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Dispersal and Kinship Patterns of a Pelagic-Spawning Riverine Fish Highlight the Value of Connectivity Over Large Spatial Scales

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ABSTRACT

Managing fish populations in regulated rivers requires an understanding of the spatial and temporal scale of their dispersal, the locations of key spawning and nursery habitats and the hydraulic processes that interplay with their life history. Golden perch (*Macquaria ambigua*), an Australian freshwater pelagic-spawning fish, highlights the worldwide challenges of managing riverine species that rely on hydraulic conditions to sustain critical metapopulation processes. This study aimed to quantify the spatial scale of early life history golden perch dispersal after a drought-breaking in-channel flow event in early 2020 in a regulated lowland river. Otolith microchemistry (⁸⁷Sr/⁸⁶Sr) and single nucleotide polymorphisms (SNPs) determined natal origins and sibling relationships, respectively, of young-of-year (YOY) caught in a floodplain nursery with larval fish captured upstream. For fish collected in the floodplain nursery, dispersal distances ranged to ~1600 km. Otolith microchemistry attributed 52% of YOY as localised in origin, 44% as originating in the midcatchment and 4% from the most upstream sample locations. Genetic analyses identified a full-sibling pair captured 900 km apart and 31 half-sibling pairs that linked YOY to larval fish captured at a diversity of upstream sites. Our study highlights the range of spatial scales over which ELH dispersal can occur for golden perch and emphasises the importance of interconnected flowing river habitats in sustaining metapopulation processes. We illustrate the positive results that increased riverine connectivity can yield for fish with similar life history strategies.

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1 | Introduction

Dispersal plays an important role in driving species' distributions, providing access to different habitats that support recruitment and promoting gene flow between subpopulations (Hanski 1998; Heggenes et al. 2006; Radinger and Wolter 2014). The construction of dams and weirs to regulate rivers has caused major losses of lotic habitats, reduced longitudinal connectivity, altered floodplain function and has ultimately resulted in biodiversity declines globally (Grill et al. 2019). The regulation of rivers significantly disrupts dispersal due to water abstraction, the conversion of lotic to lentic habitat and restricted passage over or through riverine structures such as dams and weirs (Humphries and Lake 2000; Baumgartner, Reynoldson, and Gilligan 2006; Mu et al. 2014; Pavlov, Mikheev, and Kostin 2020; Mollenhauer et al. 2021). While fish populations may survive brief periods of lost connectivity, prolonged disconnection can fragment populations, alter community structure and reduce gene flow (Kukuła and Bylak 2022; Machado et al. 2022; Martelo et al. 2024). This poses a significant threat to the long-term persistence of many species (Frankham 2022). Habitat fragmentation is further exacerbated by drought, with the interacting effects of climate and river regulation posing a compounding threat to fish population viability particularly in arid and semiarid regions (Marshall, Lobegeiger, and Starkey 2021).

In rivers, the eggs, larvae and juveniles of pelagic-spawning fish species often undergo a downstream dispersal phase, which can play a key role in distributing early life history (ELH) stages to productive nursery habitats (Lechner, Keckeis, and Humphries 2016). This downstream dispersal can occur over large spatial scales (i.e., hundreds of kilometres) for some species (Dudley and Platania 2007; Wilde and Urbanczyk 2013; Pachla et al. 2022). Investigating ELH dispersal is challenging, as traditional methods of tracking fish (e.g., using visible marks or electronic tags) are not suitable due to their small size (Cooke et al. 2013; Carnicer et al. 2023). Consequently, for many species there is a limited understanding of the spawning habitats, spatial and temporal scales of drift, nursery habitats, juvenile dispersal pathways and the underlying hydrologic and hydraulic drivers of these processes (Carnicer et al. 2023). However, several contemporary methods, such as otolith microchemistry and genetics, are providing novel insights into dispersal patterns of ELH stages (Humston et al. 2010; Woods et al. 2010; Chase et al. 2015; Ottmann et al. 2016; Reis-Santos et al. 2023). Previous studies have demonstrated that otolith chemistry, particularly the analysis of strontium isotopes ($^{87}\text{Sr}/^{86}\text{Sr}$), can reveal distinct signatures that correspond to the water chemistry in different habitats, enabling determination of natal origin and movement histories (Barrow et al. 2021; Thiem et al. 2022; Reis-Santos et al. 2023). Genetic techniques, such as kinship analysis, have also been used to study dispersal of marine (Schunter et al. 2014; Aloia et al. 2018) and freshwater fish (Furlan et al. 2024).

Golden perch (*Macquaria ambigua*) is a freshwater fish endemic to eastern Australia and is emblematic of the global challenges in managing pelagic-spawning riverine species (Dudley and Platania 2007). Hydrology and hydraulics play a major role in driving population dynamics of golden perch, affecting spawning (Koster et al. 2017; Thiem et al. 2023), recruitment (Roberts, Duivenvoorden, and Stuart 2008;

Sharpe 2011; Zampatti and Leigh 2013b) and migration of both subadults and adults (Reynolds 1983; Zampatti et al. 2018; Zampatti, Leigh, et al. 2021). ELH golden perch also undergo active and passive downstream dispersal on flow pulses (Sharpe 2011; Stuart and Sharpe 2020), with this dispersal an important influence on population structure in receiving regions (Zampatti, Leigh, et al. 2021). There is evidence suggesting that golden perch are flexible spawners (Balcombe et al. 2006; Balcombe and Arthington 2009; Ebner, Scholz, and Gawne 2009). However, existing literature indicates that spawning intensity and recruitment success are likely influenced by river flow, with higher flows and flooding generally enhancing recruitment outcomes for golden perch (Ebner, Scholz, and Gawne 2009; King, Tonkin, and Mahoney 2009; Zampatti and Leigh 2013a). As such, like other pelagic-spawning fish with drifting life history stages, golden perch are particularly susceptible to widespread river regulation and climate change threats (Koehn et al. 2020).

The northern Murray–Darling Basin (MDB) is a heavily regulated river system in eastern Australia, once characterised by a hydrologically variable flow regime (Mallen-Cooper and Zampatti 2020). While river regulation has negatively impacted golden perch in the northern MDB, successful recruitment occurs (Stuart and Sharpe 2020; Thiem et al. 2023) and through immigration has the potential to influence population dynamics in other regions where successful recruitment does not occur (Zampatti, Leigh, et al. 2021). Existing conceptual models for golden perch dispersal exist; Reynolds (1983) demonstrated long-distance upstream movement of mature golden perch in the northern MDB, suggesting that this dispersal strategy functioned to allow for downstream dispersal of drifting eggs and larvae to recruitment habitat. This was further developed by Stuart and Sharpe (2020) who proposed a conceptual model of golden perch life history in the northern MDB, which consisted of (i) flow cued upstream riverine migrations of adults and spawning within lotic main stem or tributary habitats of the Barwon–Darling catchment, (ii) downstream drift of pelagic eggs and larvae to littoral or floodplain nursery habitats, such as the Menindee Lakes, (iii) rapid juvenile growth in productive off-channel and littoral habitats, such as the Menindee Lakes, followed by (iv) juvenile dispersal both upstream (Barwon–Darling River and tributaries) and downstream (Lower Darling Baaka River (LDBR)).

This study aimed to investigate how large-scale longitudinal connectivity influences ELH dispersal, by quantifying the dispersal distances of young-of-year (YOY or Age 0) golden perch. This required estimation of the natal origin of YOY golden perch captured in a known floodplain nursery habitat (the Menindee Lakes, the terminus of the northern MDB) and quantification of dispersal distances from natal locations to the nursery. We combined otolith chemistry and genetic techniques to explore the spatial and temporal dispersal patterns of ELH golden perch during a moderate flow event that occurred in early 2020, connecting over 1800 km of riverine habitat in the northern MDB (Craik and Claydon 2020; Thiem et al. 2023). Considering the antecedent conditions of prolonged loss of connectivity in the northern MDB, results are discussed within the context of their relevance for water allocation and operational flow management to support large-scale river habitat connectivity and ELH dispersal of pelagic-spawning fish over appropriate spatial and temporal scales.

2 | Methods

2.1 | Study Region and Fish Surveys

This study was conducted in the Barwon–Darling catchment within the New South Wales section of the northern MDB, Australia (Figure 1). The Barwon–Darling catchment was historically characterised by near-perennial flows with continuous reaches of lotic habitat often extending for hundreds of kilometres (Mallen-Cooper and Zampatti 2020), to the downstream Menindee Lakes. These nine large, but shallow, regulated lakes are well-established floodplain nursery habitats (Sharpe 2011). However, river regulation, flow storage, water diversion and

climate change have increased the frequency and duration of zero or near-zero flow periods, resulting in a major reduction in the availability and persistence of lotic habitat in the Barwon–Darling, while also reducing regular filling and connection between the nine Menindee Lakes (Mallen-Cooper and Zampatti 2020). This study was conducted during a moderate in-channel flow event that occurred in early 2020, after three years of severe drought. The maximum flow volumes reached during the event are relatively common, occurring approximately 15% of the time postregulation (see Thiem et al. (2023) for a detailed description and analysis of the flow event). Due to the antecedent conditions, including prolonged periods of zero-flow from 2017 to 2019, a legal intervention order was implemented to

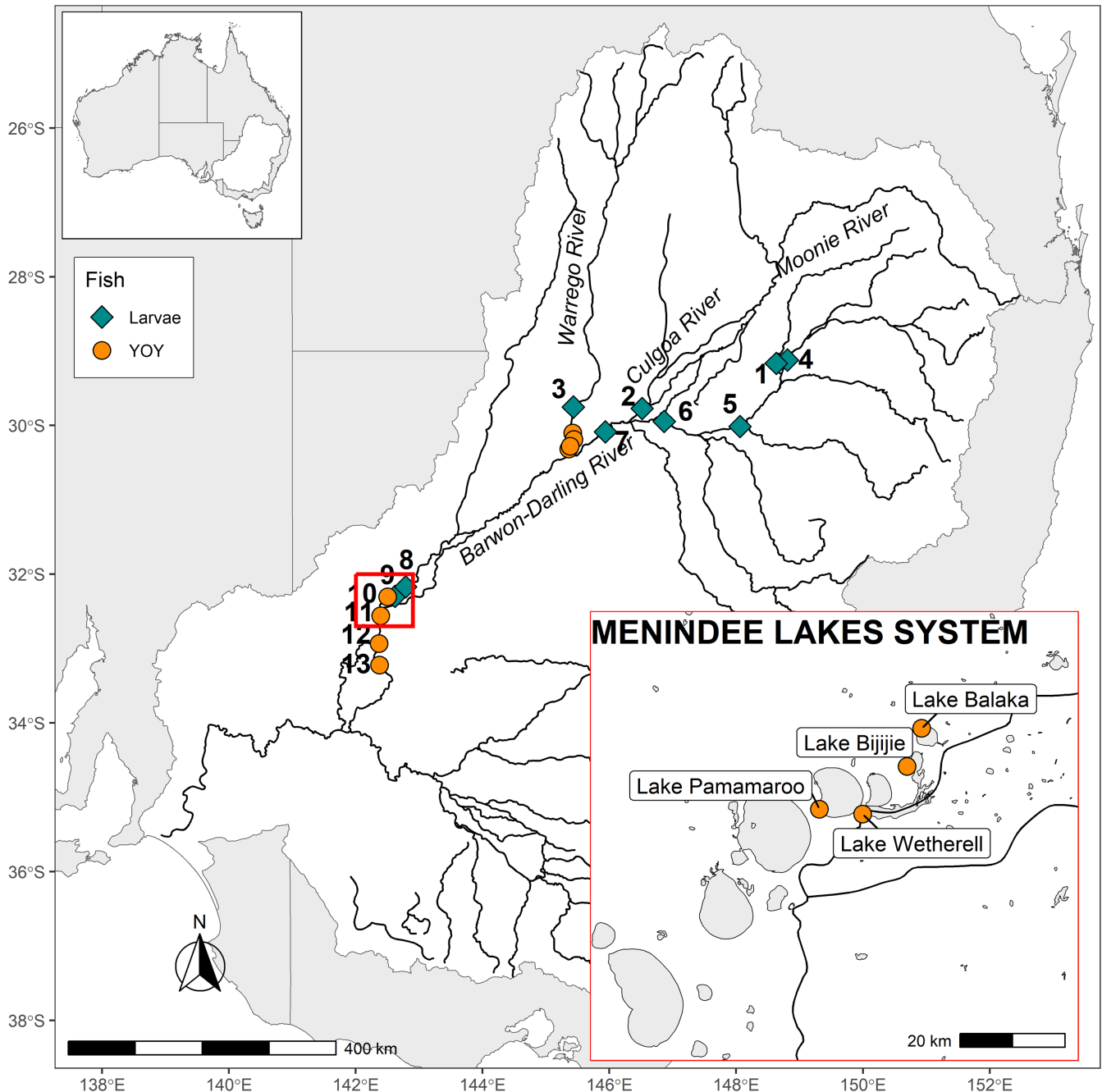


FIGURE 1 | The Murray–Darling Basin and the Menindee Lakes system showing golden perch sampling locations. Green diamonds represent larval sampling sites and orange circles represent young-of-year sampling sites. Refer to Table 1 for site details.

TABLE 1 | Details of golden perch larvae and young-of-year (YOY) sampling sites and associated 'system' (group of sites within the same general region). Site numbers correlate to those depicted in Figure 1. River distance is the distance (kilometre) from the downstream extent of Lake Wetherell (a central location to the four Menindee Lake sites) to the site, in either an upstream or downstream direction (–).

Site (number)	System	Date sampled	River distance from Menindee Lakes (km)
Larval drift netting sites			
Moonie River Bridge (1)	Moonie	5/03/2020	1593
Lower Culgoa (2)	Culgoa	26/03/2020	1044
Fords Bridge (3)	Warrego	26/03/2020	860
D/S Little Weir (4)	Barwon	5/03/2020	1625
Walgett (5)	Barwon	4/03/2020	1374
Brewarrina (6)	Barwon	5/03/2020	1122
Bourke (7)	Darling	4/03/2020 and 26/03/2020	917
Viewmont (8)	Darling	20/03/2020	62
3 Mile Creek Bridge (9)	Darling	20/03/2020	10
YOY sampling sites			
Boera Dam	Warrego	22/07/2020	811
Booka Dam	Warrego	22/07/2020	798
Homestead Dam	Warrego	21/07/2020	782
Dicks Dam	Warrego	22/07/2020	775
Junction of Warrego and Darling	Darling	23/07/2020	762
Lake Bijijie	Menindee Lakes	3/11/2020	25
Lake Pamamaroo	Menindee Lakes	5/11/2020	1.5
Lake Wetherell	Menindee Lakes	3/11/2020	0
Lake Balaka	Menindee Lakes	4/11/2020	45
Lake Wetherell Outlet (10)	LDBR	7/10/2020	–2
Bono (11)	LDBR	11/10/2020	–74
Karoola (12)	LDBR	20/10/2020	–159
Moorara (13)	LDBR	8/12/2020	–237

prevent extraction during the flow event to promote large-scale longitudinal connectivity and aid the restoration of this highly stressed riverine ecosystem (Craik and Claydon 2020). As a result, the 2020 flow event provided the first long-distance (i.e., > 1800 km) hydroecological connectivity for over three years.

Fish survey locations ($n=22$) spanned over 1830 km to encompass riverine sites in the Barwon–Darling River and its major northern tributaries, sites in the Menindee Lakes at the terminus of the Barwon–Darling catchment and sites in the LDBR, downstream of the Menindee Lakes (Figure 1 and Table 1). Larval fish were sampled throughout the protected flow event in March 2020 given this was predicted to induce golden perch spawning (Thiem et al. 2023) (Table 1). YOY sampling was carried out in winter (July) or spring (October and November) of 2020 after flows had subsided (Table 1). Sampling of YOY was conducted at four sites in the Warrego River, one site at the junction of the Warrego and the Darling rivers, a site in four of the

Menindee Lakes (Balaka, Bijijie, Pamamaroo, Wetherell) and at four sites in the LDBR (Figure 1 and Table 1).

Standardised larval drift-netting surveys were conducted to capture drifting fish within the river channel. Three drift nets (1.5 m long, 500- μ m mesh, 50-cm diameter opening) were set at each site overnight (~18 h), suspended in the flow off instream wood habitat, to sample the top 0.5 m of the water column. Drift-netting samples were preserved in 90% ethanol (see Thiem et al. (2023) for more detailed description). YOY sampling in the Warrego River and Menindee Lakes was conducted using fyke nets (Mika et al. 2022; Stuart et al. 2023). The LDBR was sampled by boat electrofishing (7.5 kW Smith-Root model GPP 7.5 H/L boat-mounted electrofishing unit), where 12 replicate 90-s electrofishing operations were performed according to standardised methods (Crook et al. 2023). YOY golden perch collected by both fyke netting and electrofishing were euthanized using an Aquis overdose, measured

(total length (TL), millimetre) and weighed (gram) in the field before being stored frozen.

All YOY and a subsample of fish captured in the larval surveys (fish caught in larval drift nets were a combination of larvae and juveniles) were prepared for genetic and otolith analyses. The subsampling protocol was designed to equally encompass the entire size range of the catch at each site; 30 fish were subsampled per site, where one fish was sampled from each 1/30th of the total size range. Where there were fewer than 30 fish captured at a site, all fish were prepared (Thiem et al. 2023). The total number of fish used in each type of analysis varied slightly to ensure that only samples in good condition were used and to account for minimum otolith size requirements ($>100\mu\text{m}$) for the otolith chemistry analysis. All fish used in the genetic and otolith analyses were remeasured (TL: millimetre), the sagittal otoliths were removed and a fin clip sample ($\sim 2 \times 2\text{mm}$) was taken from the tail fin or body tissue and preserved in 90% ethanol for genetic analyses.

2.2 | Otolith Analysis

Otolith chemistry analyses and daily ageing were used to estimate dispersal distances of YOY (i.e., Age 0) golden perch. One sagittal otolith from each fish (YOY; $n = 165$, larvae; $n = 252$), was mounted whole on a glass microscope slide using Crystalbond (Ted Pella Inc., United States) and prepared for posthatch age estimation. Further description of the daily ageing protocol used is detailed in Thiem et al. (2023), with daily age increment formation in golden perch validated by Brown and Wooden (2007). For the YOY fish, ages were only used to confirm their YOY status, thereby confirming that they originated within the temporal scope of the study.

Sectioned otoliths were transferred to master slides for the microchemistry analyses, with the master slides holding approximately 20 otoliths each. Wetted lapping film ($3\mu\text{m}$) was used to polish the otolith to the primordium and remove any remaining Crystalbond from the surface of the otolith. A total of 365 otoliths (YOY, $n = 149$; larvae, $n = 216$) were used for analysis of strontium isotope ratios ($^{87}\text{Sr}/^{86}\text{Sr}$) (Melbourne University Isotope and Trace Element Geochemistry Laboratory). The analysis consisted of an Applied Spectra RESolution excimer laser ablation system (Applied Spectra, West Sacramento, California, United States) coupled to a multicollector inductively coupled plasma mass spectrometer (MC-ICPMS). Four master slides were contained within the laser ablation system at a time, video imaging of the slides enabled digitisation of the intended ablation spot or path within GeoStar software (ver. 6.14, Applied Spectra).

For larval fish, $80\text{-}\mu\text{m}$ ablation spots measured $^{87}\text{Sr}/^{86}\text{Sr}$; the laser was operated to provide a fluence of 3Jcm^{-1} at the sample surface and was pulsed at 5Hz. Ablation was undertaken under pure He to minimise deposition of ablated material. Ablation spots were taken from the edge of the otolith to provide an estimate of the $^{87}\text{Sr}/^{86}\text{Sr}$ signatures from the known capture location (Macdonald, McNeil, and Crook 2012). Each analysis consisted of 30s of ablation, separated by 30s of gas blank measurement. Ablation paths ($50\text{-}\mu\text{m}$ spot, $5\mu\text{m}\cdot\text{s}^{-1}$) were taken on

YOY otoliths from the primordium to the edge to assess potential changes in $^{87}\text{Sr}/^{86}\text{Sr}$ from birth to capture. Ablation was conducted at 10Hz for transects. Each analysis varied in the duration of the ablation due to the differing size of the otoliths and the desired ablation path; each analysis was separated by 30s of gas blank measurement. A marine carbonate standard composed of mollusc shells ($^{87}\text{Sr}/^{86}\text{Sr} = 0.709160$) was analysed after every 10th sample to calculate external precision and assess the accuracy of the isotopic results.

Mean $^{87}\text{Sr}/^{86}\text{Sr}$ values were calculated from the otolith spot measures in larvae, and a single-factor analysis of variance (ANOVA) was conducted to examine variation in $^{87}\text{Sr}/^{86}\text{Sr}$ otolith signatures between sites. As site had a significant effect, a pairwise (Tukey's adjustment) post hoc analysis was used to assess site-wise differences. Results were compared to an existing isoscape for the MDB (Zampatti, Fanson, et al. 2021; Zampatti, Leigh, et al. 2021). While there was consistency between $^{87}\text{Sr}/^{86}\text{Sr}$ values in the current study and the existing isoscape in the tributaries, some discrepancies in the main channel of the mid-Darling River were evident. The variation observed between this study and the existing isoscape is likely due to the high flows originating from the northern tributaries during 2020 (Zampatti, Fanson, et al. 2021). Given this, we used $^{87}\text{Sr}/^{86}\text{Sr}$ values measured in the edge of golden perch larval otoliths to identify the potential natal sources of YOY golden perch captured in the latter half of 2020 rather than the existing isoscape values. Three broad regions of origin were delineated from the larval otolith chemistry data in the river upstream of the Menindee Lakes: Region 1, the Barwon River $>1550\text{km}$ upstream of the Menindee Lakes; Region 2, the midcatchment including sites from Walgett to Bourke and the three northern tributary inputs; Region 3, local to the Menindee Lakes in the upstream Darling River. Due to the coarse spatial resolution of the larval sampling sites, the exact boundaries of these regions could not be defined. YOY transect data was smoothed (1s moving average) and compared to regions identified through the analysis of larval samples. All statistical analyses and data visualisation were conducted in R version 3.5.1 (R Development Core Team 2019) using the vegan package (Oksanen et al. 2013), with a minimum significance level of $\alpha = 0.05$. River distance was calculated using the riverdist package version 0.15.5 (Tyers 2017).

2.3 | Genetic Analysis

Genetic analyses were used to identify related individuals (e.g., full-siblings and half-siblings) within and between YOY and larval samples. Relationships linking larvae captured in the upstream portion of the Barwon–Darling catchment with YOY captured in the Menindee Lakes and LDBR enabled identification of YOY natal origin and an estimate of dispersal distances.

A total of 376 fin clip samples were sent to Diversity Arrays Technology (DART) Pty. Ltd. for DNA extraction and DART sequencing. For the analysis, 153 YOY and 223 larval samples were initially prepared. Thirty-three samples failed to produce sequencing libraries due to insufficient quality and/or quantity of DNA and were removed from further analyses. Unfiltered single nucleotide polymorphism (SNP) data consisted of 14,679 SNP loci genotyped for 343 individuals. To generate

a high-quality genetic dataset for analysis, additional filters were applied to the unfiltered SNP data using the dartR V1.1.11 package (Gruber et al. 2018) in R version 3.5.1 (R Development Core Team 2019). The filters included retaining only individuals that were genotyped for more than 75% of loci, retaining only loci that were genotyped for 95% of individuals, application of a minor allele filter of 0.01, retaining one SNP per RAD tag (to control for physical linkage) and including only those SNPs that were fully reproducible across all technical replicates ($t = 1$). The filtered dataset consisted of 1489 biallelic SNPs genotyped for a total of 319 individuals.

In the filtered dataset, there were 80 individuals detected with unusually high individual heterozygosity (PHt, 0.05–0.45). Because their inclusion can bias kinship assignments, the highly heterozygous individuals were also filtered from the analysis. Previous work on a cryptic species of golden perch in the Dawson River also detected individuals with high heterozygosity (0.39), which was attributed to potential hybridisation between lineages occurring within hatcheries that stock golden perch into the Dawson River (Beheregaray et al. 2017). Given that individuals with partial ancestry from other cryptic species of golden perch (the Fitzroy and Lake Eyre Basin lineages) have also been detected in the Darling–Baaka River (Attard et al. 2022), it is possible that the highly heterozygous individuals detected in the current study could be the offspring of hybrid lineages. Following removal of highly heterozygous individuals, there were 239 individuals retained for the kinship analysis.

Full-sibling and half-sibling pairs were identified using Colony2 v2.0.6.8 (Jones and Wang 2010). Colony2 was run three times with the following settings: not updating allele frequencies, dioecious species, assumed non-inbreeding (recommended for dioecious with no or low-level inbreeding), diploidy, polygamy for both males and females (i.e., allowing half-siblings), sibship size scaling, no sibship prior, calculating allele frequencies, medium

run length, full-likelihood method and high precision. Markers were assumed to be codominant. Sibling pair assignments with a probability < 95% were disregarded. Sibling pairs were only included in the analyses if they were consistently identified in the three runs conducted; this conservative method may result in some true sibling pairs remaining unidentified but considerably reduces potential false-positive rates.

3 | Results

3.1 | Otolith Analysis

Golden perch captured in the March 2020 drift net surveys were aged between 1 and 82 days posthatch (a combination of larvae and juveniles), with most of the fish sampled estimated to be < 40 days old (mostly hatched in February–early March). There was significant variation in the $^{87}\text{Sr}/^{86}\text{Sr}$ among sites as measured from ablation spots taken from the edge (indicating the capture location) of the larval otoliths ($F_{7,124} = 206.8$, $p < 0.001$, Figure 2). At the most upstream site (~1600 km upstream of the Menindee Lakes), $^{87}\text{Sr}/^{86}\text{Sr}$ values had an average of 0.7081. The three tributaries (Moonie, Culgoa and Warrego rivers) and Barwon–Darling sites at Bourke and Brewarrina had the lowest $^{87}\text{Sr}/^{86}\text{Sr}$ values and were not significantly different from each other ($p > 0.05$), ranging from 0.7064 to 0.7067. Sites upstream of the Menindee Lakes (Viewmont and 3 Mile Creek Bridge, 62 and 10 km upstream, respectively) had average $^{87}\text{Sr}/^{86}\text{Sr}$ values of 0.7070 and 0.7072 respectively, with the $^{87}\text{Sr}/^{86}\text{Sr}$ values increasing near the Menindee Lakes. The wide variation in the $^{87}\text{Sr}/^{86}\text{Sr}$ values identified at Walgett was likely due to the larvae sampled being a mix of fish from the Moonie, Namoi and Barwon rivers.

These results were used to delineate three broadscale regions to facilitate the comparison of $^{87}\text{Sr}/^{86}\text{Sr}$ values within YOY otolith transects. Region 1 (depicted in red, Figure 2) is composed of the

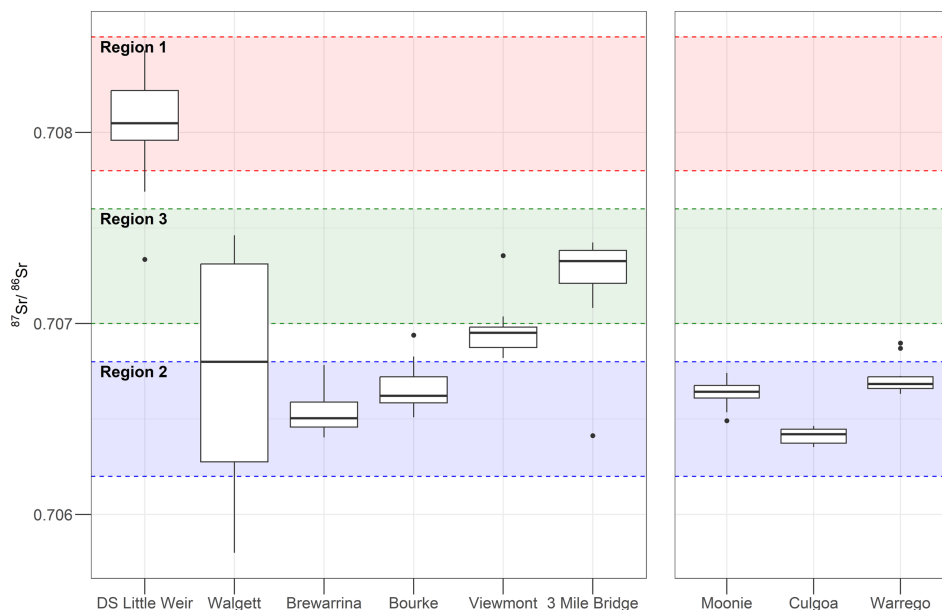


FIGURE 2 | Boxplot of the $^{87}\text{Sr}/^{86}\text{Sr}$ ratios for each larval sampling site from measurements taken at the edges of larval fish otoliths. Coloured shading shows the $^{87}\text{Sr}/^{86}\text{Sr}$ ranges chosen to delineate three regions within the Barwon–Darling catchment. The figure is divided into two sections: mainstem (left) and tributary sites (right), with sites arranged from upstream to downstream.

Barwon River upstream of the Barwon–Moonie junction, characterised by $^{87}\text{Sr}/^{86}\text{Sr}$ values > 0.7078 . Region 2 (depicted in blue, Figure 2) encompassed the middle of the catchment, including sites at Brewarrina and Bourke, as well as the tributaries (Moonie, Culgoa and Warrego rivers) with $^{87}\text{Sr}/^{86}\text{Sr}$ values ranging between 0.7062 and 0.7068. Region 3 (depicted in green, Figure 2) encompassed sites local to the Menindee lakes in the upstream Darling River, defined by an $^{87}\text{Sr}/^{86}\text{Sr}$ range of 0.7070–0.7076.

Otolith ageing confirmed all golden perch captured between July and December 2020 were YOY. Natal origin of the YOY ($^{87}\text{Sr}/^{86}\text{Sr}$ values at the otolith core) was matched to one of three regions defined in Figure 2. Of the 127 fish captured in the Menindee Lakes, 66 (52%) were estimated to have originated locally in Region 3 (the Darling River upstream of Menindee Lakes), with consistent $^{87}\text{Sr}/^{86}\text{Sr}$ values apparent throughout their life history (Figure 3), 56 fish (44%) were estimated to have originated in Region 2 (the midcatchment, including the tributaries), with all exhibiting lower $^{87}\text{Sr}/^{86}\text{Sr}$ values at the otolith core (Figure 3). Five fish (4%) originated in Region 1 (> 1550 km upstream of the Menindee Lakes) (Figure 3). Of the YOY captured in the LDBR ($n = 17$), two were estimated to have originated in Region 2, but the majority ($n = 15$) appear to have been associated with Region 3 for their entire life history.

3.2 | Genetic Analysis

Eight full-sibling pairs and 71 half-sibling pairs were identified across the combined larval and YOY datasets. Of the full-sibling pairs, five pairs were individuals that were sampled at the same site on the same date and three pairs were of individuals that were sampled in different systems (Appendix S1). In this context, we refer to 'system' as a grouping of sites, either lake or river, that are geographically linked (e.g., Menindee Lakes comprised of four sampled lakes, the LDBR comprised of four sampled river sites); see Table 1 for classification. Larval full-sibling pairs sampled in different systems included two pairs with both pairs having one individual captured in the Moonie River and the other individual in the Barwon River (Walgett) (~218 km apart) (Appendix S1). In both cases, the larval fish were collected a day apart (4/3/20 and the 5/3/20). There was also a full-sibling pair that included a larval fish captured in March 2020 and a YOY fish captured in November 2020. The larval individual of this pair was captured in the Darling River at Bourke and the sibling YOY was captured in the Menindee Lakes, in Lake Wetherell (~900 km apart).

Among the 71 half-sibling pairs that were identified in the analysis, 18 were captured in the same system including 16 at the same site (Appendix S2). The remaining 53 half-sibling pairs

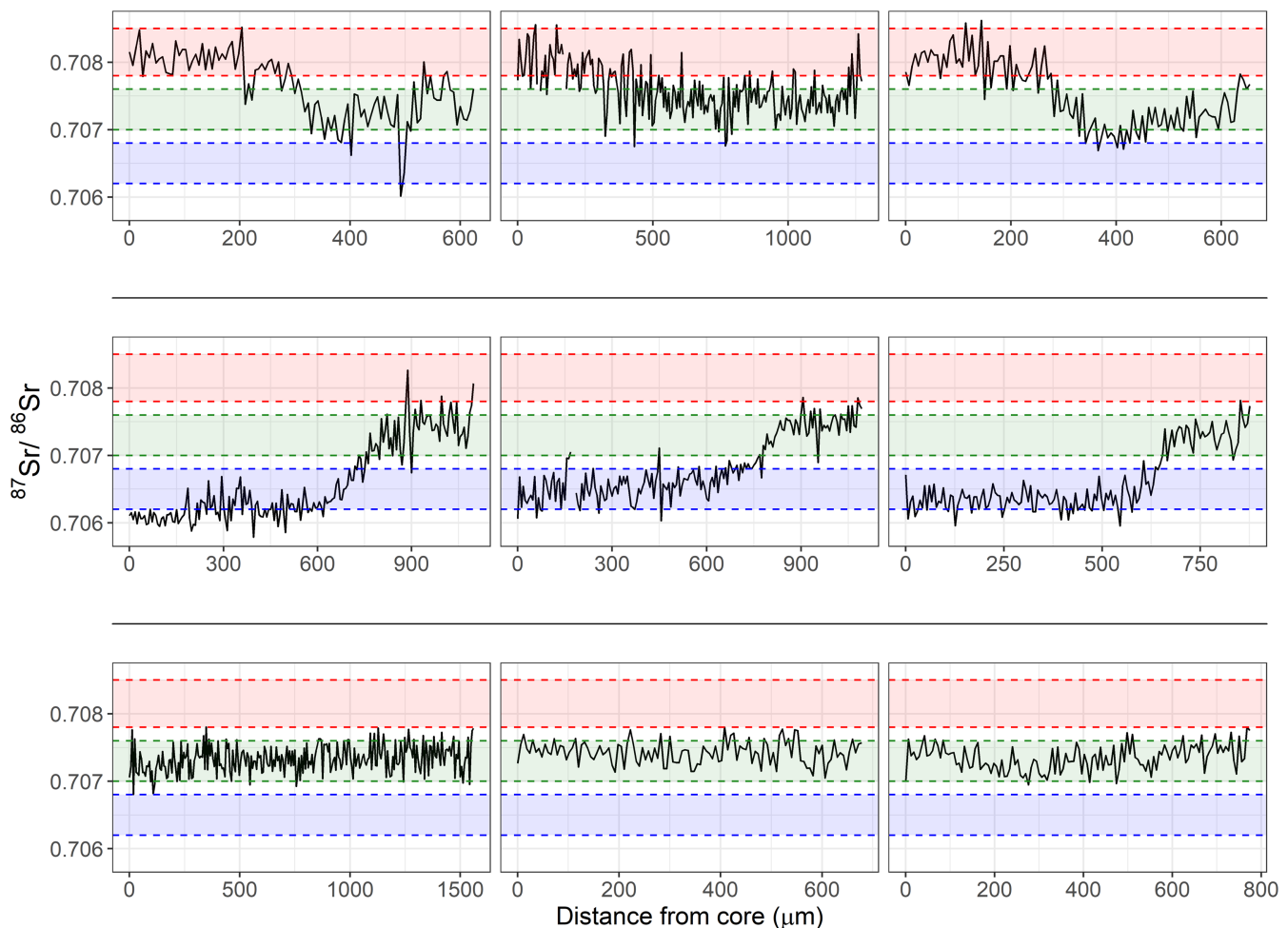


FIGURE 3 | Examples of $^{87}\text{Sr}/^{86}\text{Sr}$ transects from otoliths of YOY golden perch captured in the Menindee Lakes. Three separate regions are depicted by strontium isotope values as measured from the edge of larval and juvenile otoliths (Region 1, red; Region 2, blue; Region 3, green). Three separate movement histories were identified in YOY fish; YOY fish originating in Region 1 (top row), Region 2 (middle row) and Region 3 (bottom row).

were sampled in different systems (Appendix S3). Notably, 29 half-sibling pairs included a larval fish and a YOY fish captured in different systems (Table 2 and Figure 4). One half-sibling pair connected a YOY golden perch sampled in the Warrego River in July 2020 with a YOY sampled in the LDBR in November 2020 (> 750 km apart) (Table 2 and Figure 4). Similarly, another half-sibling YOY pair connected a fish captured in the Menindee Lakes (November 2020) with a fish captured in the LDBR (December 2020).

4 | Discussion

Insights gained from the combination of otolith chemistry and genetic kinship analyses in the current study provided a complementary approach to understanding the complexity of golden perch dispersal during ELH stages. Despite a coarse spatial resolution within the study catchment, including up to 700 km between sites, otolith chemistry provided evidence for the dispersal histories of individual fish and was able to delineate

TABLE 2 | Number of half-siblings identified between pairs of YOY and larvae/juveniles or pairs of YOY collected in the Menindee Lakes, LDBR and Warrego River (Site 1) in the latter half of 2020 with a fish captured in a different system (Site 2) in March 2020. Sites in the Menindee Lakes, LDBR and Warrego River are pooled due to their proximity.

		Site 2 (site number)						
		Larvae						YOY
		D/S Little Weir (4)	Moonie River (1)	Walgett (5)	Brewarrina (6)	Bourke (7)	Viewmont and 3 Mile Creek Bridge (8, 9)	LDBR (11–13)
Site 1 (YOY)	Menindee Lakes	8	3	6	4	1	5	1
	LDBR (11–13)						1	
	Warrego River		1					1

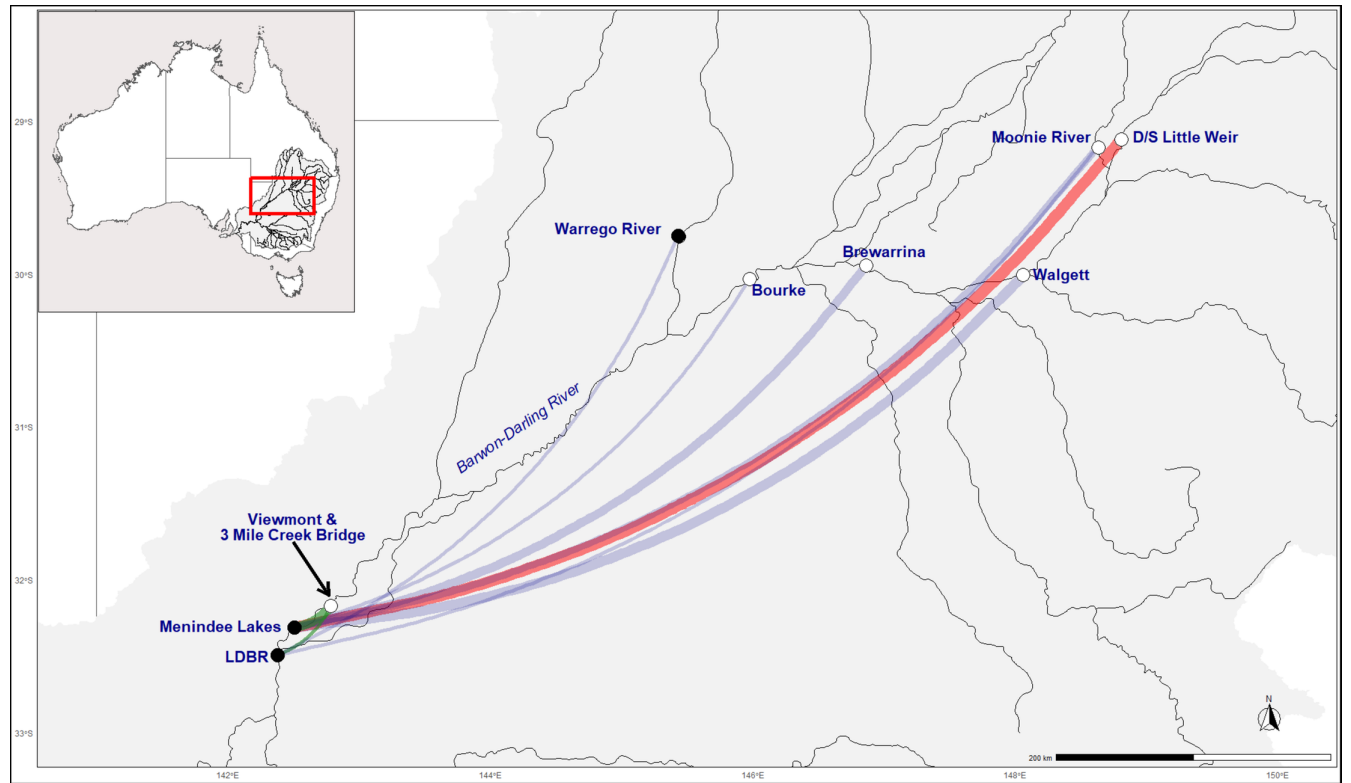


FIGURE 4 | Visual depiction of half-sibling relationships described in Table 2 for fish captured as a YOY in the Menindee Lakes, LDBR and Warrego River in the latter half of 2020 to a fish captured in a different (upstream) location. Sites where fish were captured as YOY are indicated with black circles, sites where fish were captured as larvae are indicated with white circles. Line thickness correlates to the number of half-sibling relationships between the two linked sites (thin lines, < 3 fish; medium lines, 3–5 fish; thick lines, > 5 fish). Line colour has been used to allow comparison to the regions defined in the otolith analysis, as shown in Figure 2 (Region 1, red; Region 2, blue; Region 3, green).

broad regions of estimated natal origin. The analyses of genetic kinship identified closely related individuals across a wide range of spatial scales and were able to confirm connectivity between specific sites in the study area, including the northern tributaries. Together, these data provide evidence that ELH golden perch exhibit a wide spectrum of dispersal behaviours, ranging from localised dispersal (i.e., from the Darling River upstream of the Menindee Lakes, to long distance dispersal (> 1600 km)). Confirmation of long-distance dispersal during an in-channel flow event by some fish from the upper catchment to the Menindee Lakes region supports a key element of the conceptual model of golden perch life history ecology proposed by Stuart and Sharpe (2020) after their analysis of a 2016 in-channel flow event in the Barwon–Darling catchment. Our study adds important detail to the model by demonstrating the diversity of movement behaviour that contributes to metapopulation structure in this species. This has implications for our understanding of how hydrological connectivity influences population dynamics and how this might best be represented in quantitative population models used to support management decisions (Bond et al. 2015; Hale et al. 2023).

Although variable movement traits across the lifetime of golden perch have been described previously (Barrow et al. 2021), our results provide detailed information on dispersal processes during the critical ELH stages that strongly influence recruitment into the adult population (Zampatti and Leigh 2013b). At the metapopulation level, the existence of multiple dispersal phenotypes in the ELH stages is likely to act as a buffer against fluctuating environmental conditions and resource availability (Schindler, Armstrong, and Reed 2015). Diversity in dispersal strategies facilitates connectivity between source and sink subpopulations across a wide range of scales and ensures that subpopulations do not become genetically fragmented and retain the genetic diversity necessary to adapt to environmental change (Frankham et al. 2017). In this context, our results demonstrate that the provision of free-flowing riverine habitat and hydraulic diversity to maintain connectivity between subpopulations is critical for the management and conservation of highly dispersive fish like golden perch (Dudley and Platania 2007; Mollenhauer et al. 2021). On a global scale, river regulation has negatively impacted many migratory fish species and mitigating these impacts remains a management priority for their persistence and the fisheries they support (González-Ferreras et al. 2022; Machado et al. 2022).

Golden perch are characterised by episodic recruitment with cohorts also linked to both floods and in-channel flow pulses (Mallen-Cooper and Stuart 2003; Zampatti and Leigh 2013a; Zampatti and Leigh 2013b; Zampatti, Leigh, et al. 2021). Under the existing water management regime in the Barwon–Darling River and other regulated rivers, the frequency of small and medium flow pulses has decreased and this appears to have significantly reduced the opportunities for golden perch recruitment (Mallen-Cooper and Zampatti 2018). Modelling of golden perch population viability has predicted a greater extinction risk under scenarios of increased drought frequency and localised disturbances associated with water resource development (Bond et al. 2015). The population processes detected in this study and by Thiem et al. (2023) that were supported by the 2020 flow event are particularly relevant when

considering the conditions in the preceding years; significant drought, low-to-no flow conditions (including a zero-flow for a period of 433 days at Bourke) and the cessation of tributary–mainstem connection flows (Stoffels et al. 2014; Jackson and Head 2020). With an existing lack of age structure diversity in golden perch populations in the Darling and Lower Darling Rivers that is characterised by a limited number of older fish (> 10 years), providing hydrological conditions that support ongoing spawning, dispersal and the persistence of new cohorts is imperative (Zampatti, Fanson, et al. 2021). Our data, and that of Thiem et al. (2023), demonstrates that spawning and recruitment can occur over a variety of spatial scales and that maximising the scale of interconnected flowing river habitats and access to productive floodplain nursery habitats is crucial in sustaining golden perch metapopulation processes (Stuart and Sharpe 2020; Zampatti, Fanson, et al. 2021).

Hydraulic and geomorphic diversity of river systems is likely to drive variations in the spatial and temporal patterns of ELH dispersal. For example, moderate in-channel flows, such as the 2020 flow event in the Barwon–Darling mainstem river, are likely to support high rates of longitudinal long-distance dispersal, as water residency time and physical complexity are lower than during flood events (Humphries et al. 2020; Stuart and Sharpe 2020). In contrast, high overbank flows would have different implications for the transport of drifting fish through a catchment, with the increased potential for retention of drifting larvae on inundated floodplains (Humphries et al. 2020). Additionally, geomorphically complex sections of river such as the northern tributaries may provide suitable nursery habitat for ELH fish and will impact dispersal rates as they provide greater retention of larvae as water residence time increases and eddies, slack-waters and dead zones are formed (Balcombe et al. 2006; Rolls and Wilson 2010). We detected varied dispersal rates of ELH fish in the northern tributaries, with retention of ELH golden perch in the Warrego River and two pairs of full-sibling larval fish being captured > 200 km apart, in the Moonie and Barwon rivers. Recording evidence of retention and varied dispersal rates was not a primary aim of this study, with our analysis potentially undervaluing the importance of intermediary nursery habitat within the Barwon–Darling catchment due to primarily focussing our YOY sampling in the Menindee Lakes and LDBR, at the downstream extent of the catchment. We highlight the need to prioritise research into these intermediary nursery habitats and the hydrological features that support them as they remain particularly important for the proportion of ELH golden perch that do not perform long-distance dispersals and during periods when there are limited opportunities for large scale connectivity between subcatchments (Schiemer and Hein 2008).

Effective conservation of pelagophilic fish populations requires an intimate understanding of their ELH for targeted hydrological management (Osborne et al. 2021). Many potamodromous species in floodplain river systems depend on flow events to support ELH processes, including dispersal and access to nursery areas, with river regulation and climate change posing a considerable threat to these processes (Jaeger, Olden, and Pelland 2014; Marshall, Lobegeiger, and Starkey 2021). Restoring baseflows, hydraulic diversity and large-scale connectivity is critical for flow- and

flood-pulse-dependent species; the frequency of these events is likely a key factor in promoting gene flow and increasing baseline population levels (Junk, Bayley, and Sparks 1989; Ward and Stanford 1995; Mallen-Cooper and Zampatti 2018; Kowal et al. 2024). Implementing complementary strategies to further enhance ELH survival is also critical and may involve utilising fish-friendly infrastructure and addressing water quality issues like algal blooms, hypoxia and thermal pollution (Gehrke 1991; Baumgartner, Reynoldson, and Gilligan 2006; Small et al. 2014; Michie et al. 2020; Boys et al. 2021). This research can aid our understanding of the spatial scale over which those additional measures need to be implemented to ensure management efforts are effective in their aims of building self-sustaining fish populations.

In conclusion, this research demonstrates the complexity of golden perch dispersal during the ELH stages and the broad spatial scales over which dispersal occurs. Our analyses provide additional empirical data that support existing conceptual models for golden perch dispersal and population function (Stuart and Sharpe 2020) and highlight important management priorities for their populations. These include protecting spawning and nursery habitats and the flowing water needed to connect these at large spatial scales. In this way, golden perch are emblematic of the needs for migratory riverine fishes globally (Dudley and Platania 2007; Pavlov and Mikheev 2017; Pavlov, Mikheev, and Kostin 2020; Mollenhauer et al. 2021). Basin-scale connectivity events, such as the one documented in this study, play a key role in stimulating widescale spawning and dispersal opportunities, which are essential in aiding the recovery of fish populations impacted by river regulation and reduced hydraulic diversity. Such events promote connectivity and gene flow among subpopulations, thus contributing to species resilience. In a broader context, our results demonstrate the benefits of promoting connectivity and gene flow for the conservation and restoration of riverine fish populations and their habitats worldwide.

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Ethics Statement

All research was undertaken in accordance with Fisheries NSW Scientific Collection Permit P01/0059(A)-4.0 and Fisheries NSW Animal Care and Ethics permit 14/10.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.