

## RESEARCH ARTICLE

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# A protected flow breaks the drought for golden perch (*Macquaria ambigua*) spawning along an extensive semi-arid river system

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## Abstract

Freshwater ecosystems are under extreme stress due to anthropogenic influences including changing climate, river regulation and water abstraction. Improving our understanding of the hydrological determinants of key life-history processes of fish, as well as the spatial scales over which these processes occur, is fundamental to inform effective recovery actions. We monitored the spawning response of native fish to a drought-breaking long-distance flow pulse that was protected from extraction by a legal intervention order in Australia's northern Murray–Darling Basin. Sampling sites were distributed across >1600 km of the Barwon–Darling River and three of its major tributaries. Larvae of the pelagophilic golden perch (*Macquaria ambigua*) were captured at all sites, with the size and age distribution indicative of both mainstem and tributary spawning. A mismatch between estimated hatch dates and river discharge at some locations suggested substantial flow-assisted dispersal from upstream spawning sites, although this was site-specific and more prevalent at downstream locations. Early life growth rates were the highest at tributary sites compared with mainstem sites, and within mainstem sites, golden perch grew faster in upper reaches compared with lower reaches. The present study provides insight into the environmental benefit of a post-drought protected flow event whereby connected lotic habitats promoted fish spawning and dispersal over a large spatial scale. Protection of future flow events should occur to support the conservation of golden perch and other pelagophil species, particularly following future drought periods which are forecast to become more intense and frequent.

## KEYWORDS

dispersal, flow restoration, pelagophil, periodic, riverscape

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## 1 | INTRODUCTION

River regulation provides water security for agricultural, domestic and industrial purposes in regions where hydrological regimes were once naturally diverse and dynamic (Dahm et al., 2003; Nilsson et al., 2005; Poff et al., 2007). Detrimental impacts to natural hydrology and hydraulics (i.e., quantity, timing and hydrodynamic diversity of water in rivers) and reduced connectivity (i.e., barriers and increased cease to flow events) have ensued, leading to well-documented declines in freshwater biota globally, including many fish species (Bain et al., 1988; Bunn & Arthington, 2002; Gehrke & Harris, 2001; Poff & Zimmerman, 2010). With the growing pressure of climate change posing the risk of further hydrological stress to aquatic ecosystems, the restoration and management of hydrologically diverse flow regimes is essential to support flow-dependent ecosystems (Balcombe et al., 2011; Koehn et al., 2014; Pittcock & Lankford, 2010; Tonkin et al., 2019).

Many freshwater fish species depend on complex and varied hydrological and hydraulic conditions to drive key life-history events that subsequently support the survival and persistence of their populations (Cattaneo, 2005; King et al., 2016; Tyler et al., 2021). As such, water managers must consider the life-history requirements of fish communities which requires development and implementation of actions informed by best available knowledge. This includes water sharing arrangements, delivery of water for the environment at appropriate spatial and temporal scales and protection of river flows that considers and encompasses the range of life-history strategies of entire assemblages (Baumgartner et al., 2014; Humphries et al., 2020). For example, individual species may depend on specific components of the hydrograph to cue spawning, support nesting, facilitate recruitment, enhance growth and increase the opportunities for dispersal.

Freshwater pelagophils represent one group of fish that have been disproportionately affected by river fragmentation and water extraction (Mollenhauer et al., 2021; Perkin & Gido, 2011). Characterised by a broadcast spawning strategy whereby buoyant or semi-buoyant eggs passively drift downstream in the water column (Lechner et al., 2016), pelagophilic species are dependent upon flow pulses to trigger spawning and for the subsequent downstream transport of larvae into productive nursery habitats to ensure maximum growth and survival (Durham & Wilde, 2009). A key component of this reproductive strategy requires the safe downstream transport of eggs during development, which can extend across distances >100 km (Dudley & Platania, 2007). River regulation has contributed to declines in this group of fish via the fragmentation of lotic habitats and the creation of unproductive lentic habitats (Mollenhauer et al., 2021). Further, passage past the regulating structures themselves during downstream dispersal can result in mortality (Baumgartner et al., 2006). The impacts of river regulation on pelagophils are particularly prevalent in arid and semi-arid river systems due to the extensive damming that has occurred in these systems in response to the unpredictable nature of the hydrology (Mollenhauer et al., 2021).

The northern Murray–Darling Basin (NMDB) in eastern Australia is a heavily regulated semi-arid river system that was once characterised by a highly variable hydrological regime (Mallen-Cooper &

Zampatti, 2020; Puckridge et al., 1998; Walker et al., 1995). Water management across the region is a contentious issue from an economic, environmental, social and cultural perspective (Grafton et al., 2020). Extensive regulation, diversion and extraction of water in the NMDB has vastly altered the natural hydrological and hydraulic regime (Koehn et al., 2014). The loss of flow events, increases in frequency and duration of zero and low-flow periods and reduced amplitude of flood peaks have caused widespread declines in longitudinal and lateral connectivity (Leblanc et al., 2012; Mallen-Cooper & Zampatti, 2020). In conjunction with losses of perennial and seasonal lotic habitats, there has been widespread decline of native fish populations in the region (Koehn et al., 2020; Koehn & Lintermans, 2012). Reforms to water policy and management have aimed to improve conditions for ecological assets and processes, including native fish, but recovery has been slow or non-existent for most species (Barrett, 2004; Jackson et al., 2021; Koehn, 2015; Koehn et al., 2014; Koehn & Lintermans, 2012). Given the current and projected impacts of climate change in the region, moving forward, the effective management of water resources is crucial to protect and enhance native fish populations and river health within these flow-dependant ecosystems (Balcombe et al., 2011; Cai & Cowan, 2008; Pittcock & Finlayson, 2011).

Golden perch (*Macquaria ambigua*) is one of the most widely distributed species of fish found within the Murray–Darling Basin (MDB). It is a large-bodied (commonly to 600 mm and 4 kg) fish of cultural, recreational, aquaculture and environmental value (Ebner et al., 2016; Wright et al., 2020). The species life history, particularly its reproductive strategy, is closely linked to river hydrology and hydraulics (Baumgartner et al., 2014; Gehrke & Harris, 2001; Koehn et al., 2020; Mackay, 1973). Flow pulses, in association with seasonal temperature cues, stimulate riverine spawning in golden perch (Cockayne et al., 2013; King et al., 2009; Mallen-Cooper & Stuart, 2003), and as pelagophils, they depend on lotic reaches to support egg and larval drift, dispersal and settlement (Dudley & Platania, 2007; Stuart & Sharpe, 2020). Movement and migration of adult and sub-adult golden perch is also intrinsically linked to hydrology (Faulks et al., 2010; Koster et al., 2014, 2017; Reynolds, 1983; Thiem et al., 2020), and immigration can play an important role in driving population dynamics (Thiem et al., 2022; Zampatti et al., 2021, 2022). The regulation of rivers within the natural distribution of golden perch has caused declines and reduced recruitment success among most populations (Koehn & Lintermans, 2012; Shams et al., 2020).

An absence of successful spawning and/or recruitment of golden perch in the more heavily regulated valleys highlights the need to better understand golden perch life history in the few rivers where regular recruitment remains, to inform more effective management actions (Ebner et al., 2009; Stuart, 2020). After 3 years of significant drought, exacerbated by regulation and abstraction of tributary flow pulses and long periods of zero-flow conditions in the Barwon–Darling River (2017–2019), there was significant rainfall in the northern and eastern parts of the basin (Craik & Claydon, 2020). As a result, drought-breaking in-flows to the Barwon–Darling River entered the river system via the northern tributaries (Craik & Claydon, 2020). A legal intervention order for protection of these flows (hereafter referred to as the Protected Flow Event [PFE]) was enacted with the aim being

to aid recovery of the drought-stricken region and its highly stressed riverine ecosystems including native fish populations (NSW DPIE, 2021).

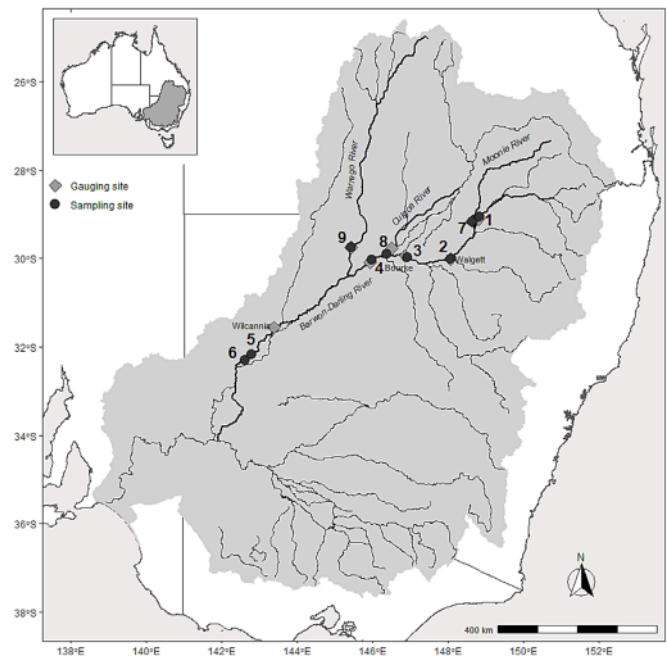
In the current study, we aimed to determine the timing of flow-related spawning of native fish species in the Barwon–Darling catchment and quantify the spatial extent of spawning in response to the PFE. Given the presence of golden perch larvae in both tributary and mainstem sites, we tested the conceptual model presented by Stuart and Sharpe (2020) for a previous post-drought flow event that occurred in 2016 whereby golden perch were reported to spawn in an unregulated tributary in the upper reaches of the NMDB and larvae were transported >1600 km downstream to nursery habitats. To do this, we expanded the previous sampling sites to encompass major tributaries and examined the size and daily age of golden perch captured throughout the NMDB. We hypothesised that if the conceptual model is transferable among flow events, then the size and corresponding age of golden perch would increase with distance downstream and that there would be an increasing disconnect (from upstream to downstream) between the timing of golden perch spawning and the PFE due to downstream dispersal. We also investigated the early growth rates of golden perch from different parts of the catchment to determine if location-specific growth rates existed. Our overarching objective was to extend the conceptual and empirical advances made recently in understanding flow-dependant reproductive strategies in golden perch. Understanding characteristics of the flow regime that support successful reproduction in an important pelagophilic species represents a key step towards developing effective and adaptive water resource management which promotes fish populations that are resilient to periods of increasing environmental stress, including water abstraction, river regulation and a changing climate.

## 2 | MATERIALS AND METHODS

### 2.1 | Study system

This study was undertaken in the NMDB, in the Barwon–Darling catchment within New South Wales (NSW), Australia. The NMDB comprises more than half of the MDB by area and includes the mainstem Barwon–Darling River and its tributary inputs upstream of the Menindee Lakes System. Major tributaries include the highly regulated Macquarie, Namoi, Gwydir, Castlereagh, Macintyre and Condamine–Balonne rivers flowing from the east and the semi-regulated Moonie, Weir, Culgoa, Warrego and Paroo rivers originating in the north (Thoms & Sheldon, 2000).

Larval and juvenile fish surveys were conducted at nine sites within the Barwon–Darling catchment during the PFE throughout March 2020, on or immediately after flow peaks. Six sites were located over a 1615 km stretch along the regulated mainstem Barwon–Darling River, with the most upstream site located in NSW on the Queensland border near Mungindi and the most downstream site located at the northern end of Lake Wetherell near the township of Menindee. Three sites were also sampled in the northern tributaries of the Barwon–Darling catchment: the semi-regulated Moonie,



**FIGURE 1** Fish survey locations (dark grey circle) and flow gauging station locations (light grey diamond) within the northern Murray–Darling Basin in south-eastern Australia (see inset). Sites 1–6 represent mainstem sites along the Barwon–Darling River, and sites 7–9 represent tributary inputs on the Moonie River (7), Culgoa River (8) and the Warrego River (9).

Culgoa and Warrego rivers (Figure 1). Mainstem sampling sites largely replicated those sampled by Stuart and Sharpe (2020) during an earlier flow event in 2016, although in the current study, we extended further upstream, encompassing three tributary sites.

### 2.2 | Fish sampling

Drifting egg, larvae and juvenile fish samples were collected during the March 2020 PFE using three fixed drift nets set in the river channel. Nets were suspended from instream wood habitat in the top 0.5 m of the water column for approximately 18 h overnight at each site, with absolute fish captures pooled from all three nets per site. The nets were 1.5 m long, with 500  $\mu$ m mesh and a 50 cm opening tapering to a 9 cm aperture at the rear of net attached to a collection bottle. Samples were live preserved in 90% ethanol and examined in the laboratory where fish larvae were identified to species level (or to genus in the case of the carp gudgeon species complex [*Hypseleotris* spp.]) based on the key of Serafini and Humphries (2004). Golden perch were both enumerated and measured (TL; mm).

### 2.3 | Hatch date calculation of golden perch

A subsample of golden perch ( $n = 252$ ) were selected for daily ageing and to enable the back calculation of hatch dates. The subsampled fish were remeasured to both TL and standard length (SL) to ensure daily age estimates could be coupled with corresponding length. A maximum of 30 golden perch were subsampled from each site for ageing.

The aim was to develop accurate age–length relationships for golden perch from each site, using a subsampling method that encapsulated the distribution of the size structure of each sample. The size range of the total sample was divided by the number of fish to be subsampled to create distinguishable size class ‘bins’ and at least one fish was sampled from each bin if available.

The sagittal otolith from each fish was mounted on a glass microscope slide using epoxy resin Crystalbond (Ted Pella Inc, USA). Different methods were used based on the individual otolith sizes, with the smallest of the otoliths requiring no extra preparation to estimate age (see Brown & Wooden, 2007, for previous use of known age fish to validate daily growth increment formation in larval golden perch). Most otoliths required a distal grind to ensure the daily age rings were clearly distinguishable; intermediate-sized otoliths were polished on the sulcus side of the otolith to view daily rings, whereas the largest otoliths required polishing of both sides (the sulcus and non-sulcus). Where polishing was required, 1200 grit wet and dry sandpaper was first used to remove the outer portions of the otolith, followed by the use of 3  $\mu\text{m}$  lapping film to finalise the process.

Otoliths were read at 200 $\times$  magnification, with a drop of immersion oil smeared over the exposed surface to reduce surface scratches and enhance the clarity of the rings. Daily rings were counted from the primordium (nucleus) to the outer edge of the otolith along a radial transect. The first ring was assumed to coincide with hatch date. In golden perch, as for other fish, there can be some variation in the timing of the first increment formation (Brown & Wooden, 2007), but based on the similarity in the size of 1–2 day old fish in our study to the predicted hatching size, we assumed the first check to be linked to hatch (Serafini & Humphries, 2004). When daily increments were not clear, a proxy measure was used instead. Two proxy measures were calculated from other golden perch otolith samples with clearer growth rings; the first was to determine the width of the hatch mark (distance from the primordium to the first increment) in very young fish (1–2 days), and the second was to determine the location of the first 10 increments in older fish where earlier increments had lost clarity. A second reading of  $\sim 20\%$  of the samples was undertaken by an experienced second reader to ensure quality control, reduce the risk of potential reader error and to provide estimates of error around age estimates. The number of re-reads completed was considered large enough to provide sufficient data to determine both precision between readers and the expected ageing error associated with the age readings. Percentage agreement, average percent error (APE) and average coefficient of variation (ACV) were calculated using the ‘FSA’ package in R (Ogle et al., 2023; R Development Core Team, 2019). This resulted in a percentage agreement of 65.9%, APE of 1.38% and ACV of 1.96%, demonstrating acceptable precision and limited reader bias (Campana, 2001). As such, the ages estimated by the primary reader were used in further analyses.

## 2.4 | Data analyses

To determine the historic frequency of discharge rates, including placing the protected March 2020 PFE into a historical context within available records, flow duration curves were produced using daily

average discharge ( $\text{ML day}^{-1}$ ) corresponding to Walgett, Bourke and Wilcannia on the Barwon–Darling River (Figure 1) from 1973 to 2021. Hydrological data were obtained from gauging stations operated by WaterNSW (<http://realtimedata.watersw.com.au>). Sites selected for analysis of flow frequency and duration were chosen as they are key sites identified in the Long Term Water Plan (LTWP) for the Barwon–Darling River (NSW DPIE, 2020). River discharge was considered as the daily average discharge rate ( $\text{ML day}^{-1}$ ), calculated from measurements recorded at 15 min intervals. Historical hydrological analysis was conducted using the HydroTSM package (Zambrano-Bigiarini, 2020), and where reported, river distances were calculated using the riverdist package (Tyers, 2017).

To compare golden perch spawning overlap with the PFE, hatch dates were back calculated from the otolith daily age estimation (generally from a subsample of the catch) and the known sample date at each site and plotted against river discharge at each sample site. Discharge rates (presented as average discharge in  $\text{ML day}^{-1}$ ) were obtained from January to July 2020 at eight locations in the Barwon–Darling catchment upstream of Menindee Lakes that corresponded as closely as possible to fish survey sites, generally within 10 km (Figure 1). This included five mainstem sites in the Barwon–Darling River and three tributary sites (one in each of the Moonie, Culgoa and Warrego rivers). Exceptions were the Viewmont and 3 Mile Creek Bridge sites, where the upstream gauge of Wilcannia was selected as it reliably depicted water flow at the sampling sites.

To quantify the proportion of golden perch hatched before compared with during the PFE, site-specific linear growth models (see details below) were used to determine a length threshold (as a proxy for daily age) applied to the entire catch at which the onset of the PFE reached each site. This was based on the difference (cumulative number of days) between the site-specific sampling date and the presence of a measurable discharge value at a relevant site gauge (range 12–37 days), with data presented as the proportion of the total sample hatched prior to the onset of the PFE.

To test for location-specific differences in growth rates of golden perch, a generalised linear growth model was fitted to golden perch age–length data ( $\text{TL} = \text{intercept} + \text{growth coefficient} * \text{age} [\text{days}]$ ) from the subset of the sample that was daily aged. A linear model was selected as best fit for this analysis due to the small age range of the fish sampled and the typically linear growth that occurs in the early life history of golden perch (Stocks et al., 2019). Capture site was included in the model to test for site-specific differences in growth rates using a parametric two-way analysis of variance (ANOVA) to test for variation in the regression equations of the different sites. As site had a significant effect, a combination of a least squared trends test and a pairwise (Tukey’s adjustment) post hoc analysis was used to assess site-wise differences. Two fish that were caught on the Darling River (site 6) were excluded from this analysis as they were estimated to be much older (63 and 82 days post hatch) than the remainder of the sample despite being of similar size. Growth coefficients (and upper and lower confidence limits) were extracted from the least squared trends test and plotted for three example sites to demonstrate the effect of site in determining age at length relationships: Moonie

River, Bourke and 3 Mile Creek Bridge. All tests were deemed significant at  $\alpha < 0.05$  and were examined statistically to ensure they met the required assumptions. All statistical analyses and data visualisation were conducted in R version 3.5.1 (R Development Core Team, 2019).

### 3 | RESULTS

#### 3.1 | Hydrology

During the PFE, flow peaks occurred at upstream mainstem Barwon–Darling sites in February 2020. At the most upstream site (DS Little Weir, 1), discharge peaked at 4250 ML day<sup>-1</sup> in late February, while in the adjacent Moonie River (7), there were two discharge peaks: one in mid-February at ~4500 ML day<sup>-1</sup> and another in early March at ~5000 ML day<sup>-1</sup>. At Walgett (2), downstream of the Moonie and Barwon rivers confluence, discharge peaked at ~14,000 ML day<sup>-1</sup> through mid-February to early March 2020, mirroring the timing of the smaller upstream peaks (Figure 2). Further downstream in the Barwon River at Brewarrina (3), discharge peaked at ~11,000 ML day<sup>-1</sup> on two occasions, for approximately 10 days in late February and again in late April 2020. The increased discharge in late April did not occur at upstream Barwon River sites, so was likely a result of inflows from the Macquarie and Castlereagh catchments, which join the Barwon River between Walgett and Brewarrina (Figure 1).

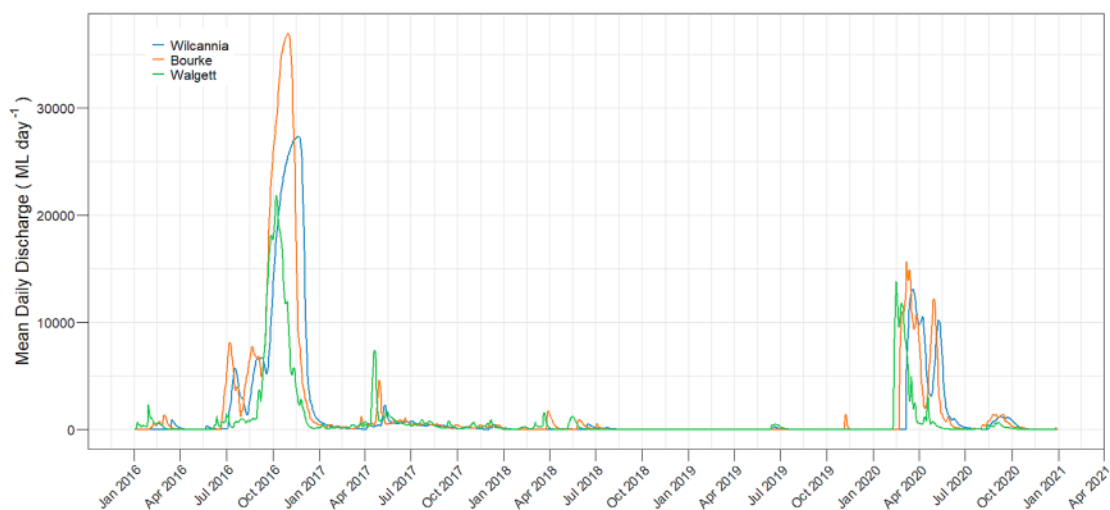
Discharge in the Culgoa River (8), which meets the Barwon River downstream of Brewarrina and upstream of Bourke, peaked in late March 2020 at ~9000 ML day<sup>-1</sup>. Downstream of the Barwon–Culgoa confluence, on the Darling River at Bourke (4), there were two peaks: the first in early March (15,000 ML day<sup>-1</sup>) and a second in late April 2020 (1250 ML day<sup>-1</sup>). In the Warrego River (9), which joins the Darling River downstream of Bourke, discharge peaked at ~3000 ML day<sup>-1</sup> in late March, and in Wilcannia (sites 5 and 6),

downstream of the confluence of the Warrego and Darling rivers, discharge peaked at ~13,000 ML day<sup>-1</sup> in mid-March and again at 10,000 ML day<sup>-1</sup> in early May 2020. Historical analysis of river discharge in the Barwon–Darling River identified that the moderate in-channel discharge peak of this 2020 PFE at Walgett (13,783 ML day<sup>-1</sup>) has only been exceeded 8% of the time since 1973, whereas at Bourke and Wilcannia, this discharge was exceeded more frequently, 12% and 15% of the time, respectively (Data S1).

#### 3.2 | Fishes

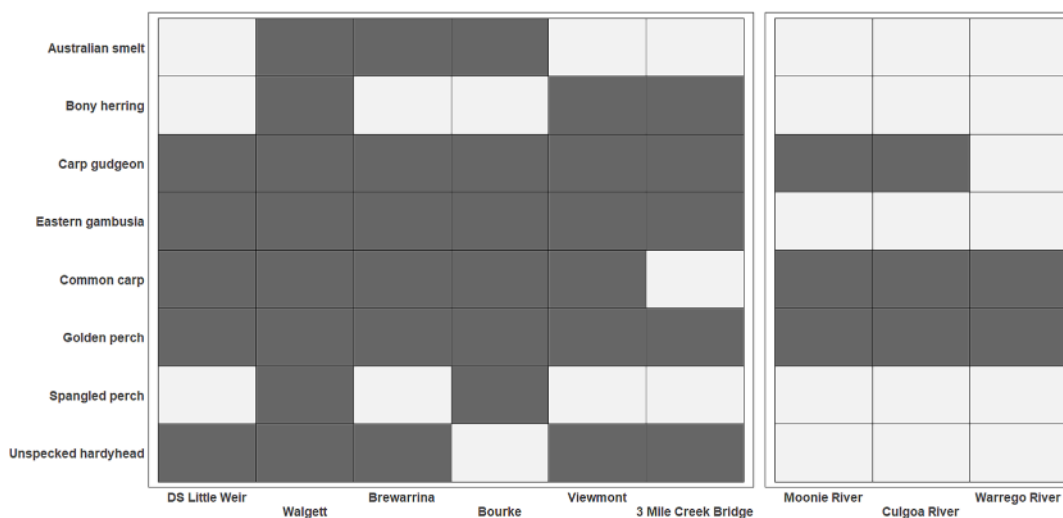
Early life stages of eight species of fish were collected, including six native species (Australian smelt, *Retropinna semoni*; bony herring, *Nematalosa erebi*; carp gudgeon, *Hypseleotris* spp.; golden perch; span-gled perch, *Leiopotherapon unicolor*; and unspoked hardyhead, *Craterocephalus stercusmuscarum fulvus*) and two introduced species (common carp, *Cyprinus carpio*; and eastern gambusia, *Gambusia holbrooki*) (Figure 3 and Data S2).

Golden perch larvae were present at all nine sites and was the most abundant species sampled with 2772 individuals captured (Figure 3 and Table 1). Catches of golden perch were higher at upstream sites on the Barwon River compared with other sites, with 1070 individuals collected at Brewarrina and 982 collected near Walgett (Table 1). Golden perch ranged from 2.23 to 38.86 mm TL, with the Moonie River and 3 Mile Creek Bridge having the broadest size distributions, 5.32–38.86 and 2.23–38.85 mm, respectively (Table 1 and Figure 4). Despite having the highest capture rates, the three Barwon River sites had the narrowest size distributions, ranging only 15 mm from largest to smallest (Table 1 and Figure 4). The length of golden perch from these sites all had similar size distributions, with as many as 100 fish in some of the 0.5 mm size class bins. The lower sites on the Darling River (sites 5 and 6) had a broad range of fish sizes



**FIGURE 2** Hydrograph highlighting recent flow events in the Barwon–Darling River from 2016 to 2020. Mean daily river discharge (ML day<sup>-1</sup>) is shown for three sites distributed along the Barwon–Darling, including Wilcannia (blue—furthest downstream), Bourke (orange) and Walgett (green—furthest upstream).





**FIGURE 3** Presence (dark) and absence (light) of larval and juvenile fish species captured at nine sites within the Barwon–Darling catchment throughout a legally protected flow event in March 2020. Sites on the left panel represent those located on the mainstem Barwon–Darling River, and sites on the right panel are located in major upstream tributaries, the Moonie River, the Culgoa River and the Warrego River.

**TABLE 1** Summary of larval and juvenile golden perch (*Macquaria ambigua*) catch numbers and size range (TL mm) from nine sites within the Barwon–Darling catchment during a protected flow event in March 2020.

Site number	River	Sampling site	Date of fish sampling	Total catch	Total length range (mm)
1	Barwon	D/S Little Weir	5/3/2020	349	4.73–14.89
2	Barwon	Walgett	4/3/2020	982	5.73–19.60
3	Barwon	Brewarrina	5/3/2020	1070	3.66–19.39
4	Barwon	Bourke	4/3/2020	65	7.10–16.90
			26/3/2020	17	14.4–30.42
5	Darling	Viewmont	20/3/2020	37	4.00–23.89
6	Darling	3 Mile Creek Bridge	20/3/2020	196	2.23–38.85
7	Moonie	Moonie River	5/3/2020	41	5.32–38.86
8	Culgoa	Culgoa River	26/3/2020	9	9.48–36.64
9	Warrego	Warrego River	26/3/2020	6	15.23–24.15

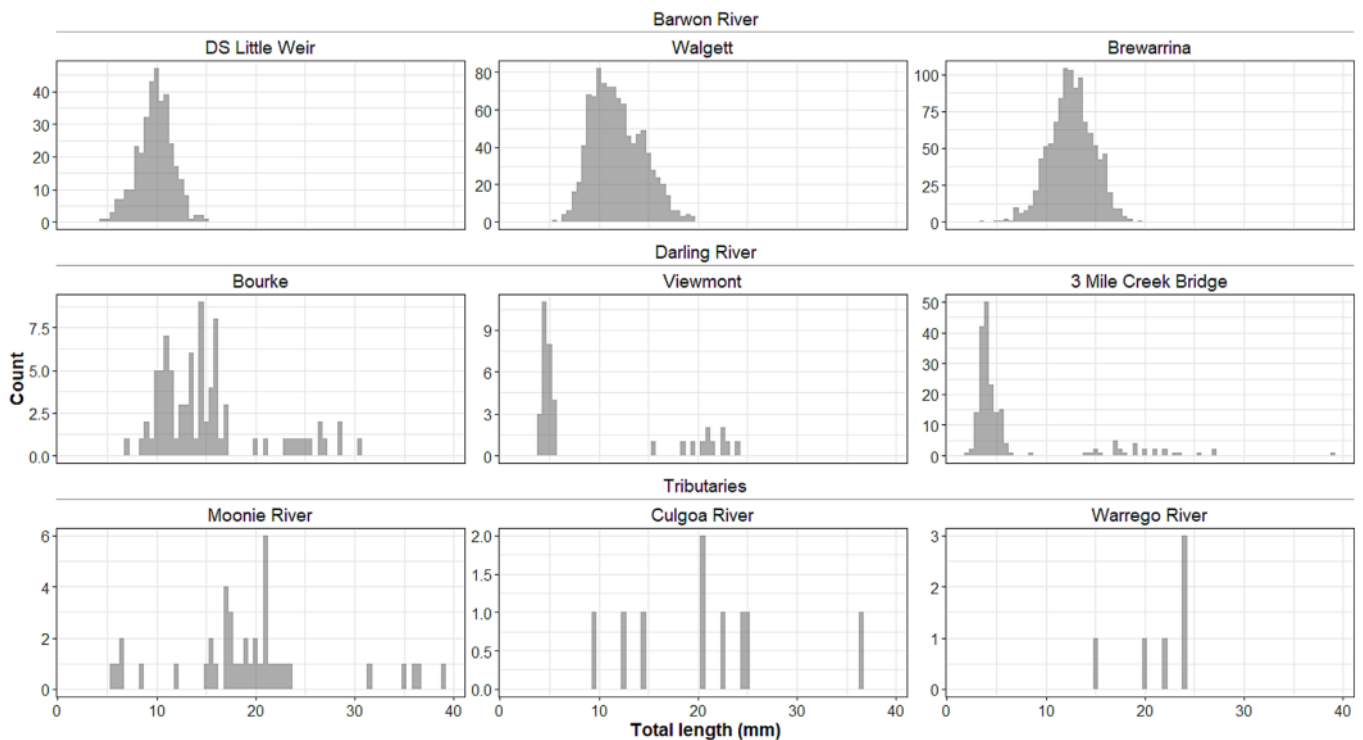
Note: Sites 1–6 are located within the mainstem Barwon–Darling River, and sites 7–9 are in upstream tributaries: the Moonie River (7), the Culgoa River (8) and the Warrego River (9).

but were dominated by 2–7 mm larvae (Table 1 and Figure 4). In contrast, fish in the tributaries had a more variable size distribution, with generally one to two fish in each 0.5 mm size class. These sites had a relatively broad range of fish sizes present within samples, despite having smaller overall sample sizes than the mainstem sites (Table 1 and Figure 4).

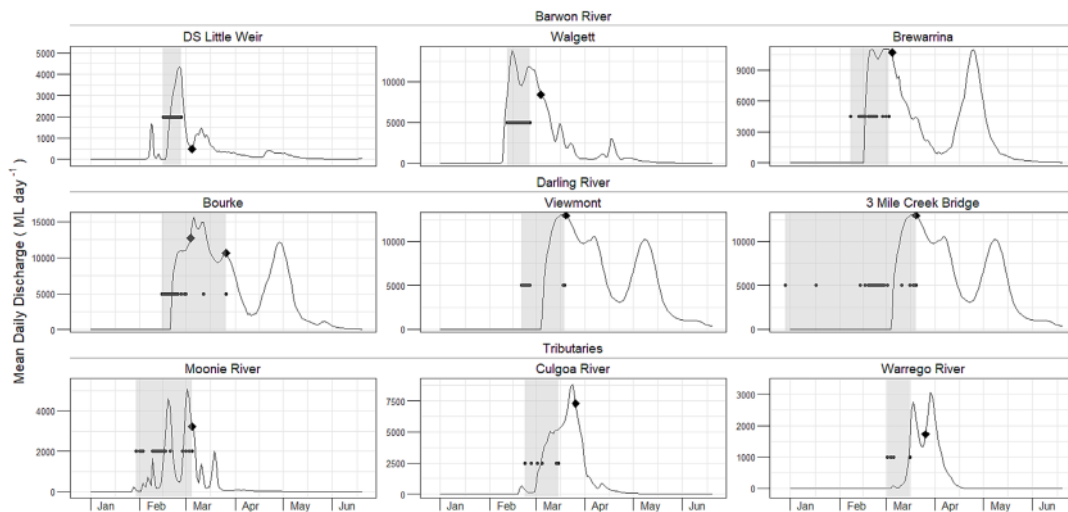
Golden perch ranged in age from 1 to 82 days old, with the earliest hatch date approximated as 29 December 2019 (Figure 5 and Data S3) immediately before the PFE. In the most upstream sites (Barwon River; sites 1 and 2), fish were aged between 7 and 20 days old, with an estimated hatch period of middle through to late February 2020. This indicates that hatching occurred for the entire sample during the PFE at these sites (Figure 5). Further downstream at Brewarrina (3) and Bourke (4), fish were aged from 2 to 26 days, with hatching occurring from middle to late February through to mid-March

2020. Approximately 0.1% of the fish captured at Brewarrina and 51% of the fish captured at Bourke had hatched prior to the onset of the PFE at their capture locations. The most downstream sites (Darling River; sites 5 and 6) had the widest range of hatch dates (29 December 2019 to 19 March 2020; Data S3), with fish ranging from 1 to 82 days old. A subset of the fish collected at sites 5 (27%) and 6 (15%) had also hatched prior to the onset of the PFE in early March 2020 at their capture locations (Figure 5), noting that these estimates are conservative as hydrological data were obtained from an upstream gauge site (Figure 1).

In the tributaries, there was mixed evidence of golden perch hatching prior to the onset of flow at their capture site (Figure 5). For example, the Moonie River had the broadest window of fish hatch dates of the tributaries, despite being sampled approximately 20 days earlier than the other two tributary sites. Fish collected on the Moonie



**FIGURE 4** Size frequency (total length [mm]) histogram of drifting golden perch (*Macquaria ambigua*) larvae and juveniles sampled during a protected flow event in March 2020 from mainstem sites along the Barwon (top panel) and Darling (middle panel) rivers, as well as major upstream tributaries (bottom panel). Counts represent number of individuals within 0.5 mm size class bins. Note that the scale on the y-axis varies. Sample sizes are included in Table 1.

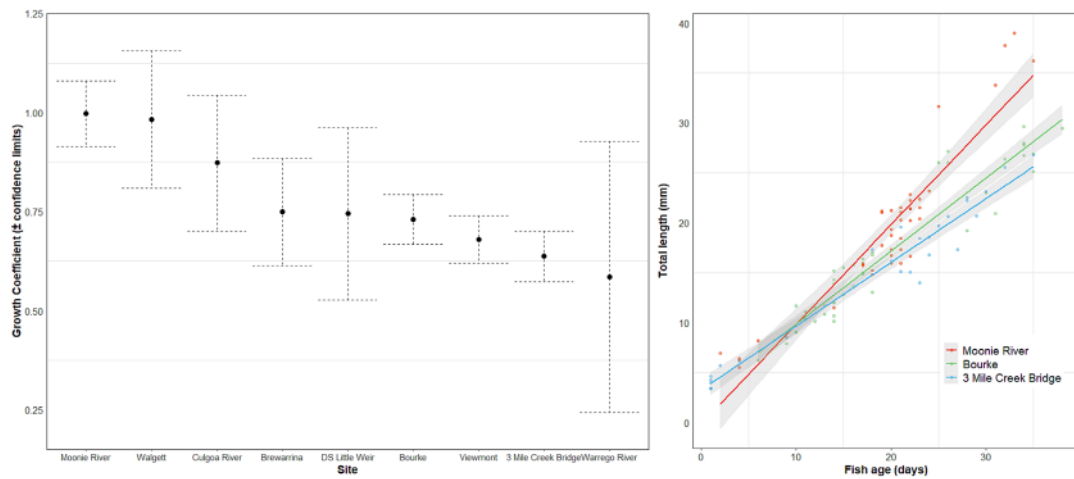


**FIGURE 5** Estimated hatch dates (black circles) of subsampled golden perch (*Macquaria ambigua*) larvae and juveniles sampled during a legally protected flow event in March 2020 from mainstem sites along the Barwon (top panel) and Darling (middle panel) rivers, as well as major upstream tributaries (bottom panel) and corresponding gauged river discharge ( $\text{ML day}^{-1}$ ; solid line). Shading indicates the time window in which potential hatching of larvae (subsampled from each site) occurred. The diamond indicates sample date. Y-axis values only relate to river discharge (solid line).

River on 5 March 2020 had hatched as early as January 2020, although there was evidence of recent spawning with fish as young as 2 days old collected in March 2020 (Figure 5 and Data S3). The Culgoa and Warrego rivers had narrower hatch date ranges, and there

was also evidence of hatching prior to the onset of flow at their capture locations (Figure 5 and Data S3).

Capture site had a significant effect on the age-length relationship of golden perch ( $F_{8, 229} = 22.160, P < 0.001$ ) (Figure 6). Pairwise



**FIGURE 6** Site-specific daily growth coefficients for golden perch (*Macquaria ambigua*), ordered from the highest (i.e., the fastest growth) to lowest (the slowest growth). Data are presented as the fitted growth coefficient estimate  $\pm$  confidence limits. (right) Modelled age-length relationships (daily age, TL) for the three example sites at the Moonie River (red), Bourke (green) and 3 Mile Creek Bridge (blue). Linear models have been applied to the data to determine growth rates of fish at each site with the 95% confidence limits applied (Moonie River,  $TL = -0.1037 + 0.997 * \text{age}$ ,  $\text{Adj } R^2 = 0.861$ ; Bourke,  $TL = 2.631 + 0.730 * \text{age}$ ,  $\text{Adj } R^2 = 0.912$ ; and 3 Mile Creek Bridge,  $TL = 3.317 + 0.638 * \text{age}$ ,  $\text{Adj } R^2 = 0.955$ ).

comparisons revealed significant differences ( $P < 0.05$ ) between the growth rates of golden perch captured from the Moonie River and the three most downstream sites on the mainstem Darling River (Bourke, Viewmont and 3 Mile Creek Bridge) and between golden perch captured at Walgett (Barwon River) and two sites on the Darling River (Viewmont and 3 Mile Creek Bridge) (Figure 6 and Data S4). Generally, growth coefficients were higher in more upstream sites, with golden perch in the Moonie River estimated to increase in total length by  $0.997 \text{ mm day}^{-1}$ , compared with  $0.574 \text{ mm day}^{-1}$  at 3 Mile Creek Bridge in the Darling River (Figure 6 and Data S4).

## 4 | DISCUSSION

The current study identifies a geographically widespread spawning response to a drought-breaking system scale flow pulse that was protected from further extraction. Specifically, larvae of the riverine pelagophil golden perch were captured at all sampling sites indicating a regional spawning response to a moderate, in-channel flow event in the mainstem Barwon-Darling River and its tributaries. The flow event peaked at  $15,000 \text{ ML day}^{-1}$  on the Darling River at Bourke, which based on post-regulation data (1973 to current) is exceeded only 12% of the time and is below bankfull height ( $\sim 25,000 \text{ ML day}^{-1}$ ). Spawning of golden perch has previously been reported in response to in-channel flow events (e.g., Gilligan & Schiller, 2003; King et al., 2016; Koster et al., 2017; Rolls et al., 2013), as well as overbank floods. However, the high ecological value of this PFE, and the associated spawning response of golden perch, is contextualised through examination of the antecedent conditions in the NMDB preceding this event. For example, Mallen-Cooper and Zampatti (2020) reported 433 days of zero flow at Bourke in 2018–2019,

representing the longest sequence of its kind in the 134 years of record keeping. In other semi-arid regions, such as the Great Plains of the United States of America, extended drought conditions have similarly contributed to recruitment failure in pelagophils (Durham & Wilde, 2009; Perkin et al., 2019). For species with life stages that rely on access to extended reaches of lotic habitats to complete their life cycle, it is essential to protect flow events following periods of prolonged drought as was experienced across the NMDB in the years preceding our study.

The occurrence of golden perch larvae at multiple locations within the mainstem Barwon-Darling River, and in all three tributaries sampled, suggests numerous spawning events spanning a vast geographic area on a single flow event. Given the connected nature of this flow event and the slow movement of water (weeks to months) between the upper and lower reaches of the system, the breadth of hatch dates from early-stage larvae represents an unfolding series of localised spawning events. Stuart and Sharpe (2020) reported golden perch predominantly spawning in the upper reaches of the system during an overbank flow in 2016/2017, including potentially in the Macintyre and Weir rivers, and long-distance flow-assisted transport of a single cohort into the Menindee Lakes. In an extension of these results and the associated conceptual model presented by Stuart and Sharpe (2020), capture of early-stage larvae in this study provides more detail of widespread spawning than has previously been shown. Our study indicates localised spawning occurred immediately upstream of the Menindee Lakes and higher upstream in the main channel and in the Warrego, Culgoa and Moonie rivers in the north-west and east of the basin.

While the design of our study did not enable identification of local habitat features conducive to spawning locations of golden perch, our results suggest that these locations occur throughout the



Barwon–Darling system rather than being concentrated in a single location. This result is supported somewhat by the vast spatial expanse of Indigenous fish traps in the system that exploited the propensity for adult golden perch to undertake pre-spawning movements on flow events (Martin et al., 2023). It may be that physical attributes in the landscape interact with river hydrology to form localised meeting points for spawning locations of golden perch, such as at the junction of rivers (O'Connor et al., 2005). Utilising a unifying framework, such as the meeting point hypothesis proposed by Fréon and Dagorn (2000) to explain the association between pelagic fish and other animate and inanimate objects including landscape features, may help elucidate associative behaviour in golden perch.

Spawning of golden perch occurred during Summer and early Autumn in 2020 in the current study. Ebner et al. (2009) reported spawning in Autumn, Winter and Spring, and Stuart and Sharpe (2020) also provide evidence of spawning in Spring. Collectively, these studies suggest that time of year is not a contributing factor to golden perch spawning in the NMDB. Rather suitable discharge, and associated connectivity and lotic hydraulics at a scale that is ecologically meaningful, appears fundamental to widespread spawning and recruitment outcomes. We recommend protecting flow events at spatial and temporal scales that support golden perch life-history processes by accounting for tributary–mainstem connectivity and floodplain connections to promote regional benefits for golden perch. In analogous situations where anthropogenic water demand constrains the recruitment of fishes, prioritisation of river reaches for protection from fragmentation and prioritising flow restoration has ensued (Dudley & Platania, 2007; Mu et al., 2014; Perkin et al., 2015). In the current circumstance, flow events are required that span 500–1000 river kilometres and result in the reconnection of waterholes and adult fish communities (Marshall & Lobegiger, 2020) and activate food webs to ensure adequate microcrustacean food for early recruits (Humphries et al., 2020; Rowland, 1996; Sharpe, 2011).

The pelagophil life-history strategy in riverine fishes is characterised by pelagic broadcast spawning and a period of passive flow-assisted downstream drift of eggs (Lechner et al., 2016). This reproductive specialisation offers several advantages over competitors but increases species' vulnerability in relation to river regulation (Dudley & Platania, 2007; Hoagstrom & Turner, 2015; Mollenhauer et al., 2021). A previous study of golden perch in the Barwon–Darling documented flow-assisted delivery of eggs, larvae and juveniles into productive ephemeral floodplain nursery habitats >1000 km from spawning grounds (Stuart & Sharpe, 2020). In the current study, a mismatch between estimated hatch dates and river hydrology at some locations indicates flow-assisted dispersal, although this was site-specific and most prevalent at downstream sampling sites. For example, hatch dates of golden perch captured in the upper reaches of the system generally overlapped with the flow pulse, although sites in the lower system as well as the lower parts of tributaries more commonly comprised a proportion of individuals hatched prior to the onset of the flow. We propose this provides evidence of downstream transport of eggs and larvae over an unquantified distance, although acknowledge zero-flow spawning and recruitment from the Warrego

River (Balcombe et al., 2006) and neighbouring catchments (Balcombe & Arthington, 2009; Kerezszy et al., 2011) means this evidence is not conclusive and spawning prior to the PFE cannot be entirely ruled out. In combination with evidence of system-wide spawning, our interpretation of the data collectively suggests that landscape position determines the possibility of entrainment of multiple larval cohorts in the drift and that logically, when the longitudinal integrity of a flow remains intact, sites in the lower system are more likely to comprise individuals derived from both local spawning and long-distance dispersers. This highlights the ecohydraulic requirements of pelagophilic spawners with periodic or opportunistic life-history strategies and their dependence on a range of mainstem and tributary discharge events (Humphries et al., 2020; Winemiller & Rose, 1992). The protection of flow events should also extend to minimising or preventing direct removal of early recruits from the ecosystem in association with floodplain water harvesting, the capture of water for consumptive use, mortality associated with downstream passage past instream structures and the settlement of juveniles in unproductive weir pool habitats (Baumgartner et al., 2006; Bice et al., 2017; Boys et al., 2021; King & O'Connor, 2007).

The early life stages of five other native fish species were also captured in the current study, although a number of species were notably absent likely reflecting a combination of historical species declines and antecedent conditions that preceded this PFE. For example, we failed to detect another species with a pelagophilic and periodic life-history strategy that was once abundant throughout the NMDB (Reid et al., 1997) but is now virtually extirpated, the silver perch (*Bidyanus bidyanus*). An absence of Murray cod (*Maccullochella peelii*), an equilibrium species with high investment in parental care, is also mostly likely reflective of a combination of low adult abundance in the region in combination with the flow event falling outside of their reproductive period (Butler et al., 2022; Stuart & Sharpe, 2022). Carp gudgeon, a species complex of small-bodied fishes (Bertozzi et al., 2000), were relatively widespread and produce hundreds of eggs that hatch after a brief period of parental care (Lake, 1967; Lintermans & Cottingham, 2007). Numerous studies have linked carp gudgeon recruitment to elevated flow or flooding (Ho et al., 2013); however, they do not require flow to trigger spawning (Humphries et al., 1999; Kerezszy et al., 2011) and are best considered an opportunist (Humphries et al., 2020). For completeness, it is also worth mentioning the presence of two introduced species, common carp and eastern gambusia collected as early recruits here. Both species have been established in the catchment for decades and are both abundant and widespread (Lintermans & Cottingham, 2007; Rolls et al., 2013). In the current degraded state, the NMDB retains few competitors for golden perch, especially when the flow regime favours a flexible and opportunistic reproductive strategy. Hoagstrom and Turner (2015) proposed that the pelagophil reproductive strategy in riverine fish, in combination with high-flow events, creates a number of potential 'loopholes' from competition and predation, including (but not limited to) the ability to saturate habitats due to high fecundity and the colonisation of temporary nursery habitats.

We found somatic growth of early-stage golden perch to vary among sites, likely reflecting the timing of spawning, as well as the diversity of river and tributary habitats, varied water temperatures and associated productivity. Overall, the growth rates of golden perch in the current study were slower than those reported from pond-reared early recruits by Arumugam and Geddes (1986) and were comparable with that of pond-reared recruits reported by Rowland (1996). The growth rates observed in the current study were faster than previous field observations, including those reported by Ebner et al. (2009) in the Menindee Lakes and Stuart and Sharpe (2020) in both the Barwon River at Walgett and in the Menindee Lakes. This may be partly a function of temperature, since the pond-reared examples are based on spring growth, whereas the study by Ebner et al. (2009) was based on several recruits that had overwintered (presumably in the Menindee Lakes). As such, the only genuinely comparable growth rates from drifting recruits are those from Stuart and Sharpe (2020) from Walgett. Those fish were the progeny of early spring spawners, collected at a water temperature of approximately 23°C. However, the river temperature was substantially lower (16–22°C) in the months that these fish were drifting (Stuart & Sharpe, 2020). It is worthwhile noting that our growth estimates apply only to drifting larvae actively or passively entrained in the current, some of which may have traversed long distances prior to capture. Comparable growth rates of individuals that have settled and are retained in nursery habitats remain unknown; although as settlement increases with increasing drift distance (Dudley & Platania, 2007), this information would be useful to contrast the advantages and disadvantages of active dispersal with settlement.

## 5 | CONCLUSION

The current study identified substantial spawning of pelagophilic golden perch across a broad geographic area and in response to a PFE in a semi-arid river system following an extended drought. In an extension of previous results from Stuart and Sharpe (2020), catchment-wide tributary and mainstem spawning was confirmed and evidence of flow-assisted dispersal was identified. Recruitment success was not measured in this study, and while Humphries et al. (2020) propose that recruitment of periodic species such as golden perch would be maximised during overbank floods as opposed to in-channel flows, this does not account for antecedent conditions. The prevailing drought conditions precluded any opportunity for spawning or recruitment of golden perch in the Barwon–Darling in years preceding the 2020 PFE (as a function of water extraction, diversion and climate change). Similarly, processes have contributed to recruitment failure in pelagophils occupying other semi-arid rivers (Durham & Wilde, 2009; Perkin et al., 2019).

Globally, river regulation continues to threaten freshwater biodiversity (Dudgeon, 2019) and, in particular, pelagophils as their life-history characteristics are highly susceptible to altered flow regimes and landscape fragmentation (Dudley & Platania, 2007; Mollenhauer et al., 2021). In the context of the Barwon–Darling River system, the 2020 PFE provided opportunity for widespread spawning of golden

perch. Protection of future flow events is essential to support golden perch life history in the Barwon–Darling system, especially when antecedent conditions include extended low flow or cease-to-flow events. We acknowledge that protecting immediate post-drought flows is just one of the important elements of a complete pelagophil conservation strategy that must also include a range of complementary measures to ensure long-term population viability (Baumgartner et al., 2020).

## AUTHOR CONTRIBUTIONS

**Jason Thiem:** Conceptualisation; data analyses; writing—original draft. **Laura Michie:** Methodology; data analyses; writing—review. **Gavin Butler:** Conceptualisation; editing. **Brendan Ebner:** Writing—review; editing. **Clayton Sharpe:** Conceptualisation; editing. **Ivor Stuart:** Conceptualisation; editing. **Anthony Townsend:** Conceptualisation; editing; funding acquisition.

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## 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 at the end of this article.

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