (Swan Hill, 1408 rkm, open symbols and half-filled symbols for zero flow) of mid-Murray irrigation areas, with a shaded period when irrigation pumps on the Murray upstream of Swan Hill were stopped

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 mainstem of the Murray River between 1638 rkm (Torrumbarry) and 320 rkm (Morgan) at all major irrigation settlements[6]; one at 878 rkm (Mildura) reportedly backing water up for 40 kilometres and storing two 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

---

[6] Murray Pioneer and Australian River Record (Renmark, SA.: 1913-1942), 21 January 1915, page 4
[7] Murray Pioneer and Australian River Record (Renmark, SA.: 1913-1942), 3 December 1914, page 2

diverted all flow causing short-term, localised zero flow downstream of individual dams[8].

The temporary dams are the likely source of the "ambiguous" data at Renmark (571 rkm) because: i) flows were fully regulated between dams, and ii) 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 rkm to 384 rkm, all reported brackish water at these low flows, but still suitable for irrigation[9], so 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 1000 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.

4.1.4   *Modelled natural flows*

Modelled natural daily flow from 1895 to 2009 show the river is perennial at upstream sites (1415, 1638 and 2198 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

---

[8] Daily Herald (Adelaide, SA : 1910-1924) 1 Jan 1915, Page 2
[9] Kadina and Wallaroo Times (SA: 1888- 1954) 1 May 1915, Page 4
[10] Murray Pioneer and Australian River Record (Renmark, SA.: 1913-1942), 25 March 1915, page 4
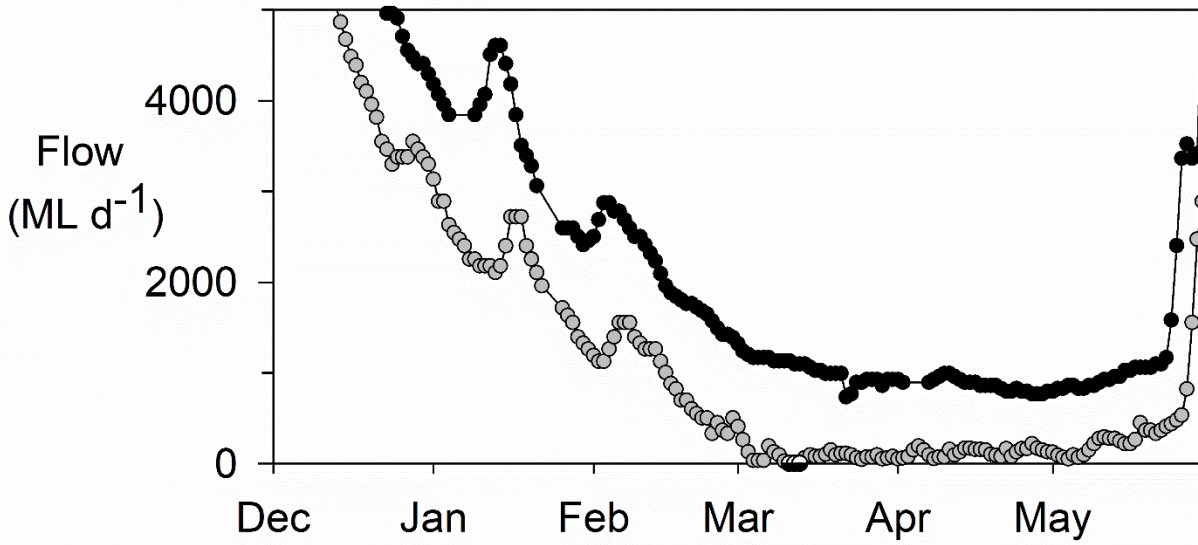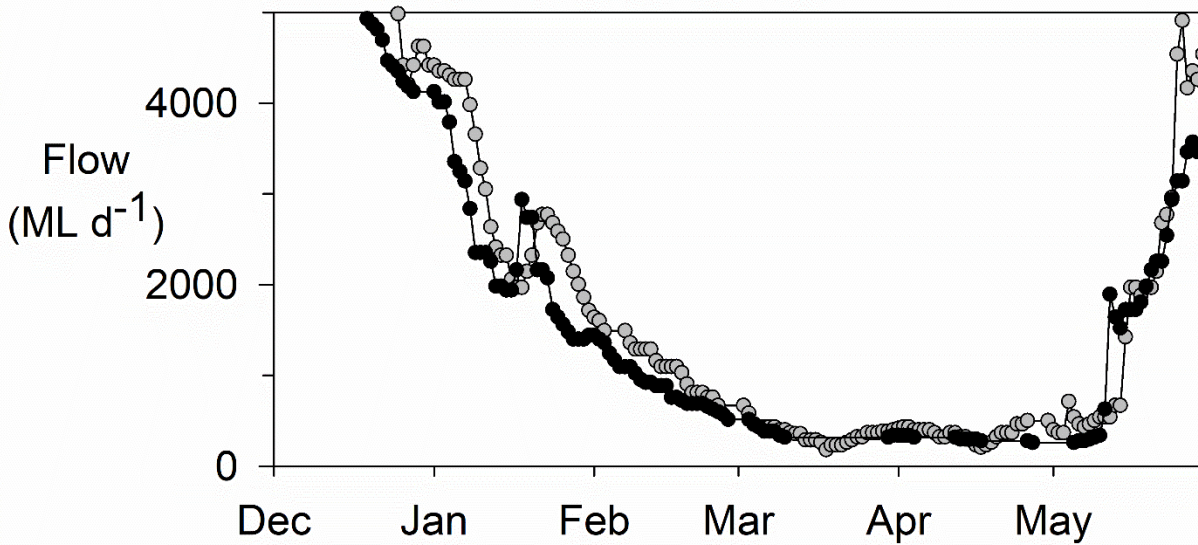
FIGURE 7 Discharge at Torrumbarry (1638 rkm) and Swan Hill (1408 rkm): a) in 1923 when irrigation was by pumps from the river and b) in 1927 when irrigation was by gravity diversion upstream of the Torrumbarry gauge

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 recognisable 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).

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 (1394 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

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 multiyear droughts resulted in multiyear suppression of flows and loss of seasonality. We compared gauged flows at Mildura (880 rkm) for three 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, while 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 8553 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: i) historical gauging from Overland Corner (425 rkm) and Morgan (320 rkm) from 1876-1913, a 37-year period that is prior to upland main-stem dams and lowland weirs, and includes the Federation Drought (1895-1903); and ii) 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 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 two months duration in autumn, and then in the Federation Drought for two to five 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 five. 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 net flow to the sea. In droughts, evaporation exceeds inflows into the Lower Lakes for a maximum continuous period of five months, leading to saltwater intrusion and brackish salinities, but over the long-term the lakes could be fresh for up to 22 years continuously.
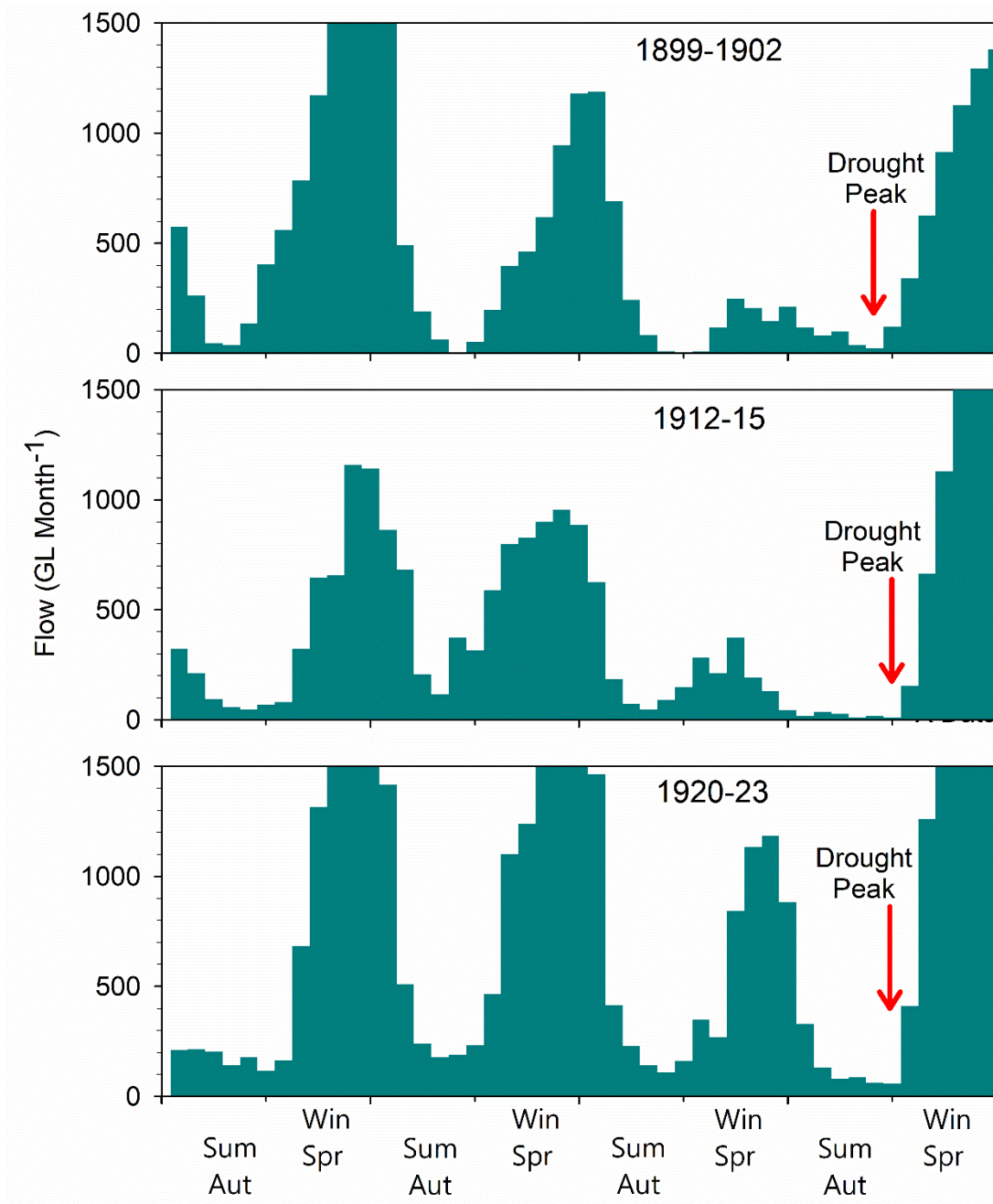
FIGURE 9 Monthly discharge (GL) at Mildura (878 rkm) for the three years preceding the peaks of the three major droughts prior to the construction of large upstream dams from the mid-1930s
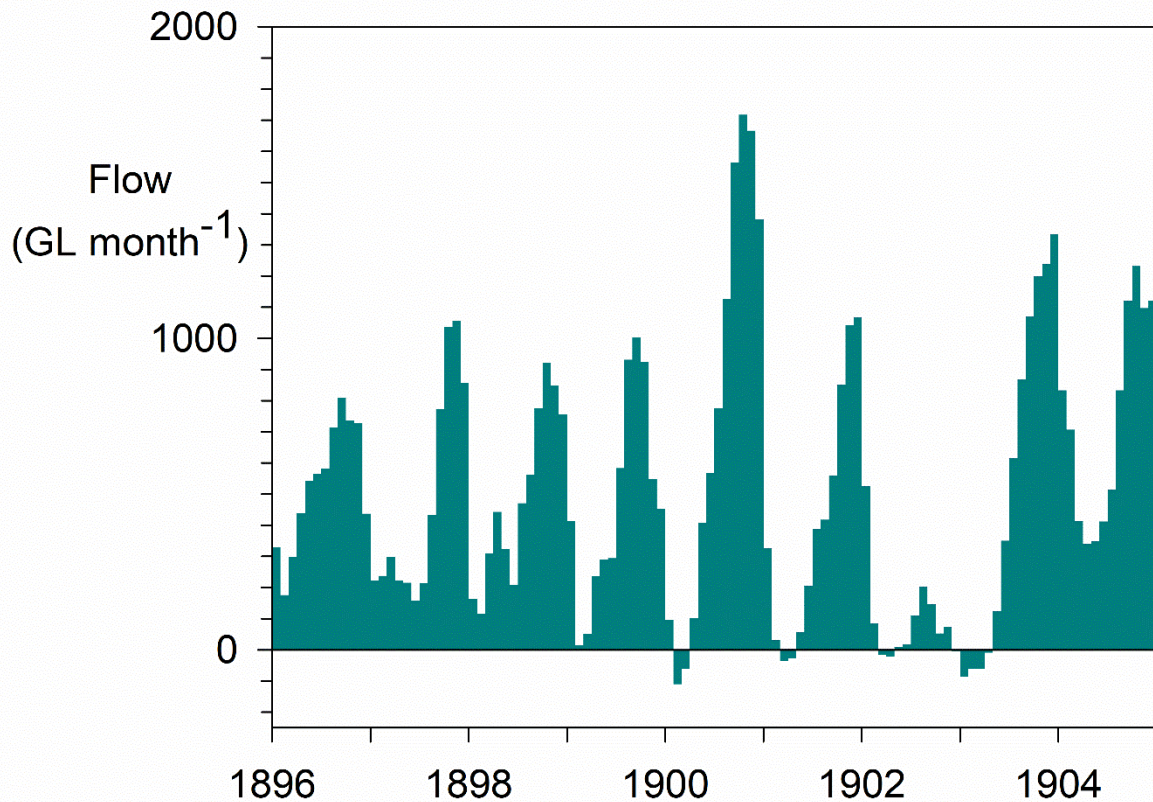
FIGURE 10 Net flow at the Murray mouth during the Federation drought from 1896 to 1903 using monthly gauged flow at Morgan (320 rkm) less evaporation from the river and Lower Lakes. Negative values indicate a net inflow of seawater into the Lower Lakes

4.2 Hydrodynamics

4.2.1 Modelling of historical data

Seasonal hydrodynamics for Morgan (320 rkm) from 1886-1913 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, Kalogianni, Papadaki, Vavalidis, Mentzafou, & Koutsoubas, 2017). These data show a strong seasonal trend in mean channel water velocities with: i) higher velocities and predominantly lotic conditions in spring, and ii) lower velocities and a mix of lotic and lentic conditions in late summer and autumn, directly reflecting reduced discharge (Figure 11). Historical data from Mildura and Euston, upstream of Morgan, show similar results.
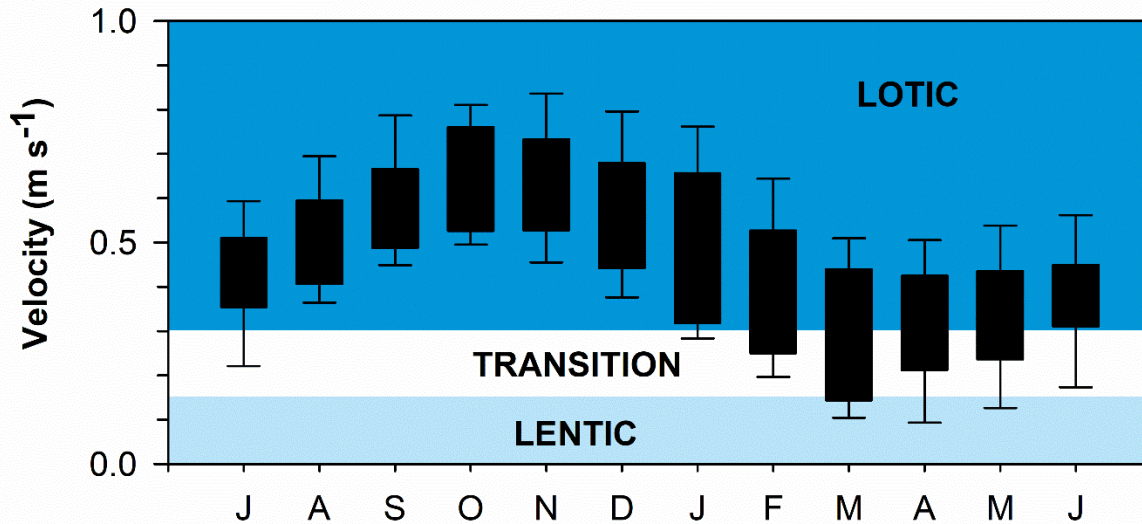
FIGURE 11 Box plot (5, 25, 75, 95 %iles) of monthly channel velocity, using mean flow, of the Murray River at Morgan (320 rkm) from 1886 to 1913. For comparison, lotic and lentic are shaded dark blue and light blue, while transition between the two is unshaded

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: i) natural, ii) gauged flows and existing weirs, and iii) gauged 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

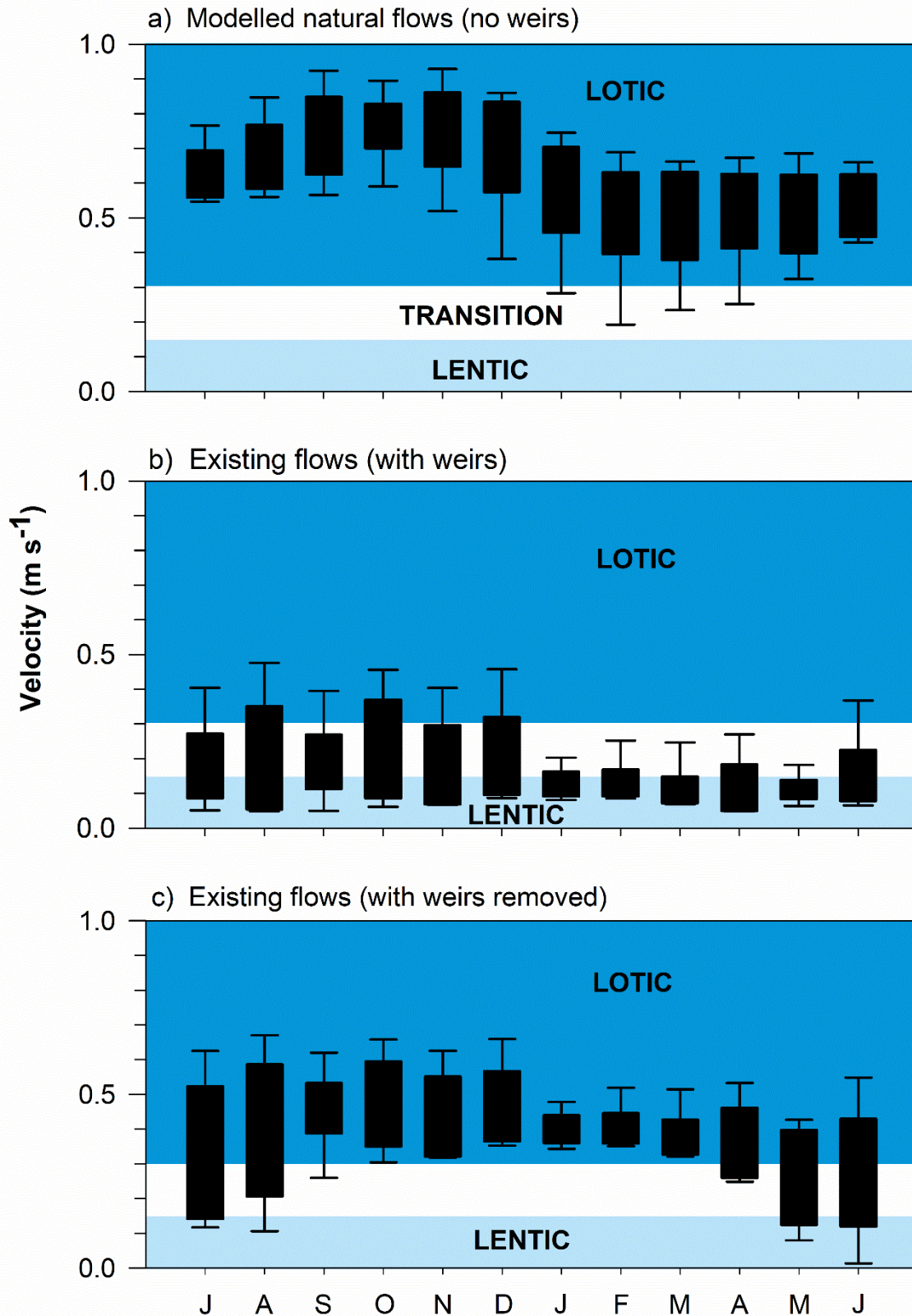**FIGURE 12** Box plot (5, 25, 75, 95 %iles) of monthly channel velocity using a mean of 119 cross-sections of the Murray River from 562 to 697 rkm and mean monthly flow, from 1995 to 2003: a) modelled natural flows with no weirs, b) gauged flows with weirs and c) gauged flows with weirs removed. For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

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 existing 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 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 pre-regulation 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 pre-regulation 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 yr^{-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 firstly 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 Murray-Darling Basin, including the Murray River, are commonly categorised as *dryland* rivers; a grouping that includes intermittently-flowing rivers without dominant, regular, annual or seasonal cycles (Walker, Sheldon, & Puckridge, 1995; Davies, Thoms, Walker, O'Keeffe, & Gore, 2009). 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. Humphries, King, & Koehn, 1999; Gawne et al., 2007) 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 utilise: i) permanent lotic habitats, ii) a predictable in-channel increase in hydrodynamic complexity each spring, and iii) 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 1:1500 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 Murray-Darling Basin is a natural phenomenon but multiyear suppression of spring flows in the Murray River is not.
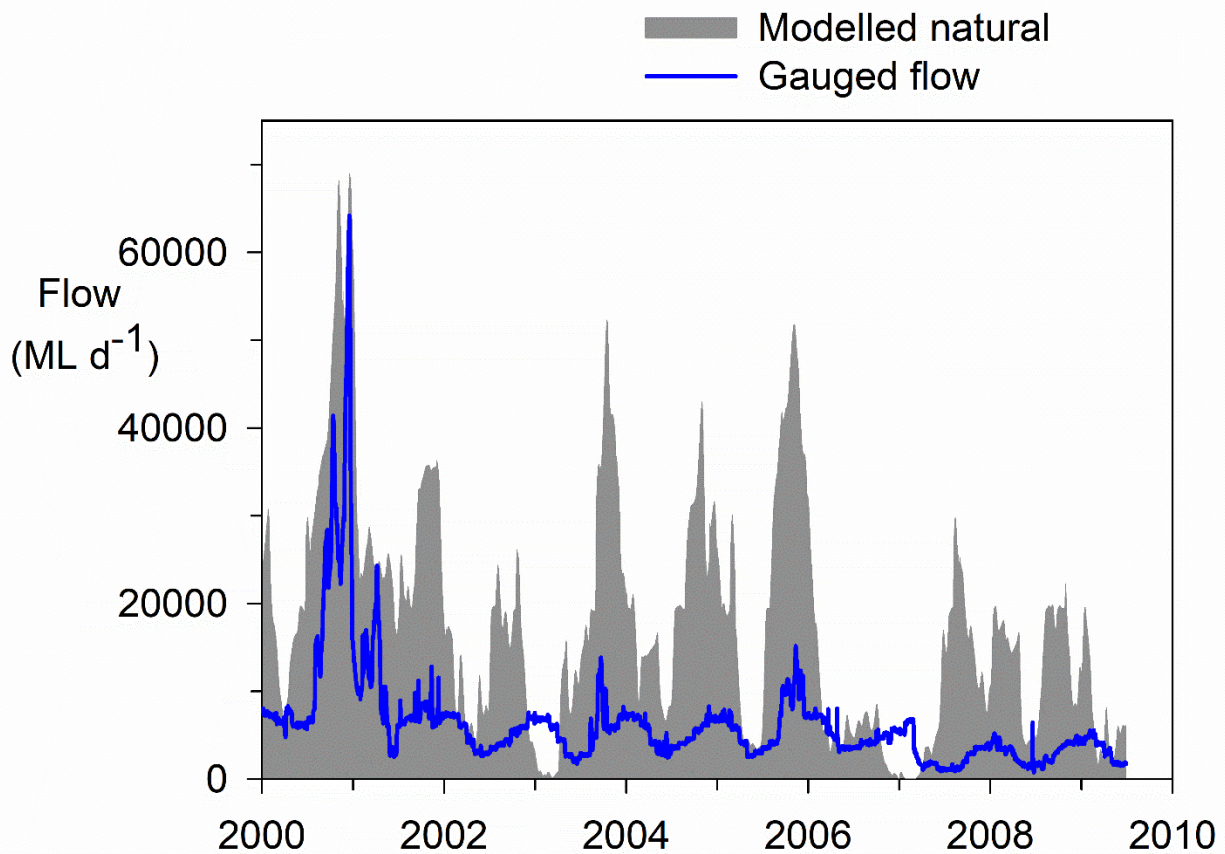

FIGURE 13 Comparison of gauged and natural daily flow (ML d^{-1}) in the lower Murray River (South Australia border) in the recent Millenium Drought (Zampatti and Leigh 2013)

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 flow 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, 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, aquatic plants) and floodplain connections. 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 (LWD) - 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 LWD 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 less affected by weirpools and generally retain much of their lotic character (Figure 14). The substantial hydrodynamic alteration and resultant habitat homogenisation in the lower river has had a profound effect on ecosystem function and form.
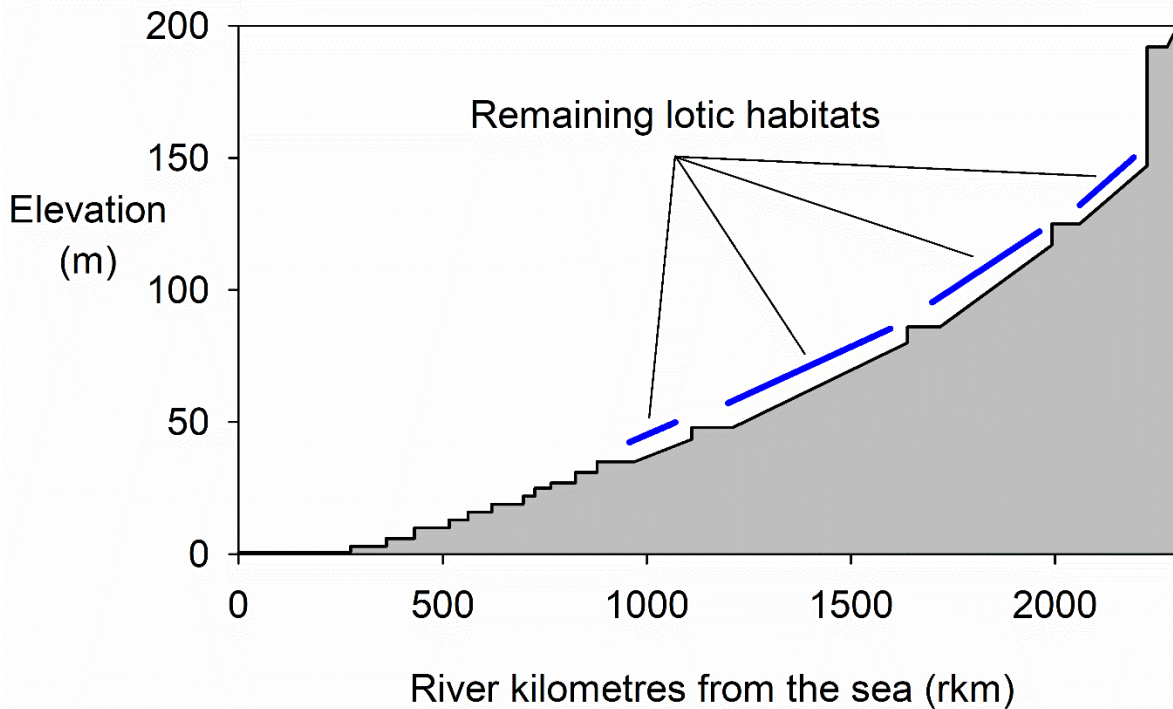
FIGURE 14 Profile of the Murray River showing weirpools and remaining lotic habitats in the main channel at low and regulated flows (<10,000 ML d^{-1}). At high flows (>50,000 ML d^{-1}) the lower weirs are removed and the channel becomes entirely lotic for the lower 1992 km

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 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 & Lake, 1992; Boulton, 2003; 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, Arthington, Foster, Thoms, Wilson, & Bunn, 2006; Bond & Lake, 2005; Sheldon, Bunn, Hughes, Arthington, Balcombe, & Fellows, 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 recognised, 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, Monti, Valade, Lamouroux, Mallet, & Grondin, 2014) and fish (Schlosser & Angermeier, 1995). In dryland rivers, lotic biota and ecology are less well recognised. Lotic bivalves and macroinvertebrates are recognised 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

homogenised 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 recognised 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 recognised. 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 generalisation 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, Gehrig, Zampatti, Nicol, Wilson, Leigh, Marsland, 2013; Cheshire, Ye, Gillanders, & King, 2016).

In contrast, riverine specialist species (Murray cod, trout cod, golden perch *Macquaria ambigua*, silver perch, Macquarie perch, 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 (Sep-Dec) (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: 1) permanent inundation of low-lying wetlands caused by weirpools (Walker et al., 1995) and 2) 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, Souter, Bean, Ross, Thompson, & Bjornsson, 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, Gell, Perga, Jeppesen, Grundell, Weller, . . . Barry, 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 exploiting a habitat niche in a river with predictable seasonal flow that maintained 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 barrages sometimes separate completely marine and completely freshwater environments leaving an estuarine ecosystem in peril (Kingsford, Walker, Lester, Young, Fairweather, Sammut, & Geddes, 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, while commercial catches of marine species that use the remnant estuary, like 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, characterised 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 characterised 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 characterised 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, while 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, characterised 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 1890's and the Federation Drought (Davis et al., 1902), while 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, while 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, anecdotal) present a consistent ecohydrological model for the Lower Lakes. Prior to irrigation, the estuary was coastal, while 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 Murray-Darling Basin (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, Beauchard, Struyf, Cox, Maris, & Meire, 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 ecohydraulic model for this perennial dryland river that integrates hydrology, hydrodynamics, 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 natural and present conditions, with three flows: a) low flows, b) a spring pulse within the channel and c) an overbank flood.

Under natural 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 low-lying terrestrial carbon store while floodplains provide a store at a higher elevation.
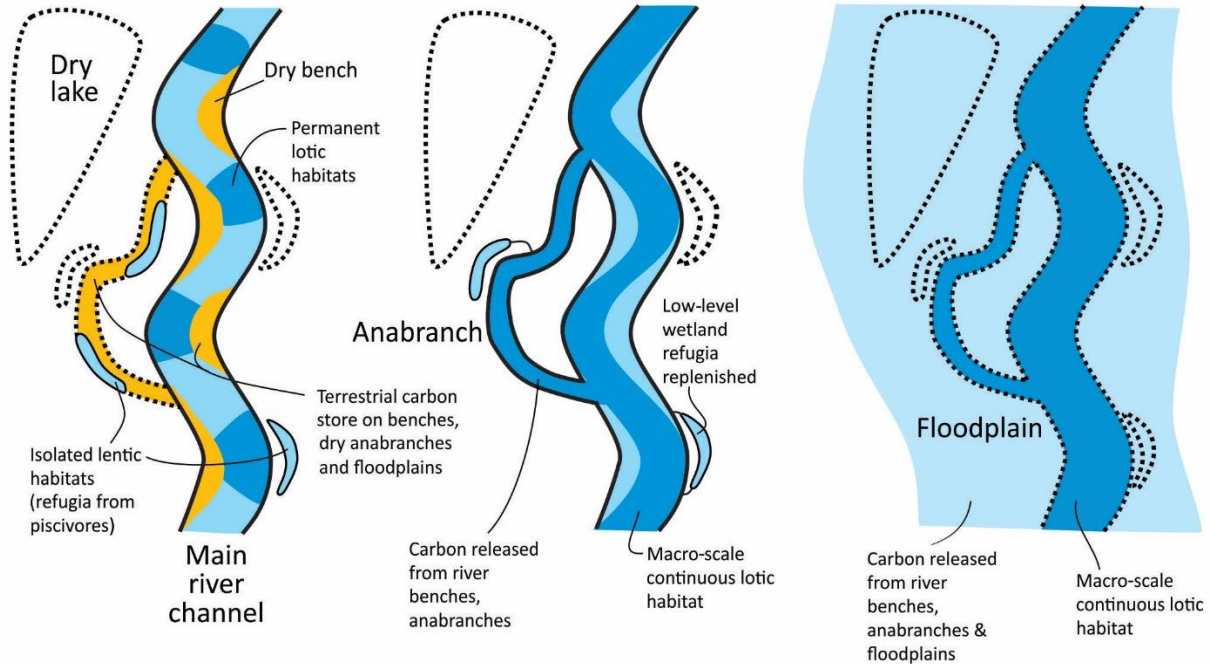
LENTIC   LOTIC

(a) Low flows   **(b) In-channel spring pulse**   **(c) Overbank flood**

PRE-REGULATION

Dry lake

Dry bench

Permanent lotic habitats

Isolated lentic habitats (refugia from piscivores)

Main river channel

Terrestrial carbon store on benches, dry anabranches and floodplains

Anabranch

Low-level wetland refugia replenished

Carbon released from river benches, anabranches

Macro-scale continuous lotic habitat

Floodplain

Carbon released from river benches, anabranches & floodplains

Macro-scale continuous lotic habitat

POST-REGULATION

Permanent lotic habitats lost from main channel and reduced to anabranches

Large lentic habitat created in weirpool

Weir

Small lentic habitats permanently connected (poor refugia from piscivores)

Carbon no longer stored on benches and dry anabranches

Less inundation and shorter duration; less carbon released from floodplains and excessive buildup between large events

Lotic habitats expand but are fragmented; with small spatial scale and shorter duration

Little carbon released from river benches and anabranches

Weir removed or submerged with unimpeded fish passage

Macro-scale continuous lotic habitat now restricted to larger flow events
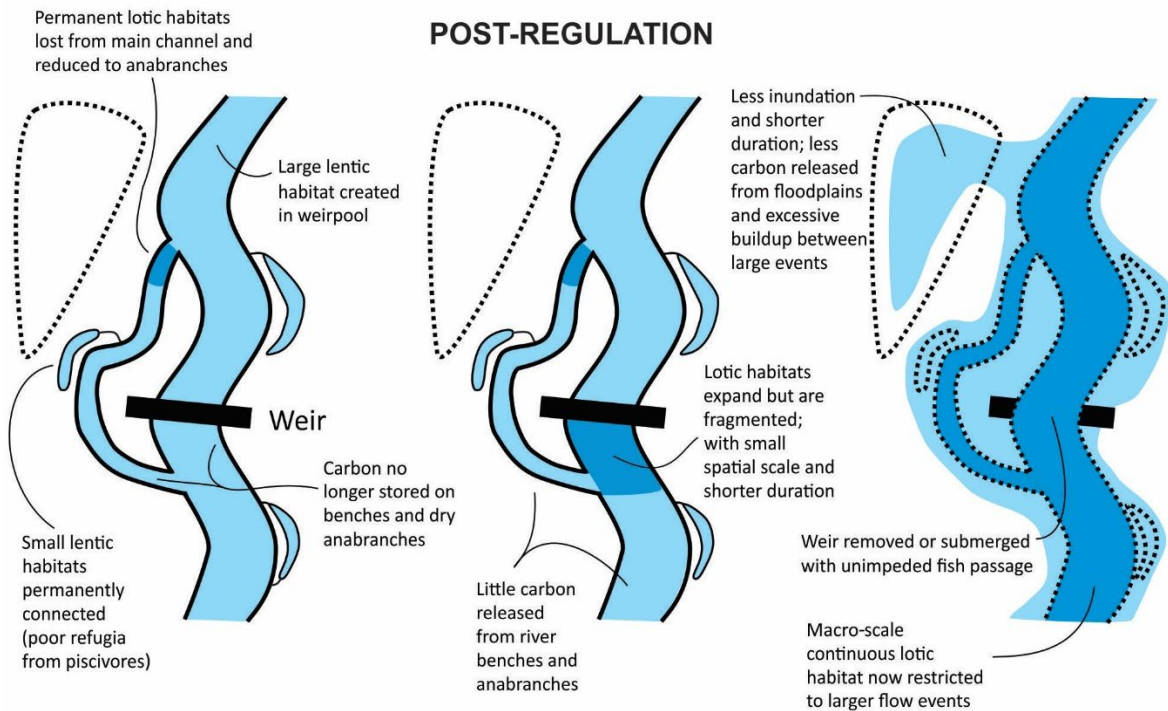
FIGURE 15   A model of a perennial dryland river integrating ecohydraulics and ecohydrology

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 mobilise 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 (100–1000s of kilometres) 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, Wilson, Baumgartner, Koster, Livore, McCasker, . . . Ye, 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 homogenisation. 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 oriental weatherloach (*Misgurnus anguillicaudatus*) - that further impact native fishes (Lintermans, 2007; Wedderburn, Hammer, Bice, Lloyd, Whiterod, & Zampatti, 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, McIntyre, Castello, Fluet-Chouinard, Giarrizzo, Nam, . . . Harrison, 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 semi-arid/dryland systems can provide a "boom" in aquatic productivity when inundated, but unlike highly seasonal rivers with permanent floodplains such as large tropical rivers, 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, Pollino, Roberts, Reid, Bond, McGinness, . . . Doody, 2014). The strategy may improve localised 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 (10s km) lentic habitats with fragmented hydrology increase. The latter will favour generalist native and non-native fish species and disadvantage specialised lotic biota, especially those with macro-scale life histories. We suggest that including objectives for hydrodynamics

and spatial integrity of flow in the Murray-Darling Basin 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). Recognising 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 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 characterising 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, Burns, Dyer, Neave, O'Brien, Pryde, & Thompson, 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^{TM}), 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, Arthington, Choy, Kennard, Mackay, Pusey, & Werren, 2002; King, Brown, & Sabet, 2003).

The ecological implications of riverine hydraulics over large spatial scales are often discussed (notably Poff, Richter, Arthington, Bunn, Naiman, Kendy, . . . & Henriksen, 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 (100s–1000s 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 South-East 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, Kamonrat, Sukumasavin, Sirimongkolthawon, Suksri, & Phila, 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 minimise 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.

REFERENCES

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

Acting Commisioner of Water Conservation and Irrigation (1915). Report of the Acting Commisioner 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. doi: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. doi:http://dx.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. 562 p.* 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 Fitzpatrick R., Mosley L., Ye Q., Hemming S., Shepherd S., & Rigney D. (Eds.), *Natural History of the Coorong, Lower Lakes and Murray Mouth*. Adelaide: Royal Society of South Australia.

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. doi: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. doi: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. doi: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. doi: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. doi: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. doi: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. doi:http://dx.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*. Institution of Engineers, Australia.

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, 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.

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: "The Rivers Handbook" Ed. P.C. Calow, G.E. Petts (Blackwell Science.)

Davis, J., Murray, S., & Burchell, F. (1902). Interstate Royal Commission on the River Murray (pp. 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. doi: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. doi: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. doi: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. doi: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 *Assessing the Ecological Integrity of Running Waters* (pp. 29-48): Springer.

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.

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*. Canberra, Australia: Murray-Darling Basin Commission.

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. doi:10.1046/j.1442-8903.2002.00092.x

Johnston, E. N. (1913). *Captains Johnstons 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. doi: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. doi: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. doi:http://dx.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. doi: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. doi: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 (pp. 50): CSIRO, Australia.

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. doi:http://dx.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.

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.

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.

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. doi: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. doi: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. doi: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. doi:http://dx.doi.org/10.1071/MF05160

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., & Postel, S. (2004). Saving Earth's Rivers. *Issues in Science and Technology, 20*(3), 31-36.

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. doi: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. doi:http://dx.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., and 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. doi:10.1002/rra.2975

Tennant, D. L. (1976). Instream Flow Regimens for Fish, Wildlife, Recreation and Related Environmental Resources. *Fisheries, 1*(4), 6-10. doi:10.1577/1548-8446(1976)001<0006:ifrffw>2.0.co;2

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.

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): John Wiley & Sons.

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. doi: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. doi: 10.1002/aqc.2735

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. doi:10.1029/2009GL041067

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.

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 für Hydrobiologie, 181*(3), 215-227. doi: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 *Perspectives in Southern Hemisphere Limnology* (pp. 111-129): 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. doi:http://dx.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*. Longman: London.

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. doi: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.