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Population demographics of golden perch (*Macquaria ambigua*) in the Darling River prior to a major fish kill: a guide for rehabilitation

Brenton P. Zampatti[A,B,N], *Benjamin G. Fanson*[C], *Lee J. Baumgartner*[D], *Gavin L. Butler*[E], *Steven G. Brooks*[F], *David A. Crook*[G], *Katherine Doyle*[D], *Alison J. King*[G], *Wayne M. Koster*[C], *Roland Maas*[H], *Aleksey Sadekov*[M], *Peter Scott*[I], *Arron Strawbridge*[B], *Jason D. Thiem*[D,J], *Zeb Tonkin*[C], *Phillipa J. Wilson*[B,K], *Jon Woodhead*[H] and *Ryan Woods*[L]

[A]CSIRO Land and Water, Locked Bag 2, Glen Osmond, SA 5064, Australia.
[B]Inland Waters and Catchment Ecology Program, South Australian Research and Development Institute (SARDI) – Aquatic Sciences, PO Box 120, Henley Beach, SA 5022, Australia.
[C]Arthur Rylah Institute for Environmental Research, Department of Environment, Land, Water and Planning, Heidelberg, Melbourne, Vic. 3084, Australia.
[D]Institute for Land, Water and Society, Charles Sturt University, PO Box 789, Albury, NSW 2640, Australia.
[E]Department of Primary Industries, Grafton Fisheries Centre, Grafton, NSW 2460, Australia.
[F]Electrofishing Services, Wamuran, Qld 4512, Australia.
[G]Centre for Freshwater Ecosystems, La Trobe University, Wodonga, Vic. 3689, Australia.
[H]School of Geography, Earth and Atmospheric Sciences, The University of Melbourne, Vic. 3010, Australia.
[I]Centre for Microscopy, Characterisation and Analysis, The University of Western Australia, Perth, WA 6009, Australia.
[J]Department of Primary Industries, Narrandera Fisheries Centre, Narrandera, NSW 2700, Australia.
[K]Australian Institute of Marine Science, Indian Ocean Marine Research Centre, The University of Western Australia (M096), Perth, WA 6009, Australia.
[L]Department of Environment and Science, Ecosciences Precinct, GPO Box 5078, Brisbane, Qld 4001, Australia.
[M]Ocean Graduate School, The University of Western Australia, Perth, WA 6009, Australia.
[N]Corresponding author. Email: brenton.zampatti@csiro.au

Abstract. An understanding of population demographics and life history processes is integral to the rehabilitation of fish populations. In Australia's highly modified Murray–Darling Basin, native fish are imperilled and fish deaths in the Darling River in 2018–19 highlighted their vulnerability. Golden perch (*Macquaria ambigua*) is a long-lived percichthyid that was conspicuous in the fish kills. To guide population rehabilitation in the Darling River, pre-fish kill age structure, provenance and movement of golden perch were explored using otolith microstructure and chemistry ($^{87}Sr/^{86}Sr$). Across the Lower and Mid-Darling River, recruitment was episodic, with dominant cohorts associated with years characterised by elevated discharge. There was substantial variability in age structure, recruitment source and movement patterns between the Lower and Mid-Darling River. In the Mid-Darling River, tributaries were an important recruitment source, whereas in the Lower Darling fish predominantly originated in the Darling River itself. Downstream movement of juveniles, upstream migration of adults and return movements to natal locations were important drivers of population structure. Restoring resilient golden perch populations in the Darling River will be reliant on mitigating barriers to movement, promoting a connected mosaic of recruitment sources and reinstating the hydrological and hydraulic factors associated with spawning, recruitment and dispersal. Globally, increasing water resource development and climate change will necessitate such integrated approaches to the management of long-lived migratory riverine fishes.

Keywords: dryland river, migration, Murray–Darling Basin, otolith chemistry, river regulation, strontium isotopes.

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Introduction

The ecological integrity of many of the world's rivers is compromised by water resource development for hydropower and consumptive use (Best 2019). Dams and other regulating structures fragment habitats and alter hydrological regimes, leading to species decline and biodiversity loss (Poff *et al.* 2007; Grill *et al.* 2015). This is exacerbated by climate change and a range of other human disturbances (Kingsford 2011; Arnell and Gosling 2013). In light of these effects, hydromorphological restoration to rehabilitate the health of riverine ecosystems is becoming more prevalent (Murray–Darling Basin Authority 2014; Kail *et al.* 2015; Schmutz *et al.* 2016).

The effective management and rehabilitation of rivers is reliant on knowledge of ecosystem function and form (Ward *et al.* 2001; Lake 2005). As the increasing prevalence of extreme climatic events causes further degradation, including fish kills, an understanding of biological mechanisms, as well as patterns, is essential to guide the adaptive management of rivers (Tonkin *et al.* 2019). Knowledge of demographic structure before catastrophic events can provide a template for species rehabilitation and be used to develop management objectives and targets (Kondolf 1995). To this end, natural baselines can be unrealistic (Stanford *et al.* 1996; Dufour and Piégay 2009), and contemporary or Anthropocene baselines may provide a more representative surrogate (Humphries and Winemiller 2009; Kopf *et al.* 2015). Simultaneously, there is a need for robust understanding of life histories and the processes that influence population and community dynamics, and their relationships with hydrology (Arthington *et al.* 2006; Humphries *et al.* 2020). This will also help identify potential lags in recovery due to variability among taxa and species driven by longevity and life history traits (Thompson *et al.* 2018).

For riverine fish populations, successful management and rehabilitation require detailed knowledge of the spatial scale of life history processes, including how recruitment source, connectivity and movement influence population demographics (Fausch *et al.* 2002; Shenton *et al.* 2012; Cooke *et al.* 2016). Management interventions can directly affect these drivers of population structure. For example, barriers to migration that interrupt connectivity may be mitigated with fishways (Lucas and Baras 2001). Globally, however, there remains a paucity of data on the population structures and life history processes of many riverine fishes (Reynolds *et al.* 2005; Cooke *et al.* 2012).

Australia's Murray–Darling Basin (MDB) is typical of many river systems worldwide where river regulation, in the form of altered flow regimes and dams and weirs, has caused substantial declines in native fish populations (Barrett 2004). Although the effects of river regulation are widespread across the MDB, they came to the fore in the Darling River in 2018–19 when drought and overextraction of water caused hypoxic conditions that resulted in the deaths of millions of fish (Vertessy *et al.* 2019), garnering national and worldwide attention (Normile 2019). Fish deaths occurred primarily in a 40-km reach of the Darling River between two regulating structures, but upstream and downstream reaches also received little to no flow over the preceding 18 months (Mallen-Cooper and Zampatti 2020). A range of fish species was conspicuous in the 2018–19 fish kills, including golden perch (*Macquaria ambigua*) (Thiem *et al.* 2021).

Golden perch are distributed broadly across the lowland rivers of the MDB (Lintermans 2007). In the Darling River, the species has provided a food source for Aboriginal people for tens of thousands of years (Balme 1995), once supported a commercial fishery (Reid *et al.* 1997), and remains a popular angling species (Forbes *et al.* 2015*b*). Golden perch are a long-lived (~27 years; Forbes *et al.* 2015*a*) potamodromous fish that exhibit a periodic life history strategy (*sensu* Winemiller and Rose 1992). Consequently, like other wide-ranging riverine fishes that exhibit episodic recruitment, golden perch are susceptible to flow regulation and barriers to movement, which ultimately reduce demographic resilience (Winemiller 2005; Olden *et al.* 2006; Zampatti 2019). In the MDB, altered flow regimes and fragmentation are considered primary causes of declines in golden perch populations and reductions in their range (Cadwallader 1978; Baumgartner *et al.* 2006; Shams *et al.* 2020). To arrest this decline and rehabilitate populations, enhancing reproduction, recruitment and movement of golden perch are key objectives for flow management and environmental water allocations throughout the MDB (Koehn *et al.* 2014; King *et al.* 2016; Koster *et al.* 2017).

For rehabilitation programs to be successful, knowledge of population demographics and drivers of population change is essential (Cooke *et al.* 2012). In the MDB, rehabilitation of native fish populations, including golden perch, constitutes a focus of contemporary and emerging fish management initiatives, particularly following the 2018–19 fish kills in the Darling River (MDBA 2020). Consequently, an understanding of pre-fish kill population demographics of golden perch in the Darling River, and the spatiotemporal characteristics of population processes (recruitment, movement) that influence these, is urgently needed to guide rehabilitation and subsequently assess effectiveness.

In this study, otoliths from golden perch collected in the Darling River in years before the 2018–19 fish kill were used to determine population age structure and the effect of recruitment source and riverine connectivity on population demographics. To reconcile spatial aspects of key life history processes, otolith chemistry was used as a natural tag. Specifically, the delineation in dissolved strontium isotope ratios ($^{87}Sr/^{86}Sr$) in water samples from across rivers of the MDB (Douglas *et al.* 1995; Zampatti 2019) was related to otolith $^{87}Sr/^{86}Sr$ to reconstruct natal origin and lifetime movements. The specific objectives of this study were to: (1) characterise the age structure of golden perch in the Lower and Mid-Darling River; (2) examine $^{87}Sr/^{86}Sr$ in otolith cores in relation to water $^{87}Sr/^{86}Sr$ across rivers of the MDB to determine fish provenance; (3) measure $^{87}Sr/^{86}Sr$ along transects from otolith core to edge to reconstruct the movement history of fish; and (4) compare age structures, natal source and movement histories between fish from the Lower and Mid-Darling River. By integrating knowledge on demographic patterns and underlying population processes, we provide an insight into the factors needed to rehabilitate golden perch populations in the Darling River. The approach used is also applicable to the management of other imperilled long-lived and wide-ranging riverine fishes, particularly in the face of continuing water resource development and climate change.

Methods

Study region

The MDB drains 1 073 000 km^2 (17% of Australia's landmass; Fig. 1). The combined length of the two major rivers, the Murray and the Darling, is ~5500 km, and both flow through predominantly semi-arid and arid landscapes. In their natural states, the Murray and Darling rivers were characterised by highly variable hydrological regimes (Walker *et al.* 1995; Puckridge *et al.* 1998), yet they also exhibited distinct but predictable hydrological and hydraulic characteristics, such as seasonal flow pulses and largely perennial lotic habitats (Mallen-Cooper and Zampatti 2018, 2020).

This study focused on golden perch populations in the mid- and lower reaches of the Barwon–Darling river system, which drains the northern river catchments of the MDB (~650 000 km^2) and converges with the River Murray ~825 km upstream from the river mouth. The mid-reach of the Barwon–Darling (hereafter the Mid-Darling River) extends south-west for ~900 km from the confluence of the Culgoa River to the Menindee Lakes (Fig. 1); an extensive series of off-channel lakes (457 km^2; capacity 1731 GL) used to store and re-regulate water for consumptive use. The Mid-Darling River incorporates the Warrego and Paroo rivers to the west (Fig. 1), although, on average, these catchments only contribute 5% of annual flow to the Darling River, principally from the Warrego River (Thoms *et al.* 2004). The Lower Darling River extends for ~500 km in a generally southerly direction from the Menindee Lakes to its confluence with the River Murray (Fig. 1).

The hydrological, hydraulic and geomorphological characteristics of the Darling River have been profoundly altered by river

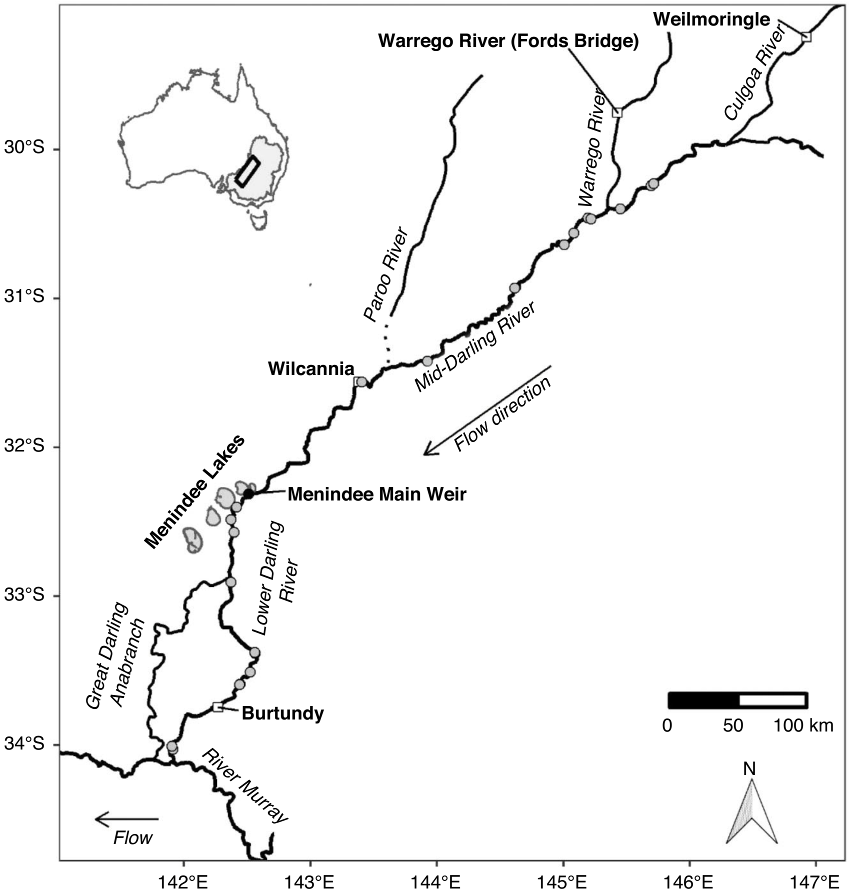

Fig. 1. Map showing the mid- and lower reaches of the Darling River, the Paroo, Warrego and Culgoa rivers and the Menindee Lakes, gauging stations (open white squares) and sampling locations (closed grey circles). Inset: the shaded area depicts the Murray–Darling Basin and black rectangle indicates the study region.

regulation in the form of headwater dams, weirs, direct extraction and floodplain harvesting (Thoms *et al.* 2004; Pearson *et al.* 2020). Flows in the Mid-Darling River are reduced by ~70%, and much of the river is fragmented and hydraulically modified by in-stream weirs (Thoms and Sheldon 2000; Mallen-Cooper and Zampatti 2020). Along the Mid- and Lower Darling River, there are at least nine substantial instream weirs, ranging from ~2 to 4.5 m high (New South Wales Department of Primary Industries 2006, 2012). Fish passage infrastructure is incorporated into some weirs, particularly those in the Lower Darling River (Baumgartner *et al.* 2014), but, for those without fishways, upstream fish passage is not feasible until the weirs are drowned-out at discharges ranging from ~2500 to 10 000 ML day^{-1} (New South Wales Department of Primary Industries 2006, 2012). In addition, the Menindee Lakes Storage Scheme (MLSS), which delineates the Lower and Mid-Darling River, comprises several weirs, regulators, levees and channels, and includes the Menindee Main Weir (Fig. 1), which has a head differential of ~12 m and does not incorporate fish passage infrastructure.

Hydrology

To relate river discharge to recruitment across the age range of golden perch collected in this study, daily mean flow (ML day^{-1}) for the period from 2005 to mid-2018 was obtained for the Lower Darling River at Burtundy (gauge number 425007), Mid-Darling River at Wilcannia (gauge number 425008), Warrego River at Ford's Bridge (gauge number 423001) and Culgoa River at Weilmoringle (gauge number 422017; Fig. 1). For all gauges, data were sourced from WaterNSW (https://realtimedata.waternsw.com.au/).

Sampling golden perch

Adult and juvenile golden perch were collected in the Lower Darling River in April 2014 and May 2018 and in the Mid-Darling River in December 2017 as components of broader investigations of golden perch population dynamics in the MDB (see Fig. 1 and Table S1 in the Supplementary material). Fish were sampled by boat electrofishing using a 5- or 7.5-kW Smith Root (Model GPP 5 or 7.5) electrofishing unit during daylight hours, and all littoral and channel habitats were fished. All fish ($n = 201$) were measured to the nearest millimetre (total length, TL) and subsamples of individuals ($n = 54$–65), proportionally representing the length frequency of golden perch collected, were retained for ageing and otolith chemistry analysis.

Ageing

Ageing methods previously validated for golden perch (Anderson *et al.* 1992; Mallen-Cooper and Stuart 2003; Zampatti and Leigh 2013) were used to establish the annual age of each individual and birth year. Briefly, golden perch retained for ageing were euthanased in the field by AQUI-S overdose (AQUI-S, Lower Hutt, New Zealand) and sagittal otoliths were removed. Whole otoliths were embedded in clear casting resin and a single transverse 400- to 600-μm section that incorporated the core was prepared from each otolith. Sections were examined using a dissecting microscope (25×) under transmitted light. Estimates of age were determined independently by three readers by counting the number of discernible opaque zones (annuli) from the primordium to the otolith edge and integrating this information with otolith edge type and capture date. A nominal birth date of 1 October was assigned to each individual. Young-of-year (YOY; <1 year old) fish were defined as individuals lacking clearly discernible annuli.

Otolith chemistry analysis

Otolith strontium isotope ratios (^{87}Sr/^{86}Sr) were used as geochemical signatures to reconstruct the natal origin and lifetime movements of golden perch. This approach has previously been used to discern the provenance and movements of golden perch in the MDB (Zampatti 2019).

Otolith ^{87}Sr/^{86}Sr was determined in a subsample of individuals of known age ($n = 43$–50), proportionally representing the age frequency of golden perch collected in each region and time period. Using the second otolith of aged fish, an additional transverse 400- to 600-μm section, incorporating the otolith core, was prepared from each otolith. Individual transverse sections were mounted collectively on 'master' slides using a thin layer of casting resin, and each section was polished using wetted lapping film (9 μm). Master slides were rinsed in Milli-Q water (Millipore) and air dried overnight in a Class 100 laminar flow cabinet at room temperature.

Laser ablation inductively coupled plasma mass spectrometry

Laser ablation inductively coupled plasma mass spectrometry (LA-ICP-MS) was used to measure ^{87}Sr/^{86}Sr in the otoliths of golden perch. Otoliths collected in the two different time periods (2014 and 2017–18) were analysed in different facilities using the same methodology, generally following Woodhead *et al.* (2005).

2014 Lower Darling fish

Analysis was undertaken by The University of Melbourne Isotope Geochemistry Laboratory. The experimental system consisted of a Nu Plasma multicollector LA-ICP-MS (Nu Instruments, Wrexham, UK) coupled to an Australian Scientific Instruments (now Applied Spectra) RESOlution laser ablation system constructed around a COMPex 110 excimer laser (Lambda Physik, Göttingen, Germany) operating at 193 nm.

Otolith mounts were placed in the sample cell and the primordium of each otolith was located visually with a 400× objective and a video imaging system. The intended ablation path on each sample was then digitally plotted using GeoStar software (ver. 6.14). Each otolith was ablated along a transect from the primordium to the dorsal margin at the widest radius using a 6- × 100-μm rectangular laser slit. The laser system was operated with a fluence of 2–3 J cm^{-2} measured at the sampling site, with a repetition rate of 10 Hz and scan speed of 5 or 10 μm s^{-1} (depending on the size of the otolith) across the sample.

Corrections for interferences and instrumental mass bias were performed within the *iolite* software environment (Paton *et al.* 2011), following protocols outlined in Woodhead *et al.* (2005). A marine carbonate standard with the isotope composition of modern seawater was run repeatedly throughout the analytical session and, using a spline fit passing through these standard analyses, all unknowns were corrected to the accepted value for modern seawater (~0.709160; e.g. Farrell *et al.* 1995). Raw values for the marine carbonate were typically within ±50 ppm from the accepted value, and thus the maximum corrections made to the $^{87}Sr/^{86}Sr$ ratio of the unknowns were of this order.

2017–18 Lower and Mid-Darling fish

Analyses were undertaken by the Advanced Geochemical Facility for Indian Ocean Research at the University of Western Australia. The experimental system consisted of a Thermo Scientific NEPTUNE Plus multicollector ICP-MS coupled with a Teledyne Analyte G2 excimer laser ablation system. Otolith mounts were placed in the sample cell and the primordium of each otolith was located visually with a 400× objective and a video imaging system. The intended ablation path on each sample was then digitally plotted. Otoliths were ablated along a transect from the primordium to the dorsal margin using a 25- × 100-µm rectangular laser slit. The laser was pulsed at 10 Hz and scanned at 10 $\mu m\ s^{-1}$ across the sample. Standardisation and Rb correction were done following Woodhead *et al.* (2005), and external reproducibility was assessed using three in-house carbonate standards with mean ± 2 s.d. $^{87}Sr/^{86}Sr$ ratios of 0.709176 ± 0.000025 ($n = 20$), 0.70592 ± 0.00012 ($n = 21$) and 0.713017 ± 0.000028 ($n = 20$). The accuracy for the standards measurements was –22, 27 and 2 ppm and was estimated as an offset between measured values and true values obtained using thermo-ionisation mass spectroscopy.

Natal origin assignment and movement history

As part of a previous study, a Bayesian mixing isotope model (BMIM) was developed to map water $^{87}Sr/^{86}Sr$ in rivers across the MDB (Zampatti *et al.* 2019). The BMIM used a similar moving average structure to the spatial stream network model used by Brennan *et al.* (2016) by incorporating the branching structure of the rivers. The BMIM was based on 726 water samples that were collected between 2011 and 2018 across the MDB and analysed for $^{87}Sr/^{86}Sr$ ratios and concentrations. The BMIM is temporally static and incorporates temporal variation into the residual error structure (Zampatti *et al.* 2019).

An assignment algorithm was also developed, based on a modified version of the Bayesian assignment approach used by Brennan and Schindler (2017), for estimating the probability that non-transitory sections of otolith $^{87}Sr/^{86}Sr$ profiles are from each river section (Zampatti *et al.* 2019). Briefly, this assignment algorithm first divides otolith $^{87}Sr/^{86}Sr$ profiles into unique sections using a regression tree approach. Working backwards from the capture location, the algorithm assigns a probability of each stationary section of the $^{87}Sr/^{86}Sr$ profile based on the $^{87}Sr/^{86}Sr$ for that section, the estimated mean $^{87}Sr/^{86}Sr$ (and variance) for each river and the distance of the river section from the current location. The final stationary section, closest to the otolith core, represents the fish's spatial (natal) origin (for more details, see Zampatti *et al.* 2019).

Because artificially propagated golden perch are stocked into the Lower and Mid-Darling River, the algorithm includes an additional option for a potential hatchery origin. Water $^{87}Sr/^{86}Sr$ was obtained for each hatchery that potentially stocks fish into the Darling River (see Zampatti *et al.* 2019). If a fish had a distinct movement in $^{87}Sr/^{86}Sr$ between 100 and 800 µm from the otolith core, representing the time period over which a hatchery fish may be released into the wild, then the algorithm checked whether $^{87}Sr/^{86}Sr$ during this period matched that of a hatchery. If this occurred, then fish were classified as stocked.

Results

Population structure

In 2014, golden perch collected from the Lower Darling River ranged in length from 88 to 419 mm and from age-0+ to age-6+, corresponding to birth years from 2007 to 2013 (Table 1; Fig. 2). The most prominent cohorts were 2009 and 2011 (65% of the sampled population; Fig. 2). In 2018, golden perch collected in the Lower Darling River ranged in length from 97 to 451 mm and from age-1+ to age-10+, corresponding to birth years from 2007 to 2016 (Table 1; Fig. 2). The 2009 cohort remained dominant in the 2018 sample, but the 2011 cohort had diminished (Fig. 2). In addition, in 2018, a cohort of age-1+ fish, representing a 2016 birth year, accounted for 40% of the sampled population (Fig. 2).

Golden perch collected in the Mid-Darling River in 2017 ranged in length from 180 to 479 mm and from age-2+ to age-10+, corresponding to birth years from 2007 to 2015 (Table 1; Fig. 2). The sampled population was characterised by five distinct cohorts: 2007, 2011, 2012, 2014 and 2015, of which the 2014 cohort was the most prominent (32% of fish collected; Fig. 2). Across both regions and in all years, no golden perch older than age-10+ were collected.

Natal origin

Individual $^{87}Sr/^{86}Sr$ profiles revealed the Darling River was the predominant natal origin of golden perch collected from the Lower Darling River in 2014 (100%) and 2018 (92%), with the remainder of fish collected in 2018 exhibiting either a Lower River Murray (6%) or hatchery (2%) origin (Table 2; Fig. 2). For golden perch collected from the Mid-Darling River in 2017, 56% had a Darling River natal origin and 42% exhibited distinct natal $^{87}Sr/^{86}Sr$ signatures representative of the Warrego or Culgoa rivers (Table 2; Fig. 2). In particular, the prominent 2014 and 2015 cohorts in the Mid-Darling River primarily exhibited

Table 1. Summary statistics for golden perch subsamples collected in the Lower Darling River in April 2014 and May 2018 and in the Mid-Darling River in December 2017

Unless indicated otherwise, data are presented as a range (minimum–maximum)

	Lower Darling		Mid-Darling
	2014	2018	2017
Number of fish	54	65	60
Length (mm)	88–419	97–451	180–479
Age (years)	0+–6+	1+–10+	2+–10+
Nominal birth year	2007–2013	2007–2016	2007–2015

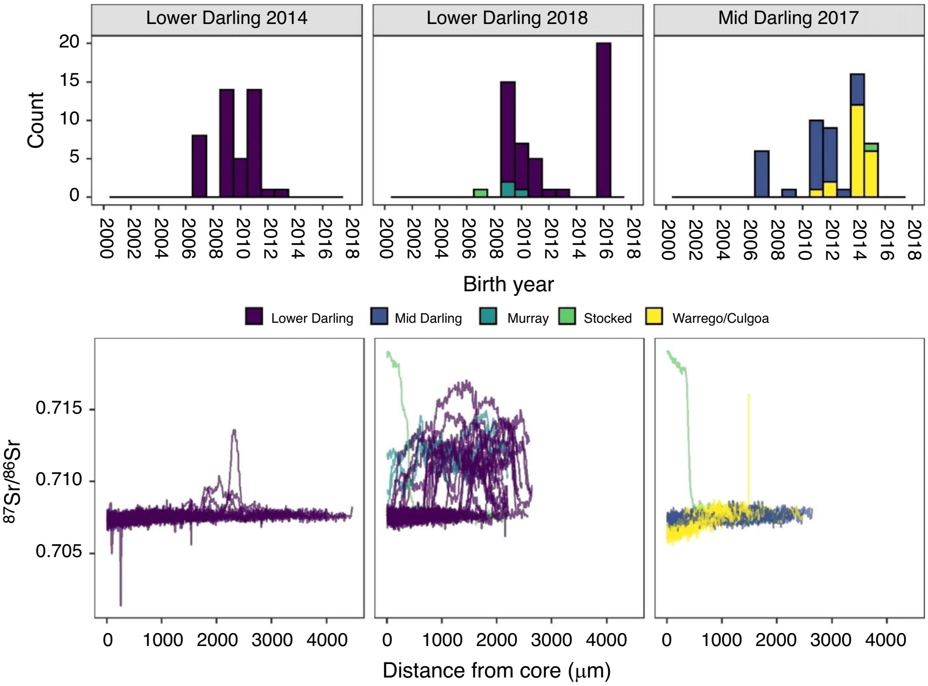

Fig. 2. Birth year distribution (top panels) for golden perch collected in the Lower Darling River in 2014 and 2018 and in the Mid-Darling River in 2017. The bottom panels show aggregated individual otolith $^{87}Sr/^{86}Sr$ profiles for fish from each region and time. Profiles indicate natal origin (colour) and lifetime variability in $^{87}Sr/^{86}Sr$.

Table 2. Summary of golden perch natal origins by sampling region: Lower Darling River and Mid-Darling River

Data show the number of fish. LD, Lower Darling; MD, Mid-Darling; LM, Lower Murray (defined as the River Murray downstream of the Darling River confluence); WR/CR, Warrego–Culgoa river

Sampling region	Year	LD	MD	LM	WR/CR	Stocked	Total
Lower Darling	2014	43	–	–	–	–	43
	2018	46	–	3	–	1	50
Mid-Darling	2017	–	28	–	21	1	50

Warrego or Culgoa river origins (Fig. 2). The natal $^{87}Sr/^{86}Sr$ signature for these fish ranged from 0.7063 to 0.7068, which is lower than fish assigned to the Mid-Darling River (Fig. 2). The Warrego and Culgoa rivers have distinctly lower water $^{87}Sr/^{86}Sr$ (mean ± s.e.m. 0.7065 ± 0.0002 and 0.7062 ± 0.0004 respectively) than the Mid-Darling River (0.7077 ± 0.0002), but similarities in water $^{87}Sr/^{86}Sr$ between the Warrego and Culgoa rivers preclude differentiation between these rivers as a recruitment source. In the Mid-Darling River in 2017, golden perch of hatchery origin accounted for 2% of fish collected (Table 2; Fig. 2).

Integrating age and natal origin enabled association of hydrological characteristics at the time and place of birth. Where golden perch originated in the Lower or Mid-Darling River, these cohorts were generally associated with overbank or within-channel flow pulses in the year of birth (Fig. 3), noting that spawning may occur throughout spring–autumn and therefore may straddle calendar years. In the Mid-Darling River, the 2014 and 2015 cohorts that predominantly exhibited a Warrego–Culgoa river natal origin (Fig. 2) were associated with either relatively minor flow events in the Warrego River that were interspersed in otherwise long periods (months–years) of cease-to-flow or, in the Culgoa River, with regular annual within-channel flow pulses (Fig. 3).

Movement

Golden perch collected in the Lower Darling River in 2014 and 2018 exhibited three lifetime movement patterns: (1) lifelong residency in the Darling River; (2) a Lower River Murray natal origin and immigration into the Lower Darling River; and (3) a Darling River natal origin, emigration to the Lower River Murray early in life (age-0+ or age-1+) and a return migration to the Lower Darling later in life (age-6+–8+; Fig. 4). In 2014, 93% of golden perch collected from the Lower Darling were lifelong residents and 7% were return migrants (see Fig. S1 in the Supplementary material). In 2018, excluding one fish of hatchery origin, 50% of fish were lifelong residents, 42% were return migrants born in the Darling River and 6% had migrated into the Darling after being born in the Lower Murray (see Fig. S2 in the Supplementary material).

In 2017, golden perch collected from the Mid-Darling River exhibited two distinct life time movement patterns: (1) lifelong residency in the Mid-Darling River; and (2) a Warrego–Culgoa river natal origin and movement into the Mid-Darling River early in life (age-0+; Fig. 4). Excluding one fish of hatchery origin, 56% of fish were lifelong residents and 42% were immigrants from tributaries (see Fig. S3 in the Supplementary material).

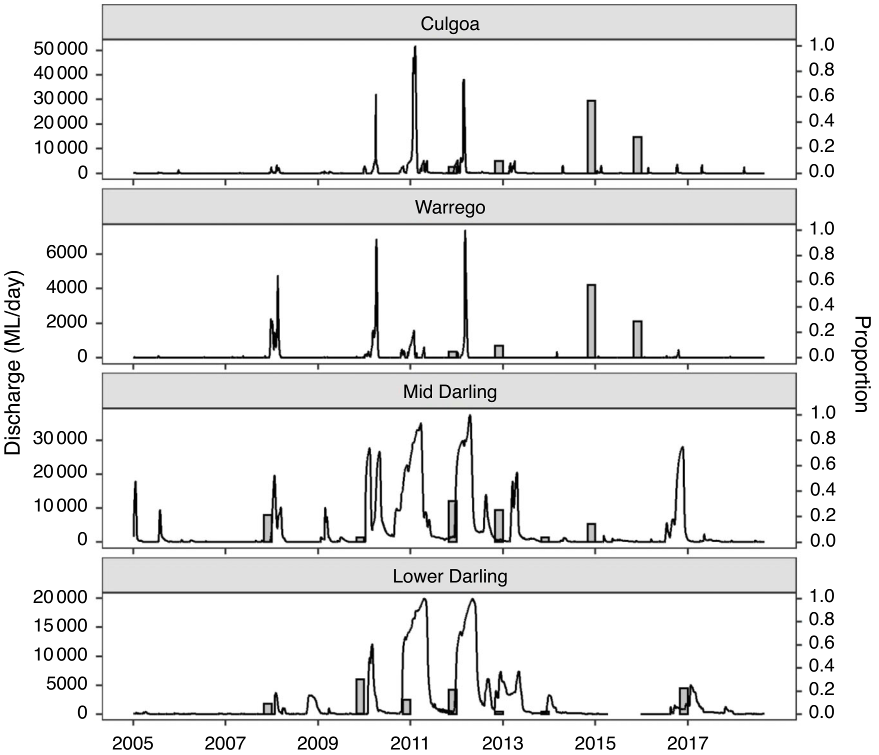

Fig. 3. River discharge over the period from 2005 to mid-2018 for the Culgoa, Warrego, Mid-Darling and Lower Darling rivers. Bars (grey shaded) depict the proportion of individuals from each cohort across all sampling years that were assigned to each river system. The same age structure data have been applied to the Warrego and Culgoa rivers because we were unable to differentiate between these rivers as a recruitment source.

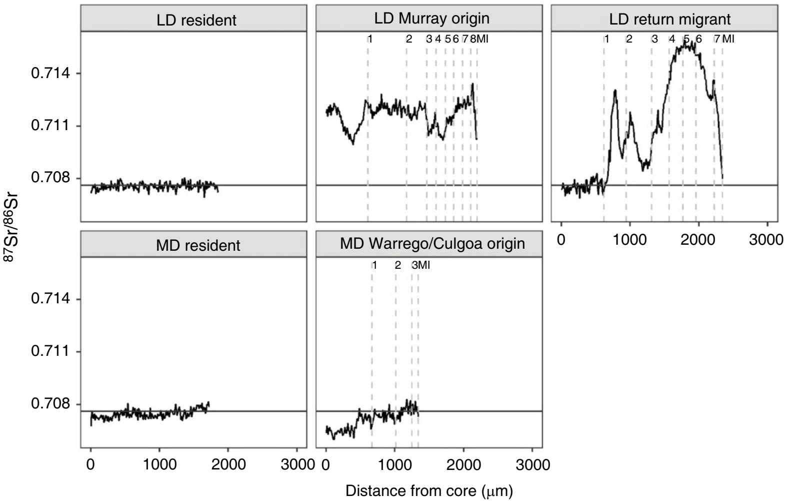

Fig. 4. The five lifetime movement patterns exhibited by golden perch collected in the Darling River based on otolith transect analysis of ^{87}Sr/^{86}Sr. Horizontal black lines indicate the ^{87}Sr/^{86}Sr of the Darling River (0.7077) and vertical dashed lines indicate annual otolith growth increments, hence age. LD resident, lifelong residency in the Darling River; LD Murray origin, Lower River Murray natal origin and immigration into the Lower Darling River, noting this fish was potentially a recent immigrant to the Darling River and had yet to integrate the Darling River ^{87}Sr/^{86}Sr signature; LD return migrant, Darling River natal origin, emigration to the Lower River Murray early in life and a return migration to the Lower Darling; MD resident, lifelong residency in the Mid-Darling River; MD Warrego–Culgoa origin, Warrego–Culgoa river natal origin and movement into the Mid-Darling River early in life. Transects for all individuals from each region and sampling occasion are provided in Fig. S1–S3.

Discussion

In rivers affected by anthropogenic alteration and climate change, knowledge of demographic patterns and underlying population processes is essential to guide the effective management of fish populations (Ward *et al.* 2001). In the years preceding the 2018–19 fish kills in the Darling River, there was substantial variability in age structure, recruitment source and movement patterns between samples of golden perch collected from the Lower and Mid-Darling River. In the Mid-Darling River, tributaries were an important recruitment source, whereas in the Lower Darling River fish predominantly originated in the Darling River. Furthermore, variation in lifetime movement patterns between the regions potentially demonstrates the effects of barriers to migration on population structure. These findings suggest that restoring a diversity of recruitment sources, and hydrological and physical connectivity throughout the Darling River, will be critical to promoting golden perch population growth and resilience.

Age structure

Golden perch populations in the Darling River in 2014 and 2017–18 (before the fish kills) were generally characterised by episodic recruitment and variation in age structure between the Lower and Mid-Darling River. The dominance of specific age classes was most marked in the Lower Darling River where, in 2014, the sampled population comprised two distinct cohorts: 2009 and 2011. By contrast, the sampled population of golden perch in the Mid-Darling River was characterised by greater age structure diversity. Across both regions, however, fish >10 years old were absent. For a long-lived fish, the absence of golden perch aged >10 years was unexpected, particularly when individuals 10–25 years old are relatively common in the adjoining River Murray (Zampatti *et al.* 2018).

Episodic recruitment is common in long-lived freshwater fishes with periodic life histories, where strong cohorts may punctuate periods of poor recruitment (Winemiller 2005). Populations of long-lived fish, like golden perch, can generally withstand these periods of recruitment failure, often caused by adverse climatic conditions (e.g. drought), because of the reproductive potential of strong cohorts (Secor 2007). However, the apparent absence of fish older than age-10+ in the Lower and Mid-Darling River and, in the case of the Lower Darling River, a lack of age structure diversity potentially render these populations susceptible to environmental perturbations (Berkeley *et al.* 2004).

Various factors could account for the truncated golden perch age structure, including a lack of recruitment, mortality and movement (Wright *et al.* 2020). Golden perch recruitment is generally associated with periods of increased flow through spring and summer (Mallen-Cooper and Stuart 2003; Zampatti and Leigh 2013). A lack of recruitment in the Darling River before 2007 could be the result of the pervasive impacts of the Millennium Drought across the MDB, leading to long periods of low or no flow (van Dijk *et al.* 2013; Mallen-Cooper and Zampatti 2020). Cease-to-flow periods in the Darling River may also have increased mortality by concentrating fish in isolated water holes, leading to predation, competition for resources or death from hypoxic or drying events (Balcombe *et al.* 2006; Close *et al.* 2014). In addition, when flow resumed, resulting in increased connectivity, fish may have migrated upstream or downstream to alternative reaches, thus restructuring populations.

This study provides a useful comparison for the demographic representativeness of golden perch collected during the 2018–19 fish kills, where an absence of older fish was also apparent (Thiem *et al.* 2021). In both studies, the 2009 cohort dominated, demonstrating the long-term persistence of this cohort in the Darling River, which has also contributed widely to the golden perch population in the River Murray (Zampatti *et al.* 2018). Nevertheless, the fish kill sample contained few fish from the 2016 cohort, which dominated in the Lower Darling River in early 2018. Either this cohort had diminished by the summer of 2018–19, when the fish kills occurred, or these juvenile fish were less susceptible to hypoxia, being smaller and having lower oxygen demands (Glencross and Felsing 2006). If these smaller, younger fish survived the hypoxic events and remain present across the $\sim$500 km of the Lower Darling River, they may convey some resilience to golden perch populations in this region.

Natal origin

Although age structures provide insight into population demographics, there is also a need to develop a mechanistic understanding of the effects of population processes (spawning, recruitment and movement) on observed patterns (Gowan and Fausch 1996; Wohl *et al.* 2005). This includes knowledge of recruitment sources and fish movement, and the effects of flow and connectivity. The Darling River was the predominant (92–100%) natal source of golden perch collected in the Lower Darling River. By contrast, in the Mid-Darling River, a large proportion (42%) of fish, particularly from the 2014 and 2015 cohorts, which were absent from the Lower Darling River, exhibited natal $^{87}Sr/^{86}Sr$ signatures representative of the Warrego or Culgoa rivers, tributaries of the Darling River. The remaining fish collected in the Mid-Darling River were predominantly of Mid-Darling River origin. Despite stocking of hatchery reared golden perch into the Darling River, pre-fish kill populations of golden perch showed little influence of stocking on population structure. The effectiveness of golden perch stocking is variable among rivers of the MDB (Crook *et al.* 2016; Thiem *et al.* 2017). As such, in rivers like the Darling, which demonstrate strong evidence of natural recruitment, a more effective approach to restoration than stocking may be to provide hydrological conditions that support *in situ* recruitment and connectivity to a diversity of spatially distinct recruitment sources.

Worldwide, there is growing recognition of the potential importance of tributaries to the population dynamics of riverine fish in flow-regulated rivers (Rice *et al.* 2008; Pracheil *et al.* 2013; Koster *et al.* 2021). Tributaries that preserve the hydrological and hydraulic conditions that promote spawning and recruitment may subsequently provide a source of recruits to flow-affected main channel habitats (Pollux *et al.* 2006; Webber *et al.* 2013). As such, preserving or reinstating the hydrological, hydraulic and habitat characteristics of tributary recruitment sources is crucial, as is enabling connectivity between tributary and main-stem rivers (Koster *et al.* 2014). In the Darling River system, a host of tributaries, particularly those with relatively intact flow regimes, may serve as recruitment sources for golden perch (Rolls *et al.* 2013; Stuart and Sharpe 2020). Furthermore, Mallen-Cooper and Zampatti (2020) highlight the opportunity to increase the diversity of potential fish recruitment sources by rehabilitating the hydrology and hydraulics of flow-affected tributaries in the Barwon–Darling river system.

The absence of tributary-derived recruits in the Lower Darling River, in particular the 2014 and 2015 cohorts, suggests that in the time frame represented in this study (2007–18), golden perch originating in the Warrego or Culgoa rivers did not make a detectable contribution to the Lower Darling River. Furthermore, the distinctive Warrego–Culgoa ^{87}Sr/^{86}Sr signature has not previously been observed in fish collected from the River Murray and its tributaries (Zampatti *et al.* 2019). It may be that fish from these regions do not disperse widely, possibly due to local-scale adaptions and migration patterns, or that only low numbers of fish may disperse large distances (Comte and Olden 2018). Nevertheless, golden perch eggs, larvae and juveniles are known to disperse hundreds of kilometres downstream along river systems (Stuart and Sharpe 2020; Zampatti *et al.* 2021). Consequently, it is likely that sequential barriers to movement along the Darling River, including aspects of the MLSS, particularly the Menindee Main Weir, may inhibit the downstream movement of golden perch at various life stages. The MLSS does not form an impenetrable barrier to all life stages, as demonstrated by the collection of juvenile golden perch dispersing downstream from the lakes (e.g. Stuart and Sharpe 2020). However, the regulating structures associated with the MLSS, and those upstream, may constitute enough of a barrier to result in distinct age structures and recruitment sources between population contingents in the Lower and Mid-Darling River.

In the Lower Darling River in 2018, the golden perch age structure included prominent 2009 and 2016 cohorts. Fish from these cohorts demonstrated a Darling River natal origin and, in the case of the 2009 Darling-derived cohort, also contributed to populations in the River Murray (Zampatti *et al.* 2021). These age-classes, however, were largely absent from the Mid-Darling River. This was despite this region experiencing high flows in these years, like the Lower Darling River, and the collection of early life stage golden perch, with a proposed origin in the northern tributaries of the Barwon–Darling river system, in association with these flows (Stuart and Sharpe 2020). The fate of these cohorts in the Mid-Darling River remains unresolved, but anthropogenic fragmentation of the river system may be a contributing factor to the disparate population structures among regions.

In the Lower Darling River, there was also a minor influence of the River Murray as a recruitment source, but these fish were absent from the Mid-Darling River, again indicating that barriers such as the Menindee Main Weir may inhibit the upstream movement of golden perch. This effect is likely to be substantial in years of low to medium flow, which are frequent in the Darling River (Thoms *et al.* 2004), but may be ameliorated during occasional large floods when bidirectional connectivity is reinstated past major barriers in the system. Indeed, a study of golden perch genetics by Faulks *et al.* (2010) found that high-flow events in arid rivers promote recruitment and connectivity that increase effective population size and genetic diversity. Consequently, mitigating the effects of Menindee Main Weir and other weirs on fish movement presents a key management priority for the Barwon–Darling river system to promote greater age structure diversity and resilience in golden perch populations, and potentially other wide-ranging species, such as silver perch *Bidyanus bidyanus* (Thiem *et al.* 2021).

Integrating otolith chemistry and age enables consideration of the spatial and temporal provenance of cohorts and associated environmental conditions, including flow (Campana and Thorrold 2001). In the Mid- and Lower Darling River, distinct cohorts of golden perch were related to recruitment events in natal locations that coincided with overbank or in-channel flow pulses. These findings concur with the hydrological characteristics documented in a range of golden perch recruitment studies (Mallen-Cooper and Stuart 2003; Roberts *et al.* 2008; Zampatti and Leigh 2013). Nevertheless, golden perch also exhibits life history flexibility across its geographic range and, in some intermittently flowing rivers of the MDB, recruitment has also been documented in cease-to-flow periods (Balcombe *et al.* 2006). In the present study, however, fish originating under this hydrological scenario did not appear to contribute to golden perch populations in the Darling River.

For fishes with periodic life histories, river regulation and climate (e.g. drought) can diminish age structure diversity and decrease population resilience (Winemiller 2005; Olden *et al.* 2006). In the present study, the year-class strength of golden perch was low when flows were low and stable or non-existent. In particular, age structures reflect the profound effect of the Millennium drought (2001–09), punctuated by one recruitment event in 2007, and the more recent drought (2013–19) in the Darling River catchment. However, in the Mid-Darling River, the effects of drought and flow regulation on age structure appear to have been partially buffered by cohorts derived from tributary rivers in association with in-channel flow pulses. These findings demonstrate that the preservation of even low-magnitude flow events in tributaries may confer improved population resilience to main-stem fish populations, if tributaries are hydrologically and physically connected to the main river. They also reinforce the need to protect the natural hydrological characteristics of arid, predominantly unregulated rivers like the Warrego to preserve ecological function (Kingsford 2000). From a management perspective, understanding the characteristics of flow associated with spawning, recruitment and movement in source tributaries could promote the efficacious use of finite environmental water resources (Poff *et al.* 2003).

Movement

This study indicates a diversity of lifetime movement patterns for golden perch in the Darling River with some variation between the mid- and lower reaches of the river. In the Mid-Darling River, immigration of YOY recruits from the Warrego or Culgoa rivers was a strong driver of population structure, but birth and lifelong residency in the Mid-Darling River was also prominent. Similarly, lifelong residency was commonplace in the Lower Darling River, particularly in fish collected in 2014. However, in 2018, a large proportion (46%) of fish exhibited a more complex lifetime movement pattern, where fish were born in the Darling River, moved downstream to the Lower Murray, commonly at age-0+ to age-1+, and then returned to the Lower Darling River later in life. The expression of alternative movement behaviours within a population has individual- and population-level impacts

(Barthel *et al.* 2008). Movement may beneficially expose fish to suitable habitats and environmental conditions for growth and reproduction, but may also increase the incidence of individual mortality (Alerstam *et al.* 2003). For example, golden perch that move among rivers or regions of the MDB exhibit faster growth rates that potentially confer fitness benefits (Barrow *et al.* 2021). Ultimately, it is likely that a combination of retentive and dispersive behaviours will promote resilience in golden perch populations in variable environments (Secor 1999).

Ontogenetic variability in habitat use has previously been described for golden perch, particularly the use of inundated floodplain habitats as nurseries (Ebner *et al.* 2009; Rolls and Wilson 2010; Sharpe 2011). In the present study, ~40% of individuals sampled in the Lower Darling River in 2018 were born in the Darling River and moved downstream into the Murray, where they remained for several years before migrating back into the Darling River. Return movements into the Darling River occurred at ages when fish were likely to have been reproductively mature (i.e. >4 years; Mallen-Cooper and Stuart 2003). Whether these movements constitute a form of natal fidelity, which is common in diadromous and some potamodromous fishes (Dittman and Quinn 1996; Duponchelle *et al.* 2016), remains to be explored; nevertheless, this complex movement pattern presents a range of considerations for river management. The dispersal of fish from the Lower Darling River, either passively as eggs and larvae or actively as juveniles, requires hydrological and physical connectivity between the Darling and Murray rivers, including unimpeded lotic environments over hundreds to thousands of kilometres (Mallen-Cooper and Zampatti 2020; Stuart and Sharpe 2020). Subsequently, the return migrations of adults require similar considerations, but also the restoration of seasonal flow pulses to cue upstream movements (Koster *et al.* 2014; Mallen-Cooper and Zampatti 2018) and a need to mitigate instream barriers to passage with effective fishways (Baumgartner *et al.* 2014).

Management implications and conclusions

In the years preceding the 2018–19 fish kills, there was substantial variability in golden perch age structure, recruitment source and movement patterns between the Lower and Mid-Darling River. These differences were potentially affected by spatially discrete recruitment sources, distinct hydrology between the regions and interrupted longitudinal connectivity. The MLSS, particularly the Menindee Main Weir, appears to delineate the population contingents. Consequently, rehabilitation of golden perch populations would benefit from the reinstatement of bidirectional connectivity at this structure, and others throughout the Barwon–Darling river system, to facilitate the upstream migration of juveniles and adults and the downstream dispersal of eggs, larvae and YOY. For all life stages, movements may occur over hundreds to thousands of kilometres, thus requiring the restoration of hydrological, hydraulic and physical connectivity at these scales (Mallen-Cooper and Zampatti 2020; Stuart and Sharpe 2020; Zambaldi and Pompeu 2020).

Considering the ongoing effects of climate change and flow regulation, promoting greater age structure diversity of golden perch in the Darling River will help safeguard populations against environmental perturbations (Berkeley *et al.* 2004) and would improve spawning outcomes, recruitment and population growth (Secor 2000). Golden perch in the Darling River, and more broadly in the MDB, have the advantage of population and life history strategies that integrate spatial and temporal bet-hedging mechanisms (Slatkin 1974; Kraus and Secor 2004). These include a combination of a periodic life history, migratory and recruitment source diversity, life history flexibility and ontogenetic variation in habitat use. In conjunction, these traits produce a portfolio effect whereby a diverse array of life history 'assets' has a stabilising effect on meta-populations due to differential responses of contingents to environmental variability (Schindler *et al.* 2010). In the case of golden perch in the Darling River, the resilience of this portfolio could be further improved by increasing the mosaic of recruitment and refuge habitats and improving the spatial processes that connect these (Kerr *et al.* 2010).

The 2018–19 fish kills in the Darling River spurred a renewed and urgent call to action for the rehabilitation of native fish populations in the MDB (Vertessy *et al.* 2019; MDBA 2020). The present study contributes to an understanding of pre-fish kill age demographics of golden perch in the Darling River, including how the spatial arrangement of recruitment sources, movement and connectivity influence population dynamics. Understanding population structure and causal mechanisms is fundamental to the rehabilitation of riverine fishes worldwide. This knowledge is key to establishing realistic rehabilitation objectives and targets, guiding restoration initiatives, such as mitigating barriers to movement and environmental flows, and ultimately measuring population response.

Conflicts of interest

Lee Baumgartner is an Associate Editor and Katherine Doyle is a Guest Editor of the 'Fish Kills in Freshwaters' special issue in *Marine and Freshwater Research.* Despite this relationship, they did not at any stage have Editor-level access to this manuscript while in peer review, as is the standard practice when handling manuscripts submitted by an editor to this Journal. *Marine and Freshwater Research* encourages its editors to publish in the Journal and they are kept totally separate from the decision-making process for their manuscripts. The authors declare that they have no further conflicts of interest.

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