# Ecology and population dynamics of golden perch in a fragmented, flow-impacted river: implications for conservation and management.

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# Declaration

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Brenton P. Zampatti

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**Cover Image:** golden perch (*Macquaria ambigua*)

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This thesis is the result of many (too many) years of work, but at the end-of-the-day it is a privilege to have an occupation where I am able to indulge a passion for the natural world and delve into the lives of fishes. I hope the knowledge generated through this thesis helps improve their lot.

*This thesis is dedicated to Keith Walker, who passed away unexpectedly in February 2016.*

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# Abstract

In rivers worldwide, human demands for water resources have fundamentally altered flow regimes and aquatic habitats, leading to profound impacts on ecosystem integrity and biodiversity. Riverine fish are prominent indicators of the impacts of river regulation because of fundamental links between flow, life histories and population dynamics. In order to effectively manage and rehabilitate riverine fish populations, there remains a considerable need to understand the life history processes and associated environmental variables that influence population structure and resilience.

In Australia's Murray-Darling Basin, native fish populations have declined in association with river regulation, yet few studies have considered the age demographics and dynamics of populations, and the processes that influence these, in an integrated manner. In this thesis, I have explored the population structure and dynamics of the migratory, pelagic spawning, golden perch (*Macquaria ambigua*), in the flow regulated and fragmented River Murray. My overarching aim was to investigate the population dynamics of golden perch and the processes (e.g. recruitment and movement) that influence population structure, including the potential effects of flow and river regulation. To understand how flow and connectivity influence population dynamics, I characterised temporal variability in age demographics over a period of hydrological extremes (drought–flood), then to elucidate the processes promoting these temporal patterns, I investigated spawning, recruitment and movement.

From 2001 to 2010, the Murray-Darling Basin (MDB) experienced severe drought. Throughout this period, golden perch age structure in the lower River Murray was characterised by intermittent recruitment and a few dominant cohorts. These distinct cohorts were predominantly recruited prior to the drought, in association with overbank floods or increased flow contained within the river channel (Chapter 2).

Despite a depauperate age structure at the end of the Millennium Drought, population growth of golden perch in association with flooding in 2010 was rapid and substantial (Chapter 3). This response superficially supports the *flood-pulse* model, where flooding promotes high

abundances of biota due primarily to recruitment driven by floodplain derived energy. Nevertheless, growth in the golden perch population was promoted by increased abundances of age 0+ and 1+ fish, the product of spawning and recruitment in the flood year and the year prior, respectively. Recruitment of age 0+ fish was substantial, demonstrating the capacity of fishes with *periodic* life histories to respond to episodic events that may promote high survival of early life stages. In addition, however, approximately 50% of the population sampled post-flooding was age 1+ fish, that were not detected in the population as age 0+ the year prior, and were assumed to have migrated from elsewhere in the system. Consequently, immigration of juvenile fish was considered a substantial driver of population growth.

In order to understand the spatial arrangement of recruitment sources, and the influence of movement on population structure, I used otolith chemistry to retrospectively determine the provenance and movement history of individuals from specific age cohorts (Chapter 4), and radio telemetry to investigate the movements of adult fish (Chapter 5). Water and otolith chemistry, specifically $^{87}Sr/^{86}Sr$, was used to delineate the provenance and movement of golden perch. Water $^{87}Sr/^{86}Sr$ was distinct among the Darling River and lower and mid-River Murray. In turn, otolith chemistry revealed that golden perch collected in the lower River Murray were the progeny of spawning in either the River Murray or Darling River, during years characterised by within-channel rises in flow, or in both rivers in a year characterised by extensive overbank flooding.

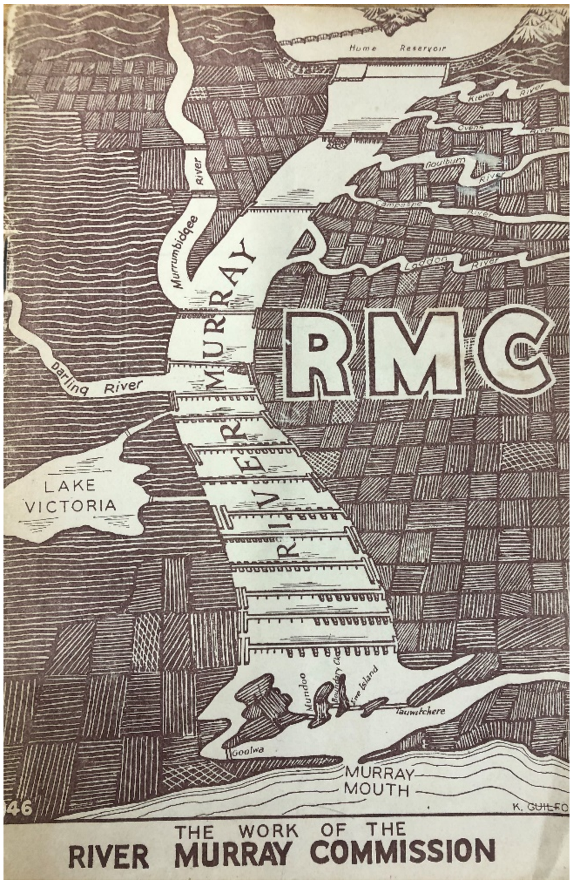
Movement of fish from the Darling River was a substantial driver of population structure in the lower River Murray, with fish dispersing from natal habitats in the Darling River either in the year of birth, as eggs and larvae, or at age 1+ in association with flooding. Importantly, the Darling River constituted a recruitment source for golden perch when environmental conditions were unsuitable for spawning and recruitment in the River Murray. In regulated river systems worldwide, the ecological importance of tributaries and tributary-mainstem junctions is increasingly recognised.

To investigate the habitat use and movement of adult golden perch in relation to flow, season and water temperature, I used a combined radio-telemetry and passive integrated transponder (PIT) tag approach. Site fidelity was common, with 36% of fish remaining at the site of capture throughout the study period (~2 years). Over the same period, however, 29% of fish migrated long distances upstream (up to 270 km), coinciding with steady, rising and falling flows. These movements were correlated with seasonal variation in water temperature and to a lesser extent, flow variability. Whilst environmental factors, such as flow, may constitute an impetus for movement, movement may also be driven by endogenous cues such as sexual maturity and age. The role of these factors in promoting movement and interactions with flow, warrant further investigation.

Golden perch in the lower River Murray appeared to exhibit partial migration, whereby some fish in a population migrate and some do not. This combination of retentive and dispersive behaviours minimises risks associated with habitat and environmental heterogeneity. For example, in large river basins, where climate variability and river regulation lead to regionally diverse flow patterns, within-population variability in migratory movements and destinations increases the chance of at least some fish being exposed to environmental conditions conducive to spawning and recruitment. For golden perch, this mechanism may contribute to the basin-wide persistence of this species.

In this thesis, I have addressed concepts relating to the autecology, population structure and movement of golden perch and provided new insights regarding the spatial structuring of populations. Globally, these factors are considered key contemporary knowledge requirements for understanding the impacts of anthropogenic disturbances on riverine fish populations. Despite increasing recognition of the need to manage freshwater fishes, and indeed ecosystem function, at the river-scale, research and management are often undertaken in a spatially disaggregated manner. Ultimately, conservation and rehabilitation of riverine fishes requires management at a spatial scale concordant with life history and population processes. Such approaches also need to integrate recruitment source, life history and migratory diversity, and the hydrological and hydraulic characteristics of rivers that support critical life history processes.

# CHAPTER 1: General Introduction



River Murray Commission (1946)

The regulated River Murray

## Chapter 1: General Introduction

### River regulation and freshwater fishes

Flow is a pervasive force in riverine ecosystems. It drives hydrological and geomorphological processes, and determines the types and amount of habitat available to aquatic biota (Poff and Ward 1989). It governs the nature of the substratum and the degree of connectivity between habitats (longitudinally, laterally, vertically and temporally), facilitates the exchange of nutrients and organisms (Vannote *et al.* 1980; Junk *et al*. 1989; Thorp and Delong 1994; Ward and Stanford 1995) and influences the physiological nature, movements and life histories of resident plants and animals (Junk *et al.* 1989; Poff *et al.* 1997).

In many regions of the world, human demands for freshwater have fundamentally altered the flow regimes of rivers, leading to profound impacts on freshwater biodiversity and the integrity of aquatic ecosystems (Dudgeon *et al*. 2006; Vorosmarty *et al*. 2010). Dams impede the flow regimes and fragment habitats of over half the world's large river systems (Nilsson *et al.* 2005). Indeed, flow regulation through dams, barrages, weirs and levees arguably is the most significant human impact on aquatic ecosystems (Petts 1984; Sparks 1995; Stanford *et al.* 1996; Ward *et al.* 1999; Pringle *et al.* 2000).

The impacts of flow-regulating structures are generally well known (Petts 1984; Ward and Stanford 1989; Walker and Thoms 1993; Bunn and Arthington 2002). Impacts occur upstream and downstream as a result of habitat fragmentation, inundation, hydraulic and hydrological alteration, and altered water physico-chemistry. Regulatory structures fragment habitats by obstructing the longitudinal and lateral dispersal and migration of aquatic organisms (Lucas and Baras 2001) leading to reductions in abundance, distribution, richness and/or diversity of aquatic communities, genetic isolation and species loss (Penczak *et al.* 1998; Ward *et al.* 1999; Gehrke *et al.* 2002; Katano *et al*. 2006). Artificially elevated water levels, upstream of regulating structures (i.e. weir pools or reservoirs), permanently connect habitats that may have been connected temporally or not at all, whilst hydraulic alteration converts lotic to lentic waters and reduces hydraulic heterogeneity (Petts 1984; Bice *et al*. 2017). This affects geomorphic (e.g. erosion,sedimentation) and biological (e.g. larval drift) processes and favours biota adapted to lentic rather than lotic systems (Copp 1990; Brown and Ford 2002; Dudley and Platania 2007)

Hydrological alteration inhibits geomorphic processes (such as channel development), isolates channel and floodplain environments and reduces floodplain productivity, alters the availability and suitability of habitats for aquatic organisms, and disadvantages biota reliant on hydrological variability and cues (Boulton and Lloyd 1992; Walker and Thoms 1993; Sparks 1995; Nesler *et al.* 1988; Pringle *et al.* 2000; Bunn and Arthington 2002). In floodplain rivers, discharge variability produces a mosaic of aquatic and terrestrial habitats that foster biota adapted to exploit spatio-temporal disturbance (Copp 1989; Ward and Stanford 1989; Ward *et al*. 1999). River regulation disrupts the natural disturbance regimes that maintain these mosaics, (Junk *et al.* 1989; Ward *et al.* 1999; Poff *et al.* 2007). In turn, this leads to a loss of faunal diversity and a change in ecosystem structure and function (Walker *et al.* 1992; Welcomme 1994).

Globally, population decline and range reduction are major issues for freshwater biodiversity (Dudgeon *et al*. 2006) and declines in large-bodied riverine fishes exemplify this (Cooke *et al*. 2012). Because of their dependence on aquatic habitats and the fundamental links between flow and life histories and population dynamics, riverine fish are prominent indicators of changes associated with river regulation (Bunn and Arthington 2002). Flow regulation can affect fish by decreasing habitat complexity and productivity, and by interrupting critical life history processes such as movement and spawning (Dudley and Platania 2007). In turn, recruitment may be compromised leading to population decline (e.g. Paragamian *et al*. 2005). Ultimately, river regulation creates conditions that favour generalist and non-indigenous species at the expense of locally-adapted native fishes (Brown and Ford 2002; Aarts *et al*. 2004; Poff *et al.* 2007).

Riverine fishes display diverse life history strategies (e.g. Humphries *et al*. 1999; Reynolds *et al*. 2005) that may determine differential susceptibility to the impacts of river regulation (Winemiller 2005; Olden *et al*. 2006). Perhaps the best known study of life history diversification in freshwater fishes and its implications for population regulation, including the impact of anthropogenic disturbance, is that of Winemiller and Rose (1992) who developed a framework based on trade-offs among three demographic variables of survival, fecundity, and onset and duration of reproductive life.

This approach was considered an improvement on guilds defined by physiological recruitment attributes that provided limited insight into the dynamics of populations (Winemiller 2005). Winemiller and Rose (1992) proposed a trilateral continuum between three primary life history strategies: 1) periodic – large, long-lived, high fecundity, contracted breeding season, 2) opportunistic – small, short-lived, high reproductive effort, extended breeding season and 3) equilibrium – intermediate size, low fecundity, large egg size, parental care. Such an approach enables prediction of populations with high or low demographic resilience as influenced by environmental variability, predictability and seasonality. Ultimately, in regulated rivers, flow modification and fragmentation influence the life-history composition of fish assemblages (Olden and Kennard 2010). Fishes with periodic life-history strategies and high recruitment variation/low demographic resilience may be particularly susceptible to the hydrological modification of rivers, especially homogenisation of flow regimes; concurrently, species with opportunistic life-history strategies may prosper (Olden *et al*. 2006).

Maintenance or reinstatement of natural flow variability is considered vital to support the conservation of freshwater biota (Poff *et al*. 1997; Arthington and Pusey 2003).To facilitate integrated approaches that address water security for humans and the conservation of freshwater biodiversity (Vorosmarty *et al*. 2010), trade-offs need to be made. These trade-offs will be best informed by a knowledge of how ecosystems and their constituent biota function and respond to flow modification (Richter *et al*. 2003). Conservation of freshwater fishes requires an understanding of the life history processes that influence population dynamics, including their spatio-temporal characteristics and the relationships with environmental conditions, particularly flow. In large rivers, however, relationships between environmental variables and key life-history processes (e.g. spawning, movement) are spatio-temporally complex and inherently difficult to study (Fausch *et al*. 2002; Kraabol *et al*. 2009).

Despite many advances in the study of freshwater fishes, an understanding of the autecology of freshwater fishes remains fundamental to conservation. A lack of basic information on fish life history (e.g. where fish spawn, where they move, when they move) constitutes a major impediment to the management and conservation of fishes in large-rivers, and inhibits restoration of hydrology, habitats, fish populations and riverine ecosystems (Galat and Zwiemuller 2001; Cooke *et al*. 2012). These sentiments are echoed by Shenton *et al*. (2012), Cooke *et al*. (2016) and Crook *et al*. (2016) who collectively advocate the need for basic autecological knowledge on freshwater fishes to inform modelling of population dynamics, mitigation of barriers to fish passage and ecosystem restoration. In addition to a paucity of life-history and ecological information, data on the demographics and population dynamics of many freshwater fishes is scarce (Reynolds *et al*. 2005)

### Flow regulation in Australia's Murray-Darling Basin

Flow modification is often most severe in regions where flow variability is naturally high and where human demand for security of water supply is greatest. The flow regimes of rivers in the Murray-Darling Basin (MDB), Australia, are highly variable and many native biota have evolved to exhibit broad environmental tolerances and flexible life histories (Walker *et al.* 1992; Puckridge *et al*. 1998). Like elsewhere in the world, anthropogenic modification of flow regimes in the MDB, homogenises and fragments habitats and hydrology, disrupting a dynamic disturbance regime.

Modification of flow regimes and the structures that achieve it (hereafter termed river regulation) are considered primary factors in declines in the range and abundance of native fish in the MDB. Indeed, the MDBC *Native Fish Strategy* estimates that native fish abundances are presently 10% of their pre-European levels reflecting the effects of flow regulation, habitat degradation, lowered water quality, barriers, alien species, exploitation, diseases, and translocation and stocking (Barrett 2004). As a result, fish are a primary objective, and form a considerable focus, for environmental water delivery under contemporary river rehabilitation programs such as the Murray-Darling Basin Plan and the associated Basin Watering Strategy (Koehn *et al*. 2014).

Research on the impacts of river regulation on freshwater fish of the MDB has primarily occurred in the mid to upper reaches of the River Murray and its tributaries (i.e. the Ovens, Goulburn, Broken and Campaspe Rivers) (e.g. Mallen-Cooper 1996; Humphries and Lake 2000; King *et al.* 2003; Mallen-Cooper and Stuart 2003; O'Connor *et al*. 2005). These regions are hydrologically and hydraulically distinct from the lower reaches of the River Murray with many reaches retaining their lotic character, albeit with altered seasonality of flows, decreased flow variability and magnitude, and in some cases, cold water pollution (Maheshwari *et al*. 1995). As a consequence, life history models proposed for native and alien fish species may reflect this mid-catchment perspective (e.g. Humphries *et al.*, 1999; Stuart and Jones, 2006; Koster *et al*. 2016).

The lower River Murray, defined as the 885 km of river between the Darling River confluence and the river mouth is regulated by levies, five tidal barrages and 10 low-level (<3 m) weirs, creating a series of impounded weir pools that have lost their lotic character and, under non-flood flows, have relatively stable water levels (Walker 2006). The weirs, and associated weir pools, create barriers to the upstream and downstream movement of aquatic biota, although upstream fish passage has been addressed through installation of fishways on the tidal barrages and all main stem weirs, via the 'Sea to Hume Dam' fish passage program (Barrett and Mallen-Cooper 2006).

Upstream river regulation (i.e. headwater dams and riverine diversions) has reduced hydrological variability in the lower River Murray, leading to isolation of the floodplain, a loss of environmental cues, decreased riverine productivity and altered carbon dynamics (Boulton and Lloyd 2002; Gawne *et al*. 2007). Despite these significant changes to the natural flow regime, connectivity and productivity, there are few quantitative data to describe the impacts on fish and ultimately to inform actions to conserve and rehabilitate native fish populations.

## Freshwater fish in the Murray-Darling Basin

Overall, native fish populations in the MDB have declined in range and abundance, whilst exotic species such as common carp (*Cyprinus carpio*) have proliferated (Cadwallader 1978; Walker and Thoms 1993; Gehrke *et al*. 1995; Pollino *et al*. 2004; Mallen-Cooper and Brand 2007). In its various forms, river regulation in the MDB exacerbates other threats such as salinity, reduced water quality and alien species, and across a continuum of spatial scales (e.g. wetland to catchment), alters fish assemblages, decreases species diversity and favours exotic species (Gehrke and Harris 2000; Humphries and Lake 2000; Gehrke and Harris 2001; Humphries *et al.* 2002; Pollino *et al.* 2004; Humphries *et al.* 2008). Dams and weirs cause downstream accumulations of fish, alter the abundance and feeding habits of fishes upstream and downstream, and affect fish behaviour (Cadwallader 1977;

Mallen-Cooper 1996; O'Connor *et al.* 2006; Baumgartner 2007). Furthermore, smaller-scale floodplain regulating structures and levees interrupt lateral connectivity (Jones and Stuart 2008).

Flow regulation is implicated in the population decline of species that spawn in relation to flow cues (e.g. golden perch), or for whom increases in flow improve recruitment (e.g. Murray cod *Maccullochella peelii*) (Walker and Thoms 1993). Cold-water pollution from headwater dams, although not applicable to the lower River Murray, has also altered fish assemblages by disadvantaging native species and favouring exotic species (e.g. brown trout *Salmo trutta*) (Pollino *et al.* 2004; Todd *et al.* 2005).

The primary impacts of river regulation on fishes in the lower River Murray are reduced hydrological variability, leading to isolation of the floodplain and a loss of environmental cues, altered fluvial dynamics (conversion of lotic to lentic waters), barriers to movement and interactions with alien species. Nevertheless, there are few quantitative data to describe the consequences.

The native fishes of the MDB demonstrate three life-history modes, analogous to the three life history strategies proposed by Winemiller and Rose (1992) and reflecting the duration of spawning, spawning style and time, cues for spawning, fecundity and parental care (Humphries *et al.* 1999):

1. *Large-bodied circa-annual spawners* (relates to Humphries *et al*. (1999) Mode 1 and Winemiller and Rose (1992) equilibrium strategy). Large-bodied, long-lived species (e.g. Murray cod, freshwater catfish *Tandanus tandanus*) that spawn in spring/early summer, and at the same time each year. Spawning is temperature related and thousands to tens of thousands of eggs are laid demersally and subject to parental care.
2. L*arge-bodied flow-cued spawners* (Humphries *et al*. (1999) Mode 2 and Winemiller and Rose (1992) periodic strategy). Large-bodied, long-lived species (e.g. golden perch, silver perch *Bidyanus bidyanus*) may spawn at any time between spring and autumn. Spawning is linked to a rise in flow (or flow variability) and a temperature threshold. Hundreds of thousands of semi-buoyant (pelagic) eggs are laid and no parental care is exhibited.

3. *Small-bodied protracted* or restricted spawners (Humphries *et al*. (1999) Mode 3a and 3b, respectively and Winemiller and Rose (1992) opportunistic strategy). Mostly small-bodied species that have protracted, repeat or serial spawning from spring to autumn (e.g. Australian smelt *Retropinna semoni*, flatheaded gudgeon *Philypnodon grandiceps*) or a single spawning event from late winter through summer (e.g. carp gudgeons *Hypseleotris* spp and Murray rainbowfish *Melanotaenia fluvialtilis*). Spawning cues are uncertain; from hundreds to thousands of planktonic or demersal eggs are laid and no parental care is exhibited.

In general, the only species that require flow variability to spawn are the flow-cued spawners, golden perch and silver perch, and strong recruitment of these species coincides with in-channel rises in flow and overbank floods (Mallen-Cooper and Stuart 2003; Ye 2004). Consequently, restoration of key aspects of the hydrograph (e.g. spring flow pulses) may be particularly important for these species.

Although in many large temperate and tropical rivers there are numerous species that specifically spawn on floodplains (Copp and Penaz 1988; Gorski *et al*. 2010), it appears that in the southern MDB (and likely the MDB as a whole) there are no large-bodied native species that actually use floodplains for spawning (Humphries *et al*. 1999; King *et al*. 2003). The one large-bodied species that does is the alien common carp (King *et al.* 2003).

Most native fish species will spawn and recruit in the river channel, but it is highly likely that floodplain inundation increases productivity in the channel, benefiting recruitment (Junk *et al.* 1989). Strong recruitment in some circa-annual and flow-cued spawners (i.e. Murray cod and golden perch) has been associated with overbank flows (Ye 2004; Rowland 1996; Zampatti *et al*. 2014) and, if floods coincide with spawning, food from the floodplain is transported back into the river channel, enhancing recruitment (Humphries *et al.* 1999). Nevertheless, the role of the floodplain and overbank flows in the recruitment ecology of large-bodied fish in the lower River Murray remains unexplored.

Investigations into the ecology of freshwater fishes in the lower River Murray have predominantly been conducted on small- to medium-bodied fishes in relation to distribution, life history and taxonomy (Lloyd and Walker 1986; Puckridge and Walker 1990; Bertozzi *et al*. 2000; Hammer *et al.* 2007; Wedderburn *et al.* 2008) and more has been published on the ecology of large-bodied alien fish than large-bodied native fish (e.g. Villizzi and Walker 1999a, 1999b; Smith and Walker 2003a, 2003b, 2004). Reynolds (1983) investigated the movement of large-bodied native species and the exotic common carp, but only recently have investigations of the assemblage structure and migration ecology of entire fish communities been initiated (e.g. Baumgartner *et al.* 2008; Stuart *et al.* 2008 and Conallin *et al*. 2011).

Most of the investigations into the flow-related ecology and impacts of river regulation on fish in the MDB have been undertaken in the hydrologically and hydraulically distinct mid-reaches of the Murray River and its tributaries (e.g. Humphries and Lake 2000; Mallen-Cooper and Stuart 2003; King *et al*. 2003; O'Connor *et al*. 2005).

### Study species: golden perch (*Macquaria ambigua*)

Golden perch (*Macquaria ambigua*) is a large-bodied (up to 76 cm total length, [TL]) potamodromous fish (i.e. migrates wholly within freshwater) that is widespread in the Murray-Darling, Lake Eyre and Bulloo-Bancannia river basins (representing the Murray-Darling and Central Australian biogeographical provinces, Unmack 2001), and also occurs in the Dawson and Fitzroy Rivers, in the Eastern biogeographical province (Allen *et al.* 2002; Unmack 2001). Across these regions, golden perch are currently described as a single taxon (*M. ambigua*), but a range of studies have demonstrated various levels of genetic variation among populations (e.g. Musyl and Keenan 1992; Faulks *et al*. 2010; Beheregaray *et al*. 2017). As such, three distinct lineages are recognised across the three biogeographical provinces (Beheregaray *et al*. 2017).

Golden perch is an iconic fish in the Murray-Darling Basin; a major target species for recreational anglers and formed the primary component of a commercial fishery in the River Murray until 2002, when commercial fishing ceased in the riverine reaches of the lower River Murray (Ye 2004). A commercial fishery, however, continues to operate in the terminal lakes (Alexandrina and Albert) of the River Murray where approximately 20–200 tonnes/annum is landed (Earl 2016).

Golden perch has undergone reductions in range and abundance in the MDB (Cadwallader 1978; Walker 1979; Brumley 1987). These declines have been primarily attributed to the construction of dams and weirs altering flow regimes and creating barriers to movement (Cadwallader 1978; Gehrke *et al*. 1995; Mallen-Cooper 1996; McDowall 1996). Interestingly, the potential impacts of commercial or recreational fishing are rarely mentioned. The following sections discuss the life history of golden perch in relation to the impacts of river regulation on spawning and recruitment, and movement.

**How does hydrology influence the spawning and recruitment of golden perch?**

Golden perch exhibit a *periodic* life-history strategy (Winemiller and Rose 1992) with a life-span of over 20 years, batch fecundity of ~500,000 and high recruitment variation (Lake 1967; Stuart 2006; Mallen-Cooper and Stuart 2003). Golden perch are also pelagic broadcast-spawners (i.e. release passively drifting eggs into open water that develop as they drift downstream), a trait they potentially retained from a marine ancestor (Mackay 1973). Indeed, pelagic broadcast-spawning is common in marine fishes, and whilst is has been proposed a rare trait in freshwater fishes (Houde 1994; Hoagstrom and Turner 2015) it is relatively common in riverine fishes in tropical South America and South East Asia (Medley *et al*. 2007; Cowx *et al*. 2015)

In lotic ecosystems, pelagic broadcast-spawning is often associated with migratory reproductive behaviour and, in conjunction, such life history traits render these species particularly susceptible to the impacts of river regulation (Welcomme and Winemiller 2005). In lotic ecosystems worldwide, migratory, pelagic broadcast-spawning fishes (pelagophils) are disadvantaged by fragmentation and flow modification; spawning migrations are interrupted by barriers, hydrologic cues and hydraulic habitats for spawning are altered by flow regulation, and the obligate downstream drift of eggs and larvae, essential for the development of early life stages, is interrupted by the physical and hydraulic impacts of dams and weirs (Dudley and Platania 2007; Perkin *et al*. 2015). Many of these species also demonstrate periodic life history strategies, with high recruitment variability and low demographic resilience (Winemiller 2005).

Golden perch was originally described as flood-cued spawner by Lake (1967) and more recently as a species that has a life history that fits the Flood-Pulse Concept proposed by Junk et al. (1989) (Gehrke and Harris 1994; Schiller and Harris 2001). That is, fish spawn in association with spring floods that inundate floodplains, stimulating the production of abundant food, such as zooplankton, and facilitating high rates of survival of larval fish. This model, however, has been questioned in recent years with researchers demonstrating that spawning may occur in association with increases in flow contained within the river channel (Mallen-Cooper and Stuart 2003; Roberts *et al.* 2008; Sharpe 2011). It has also been reported that golden perch may spawn with no increase in flow (King *et al.* 2005; Balcombe *et al.* 2006). Strong recruitment into the adult population has also been associated with within-channel rises in flow (Mallen-Cooper and Stuart 2003). Golden perch in regulated rivers, however, have more variable recruitment, whereby a small number of age classes comprise a large proportion of the population, than in unregulated or lesser-regulated rivers where multiple age classes indicate more frequent recruitment (Roberts *et al.* 2008).

The collection of fish larvae can provide evidence of when, where and under what environmental conditions a particular fish species has spawned. Furthermore, fish larvae have been suggested as a useful tool to investigate the effects of river regulation and restoration (Scheidegger and Bain 1995; Humphries and Lake 2000). Numerous studies have collected the drifting eggs or larvae of golden perch but the success of subsequent recruitment in these studies was unevaluated (King *et al.* 2005; Gilligan and Schiller 2003). The presence of larval fish alone does not predicate recruitment and ultimately recruitment into the reproductive population will be a key to the restoration of native fish communities. Our knowledge on how hydrology influences the population dynamics of golden perch is growing; nevertheless, long-term studies that integrate spawning, survival, recruitment to the adult population and flow have been lacking (King *et al.* 2005; Brown and Wooden 2007).

### Movement of juvenile and adult golden perch

Golden perch exhibit a range of migration patterns from strong home range fidelity (Crook 2004) to large-scale (100s-1000s km) movements upstream and downstream (Reynolds 1983; O'Connor *et al*. 2005). Long-distance movements in spring and early summer, both in an upstream and downstream direction, are proposed to be associated with spawning, but empirical data linking movement with reproduction are rare. Nevertheless, Koster *et al*. (2017) associated golden perch movement with the spatio-temporal presence of eggs and larvae in a tributary of the River Murray.

In a tag and recapture study undertaken in the lower River Murray, golden perch were recorded travelling >1000 km in an upstream direction and >450 km downstream (Reynolds 1983). Reynolds (1983) proposed that long-distance upstream migrations were a spawning movement being undertaken by mature golden perch to ensure that pelagic eggs would not drift into saline water and die. Subsequently, monitoring of fishways in the mid-Murray has demonstrated that a large proportion (>90%) of the migratory population may, at times, be smaller immature fish, age 1+ and greater (Mallen-Cooper 1999; Mallen-Cooper and Brand 2007).

Biotelemetry techniques have been used to investigate the movement of golden perch in the mainstem and tributaries of the mid reaches of the River Murray (Crook 2004a, 2004b; O'Connor *et al.* 2005; O'Connor *et al*. 2006). O'Connor *et al*. (2005) utilised radio-telemetry to investigate the movement of adult golden perch in a relatively unobstructed 500 km lotic reach of the mid River Murray. Fish were observed to move both downstream and upstream during a rising spring flow to distinct reaches of the River Murray before making return homing movements. These movements were in the spawning season (spring–summer) and hence were considered to be associated with reproduction, while outside the spawning season there was limited movement (O'Connor *et al*. 2005). A similar non-spawning season pattern of restricted movement, strong site fidelity and established home ranges was reported in a River Murray tributary (Crook 2004a, 2004b). Yet that study was over a short time-frame (four months) and in a geomorphically constrained section of river. Consideration of the temporal and spatial scale of these investigations is important, especially with long-lived fish.

The life histories and ecological requirements of migratory, pelagic-spawning fishes, such as golden perch, expose these fishes to multiple impacts of river regulation. Understanding the ecology and mechanisms by which golden perch populations are structured in the lower River Murray can guide ecological rehabilitation in the MDB (e.g. barrier removal, hydrological and hydraulic restoration, habitat restoration). Furthermore, this knowledge can provide broader insight into the population dynamics of freshwater fishes with periodic life strategies, and guide population rehabilitation in regulated rivers.

### Study Region: The lower River Murray and Chowilla Anabranch system

The Murray-Darling Basin is the largest catchment in Australia, draining an area of 1 073 000 km$^2$ or 14% of the continent. The combined length of the two major rivers, the Murray and the Darling, is ~5 500 km. In general, the climate is arid or semi-arid and approximately half the annual discharge originates from <5% of the catchment (the headwaters of the Murray) (Walker 1992). Mean and median annual discharge are 12 300 GL and 11 883 GL, respectively, but natural discharge is highly variable (Maheshwari *et al*. 1995). Under regulated conditions approximately 36% of the natural mean annual discharge (4 915GL) reaches the sea (Walker 2006), although this has been zero several times in the past 10 years due to diversions and storage during drought (Zampatti *et al*. 2010).

Flows in the system are managed by the Murray-Darling Basin Authority (MDBA) according to a parliamentary agreement from 1914 and SA receives a guaranteed minimum annual entitlement flow of 1850 GL (Jacobs 1990). This normally comprises a minimum winter (non-irrigation season) flow (measured at the South Australian border) of approximately 3 000 ML/d and a summer (irrigation season) flow of approximately 7 000 ML/d.

Large-scale regulation commenced in the 1920s, and by the 1960s the Murray subsystem was regulated by three large headwater storages (Hume, Eildon, and Burrinjuck), main channel and tributary weirs, levees and tidal barrages. The lower River Murray, downstream of the Darling River confluence, is re-regulated by floodplain levies, five tidal barrages and 11 low level (<3 m) weirs creating a series of impounded weir pools that under non-flood flows have relatively stable water levels (Walker 2006). Weirs in the lower Murray were specifically located to provide navigation for paddle steamers in the 1920s and 30s, hence they create a continuous series of pools. Their cumulative effects on the river's ecosystem are profound. These structures have fragmented over 600 km of river into a series of 29–88 km long weir pools and transformed a highly dynamic lotic system into a homogenous series of cascading lentic environments (Walker 2006). The impacts of river regulation on the hydrology, geomorphology and ecology of the lower River Murray have been comprehensively described (see Walker *et al.* 1992; Walker and Thoms 1993; Maheshwari *et al.* 1995; Walker 2006).

One area in the lower River Murray River that does retain spatial habitat variability, including hydraulic heterogeneity, under regulated flows, is the Chowilla Anabranch system. The floodplain in this region is 5–10 km wide and is characterised by many irregularly shaped off-channel habitats including anabranches, billabongs (oxbows) and deflation basins (Walker and Thoms 1993). The Chowilla region is the largest remaining region of floodplain habitat in the lower River Murray River and in 1987 the region was listed as a *Wetland of International Importance* under the Ramsar Convention recognising its diverse birdlife and the extent of red gum (*Eucalyptus camaldulensis*) and black box (*Eucalyptus largiflorens*) woodlands.

The Chowilla Anabranch system lies on the northern floodplain of the River Murray adjacent to Lock and Weir No. 6, approximately 620 km from the river mouth. The anabranch system is a complex of perennial and ephemeral creeks, backwaters, billabongs and lakes. Data on the historical (preregulation) character of the system is scarce; nevertheless, some insight can be gained from the journal of the explorer Charles Sturt. In the summer of 1829-30, Sturt travelled by boat from the mid-reaches of the Murrumbidgee River down the River Murray to the Murray mouth. He made numerous observations of the hydraulic character of the river. In late January 1830 he described a significant 'rapid' in the vicinity of the Rufus River, then after passing the Lindsay River described the river tending southwards (the approximate present day site of Lock 6) and passing down a series of several rapids. He did not describe the Chowilla Creek confluence but described more 'rapids' and 'shoals' as he passed through the Murray gorge (Sturt 1833). The channel forms that Sturt described have now been replaced by a series of contiguous weir pools.

Due to the head differential (~3 m) created by Lock and Weir No. 6 on the Murray River, 20–90% of River Murray flows are now diverted through the Chowilla Anabranch system under low flow conditions (i.e. < 10,000 ML/d) (Stace and Greenwood 2004). Consequently, the Chowilla Anabranch system exhibits permanent lotic habitats in what previously would have been a combination of perennial and ephemeral streams. Given Sturt's 1830 description of the River Murray in this region, it appears that regulation has shifted lotic waters from the main channel into the anabranch system, and reduced these habitats regionally by hundreds of kilometres.

The uniqueness of these flowing waters in a region where main channel hydraulics have been fundamentally altered has been attributed to the maintenance of remnant populations of endangered flora and fauna that are uncommon or extinct elsewhere in the lower Murray (O'Malley and Sheldon 1990; Pierce 1990; Sharley and Huggan 1995). The region has been proposed as a significant spawning and recruitment site for golden perch and Murray cod (*Maccullochella peelii*) (Pierce 1990; Lloyd 1990), two fish species whose range and abundance have declined in the MDB (Cadwallader 1978; Walker and Thoms 1993).

## Thesis scope

River regulation is considered a dominant factor in worldwide declines in the distribution and abundance of freshwater fishes. Despite this, studies that investigate the influence of hydraulics and hydrology on the ecology of fish over a range of spatial scales and over sufficiently long temporal scales (i.e. multiple years) are rare (Fausch *et al*. 2002; Arthington and Pusey 2003; Humphries *et al*. 2008). Furthermore, whilst the potential impacts of river regulation on native fish are often discussed, there are few studies that provide causal links or direct evidence (Murchie *et al.* 2008). This is particularly true for fish populations in the Murray-Darling Basin.

In order to effectively manage and rehabilitate riverine freshwater fish populations, there remains a considerable need to understand the life histories and population dynamics of fishes, including the influence of flow on population processes (e.g. spawning, recruitment, movement) (Cooke *et al*. 2012). The *periodic* life history characteristics of golden perch, including long-distance migration, flow-cued spawning and pelagic eggs and larvae, render this species particularly susceptible to river regulation. As such, the rehabilitation of golden perch populations forms a key component of flow restoration strategies in the MDB. Nevertheless, the population dynamics of golden perch throughout the MDB remain little explored and knowledge on the ecology of golden perch remains incomplete. This information is fundamental to inform flow restoration strategies to mitigate the impacts of river regulation on golden perch and to develop robust monitoring programs to measure response.

The Chowilla Anabranch system and adjacent River Murray are considered important to the ecology and regional population dynamics of golden perch, yet the region is also subject to the range of impacts of river regulation that characterise the lower River Murray, namely altered fluvial dynamics (conversion of lotic to lentic waters), barriers to movement, and reduced hydrological variability. Consequently, Chowilla and the adjacent River Murray provide a unique region in which to study the ecology and population dynamics of golden perch.

The overarching aim of this thesis is to investigate the population dynamics of golden perch in the lower River Murray and the processes (e.g. recruitment and movement) that influence population structure, including the potential effects of flow and river regulation.

The specific objectives are to:

1. Investigate temporal variation in spawning and recruitment of golden perch, over multiple years and in relation to biologically relevant environmental parameters (e.g. discharge and water temperature), in order to inform the conservation or restoration of ecologically important components of the flow regime of the River Murray.
2. Determine the influence of hydrological extremes (i.e. drought and overbank flooding) on golden perch population demographics in the lower River Murray.
3. Use water and otolith chemistry, specifically $^{87}Sr/^{86}Sr$, to retrospectively determine the natal origin of distinct cohorts of golden perch and the migration history of these fish. Identifying the provenance of golden perch in the lower River Murray and integrating this with migration history will improve understanding of the spatial ecology of golden perch and relationships between flow and key life history processes (spawning, recruitment and movement).

4. Investigate the movement behaviour of adult golden perch to understand how movement may influence population processes and also inform barrier mitigation, habitat conservation and rehabilitation, and environmental flow delivery.

These investigations will provide new knowledge regarding the ecology and population dynamics of golden perch in a highly regulated semi-arid river, and a continuum for studies undertaken in the hydrologically and hydraulically distinct mid-reaches of the River Murray, and the Darling River (e.g. Mallen-Cooper and Stuart 2003; King *et al*. 2003; O'Connor *et al*. 2005; Sharpe 2011). This will assist in the development of conceptual and empirical population models for golden perch, which incorporate appropriate spatio-temporal scales and associated environmental drivers. Such an approach will assist in the management and rehabilitation of native fish populations in the Murray-Darling Basin, and more broadly will advance understanding of the impacts of river regulation on riverine fishes, thus aiding management and conservation.

### Thesis structure and a note on chapter styles

In this thesis, each data chapter is written in the form of a stand-alone scientific paper, several of which (Chapters 2, 3 and 5) have been published. As such, each chapter includes a separate introduction, method, results, discussion and references, and tables and figures are integrated in the text. Co-authorship is acknowledged at the start of each published chapter. All chapters are tied to the overarching aim of my thesis, and I present them as a cohesive flow of work reflecting my research objectives and culminating in a General Discussion (Chapter 6).

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# CHAPTER 2: Within-channel flows promote spawning and recruitment of golden perch - implications for environmental flow management in the River Murray, Australia

An early life-stage golden perch

# Statement of Authorship

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| Contribution to the Paper | Designed study, collected and interpreted data, wrote manuscript and acted as lead and corresponding author | | |
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By signing the Statement of Authorship, each author certifies that:

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ii. permission is granted for the candidate in include the publication in the thesis; and

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# Within-channel flows promote spawning and recruitment of golden perch, *Macquaria ambigua ambigua* – implications for environmental flow management in the River Murray, Australia

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**Abstract.** Restoring fish populations in regulated rivers requires an understanding of relationships between hydrology and population dynamics. In the present study, spawning and recruitment of golden perch, *Macquaria ambigua ambigua*, were investigated in relation to flow in the regulated lower River Murray. All life stages were sampled in three successive years, with peak flows of 8500 (2004 05), 15 000 (2005 06) and 7000 ML day$^{-1}$ (2006 07). Larvae occurred only in November/December 2005, and young of year fish only in early 2006. Counts of daily increments in otolith microstructure indicated spawning in late October/early November 2005. Back calculated birth years for adults, derived from otoliths and compared with the hydrograph for the preceding 25 years, revealed the dominance of three year classes spawned in association with increased discharge in 2000, 1998 and 1996. In 2007, an additional year class of 1 year old fish appeared, following spawning in 2005. In each case, strong recruitment followed spring summer spawning, when peak flows were $>$14 000 ML day$^{-1}$ and water temperatures would have exceeded 20°C. Restoration of within channel flows of 15 25 000 ML day$^{-1}$ from late spring through summer would promote spawning and recruitment and improve the resilience of golden perch populations in the lower Murray.

**Additional keywords:** Chowilla, freshwater fish, Murray Darling Basin, restoration, river regulation.

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## Introduction

An understanding of flow related ecology is critical to the restoration of freshwater ecosystems, in particular to inform the provision of more natural flow regimes in regulated rivers (Arthington and Pusey 2003; Poff *et al.* 2010). Fish are a prominent indicator of anthropogenically induced changes to the natural flow regime. Worldwide, flow regulation affects fish by decreasing habitat complexity and productivity, impeding movement and disrupting life histories (Lucas and Baras 2001; Brown and Ford 2002; Poff *et al.* 2007). Many studies highlight the potential effects of river regulation on fish, yet there remains considerable need to quantify ecological responses to flow alteration, using rigorously designed experiments conducted over appropriate spatio temporal scales (Humphries *et al.* 2008; Souchon *et al.* 2008; Poff and Zimmerman 2010; Bradford *et al.* 2011).

Flow regulation is considered a key threat to native fish in the Murray Darling Basin (MDB), Australia (Cadwallader 1978; Gehrke *et al.* 1995), and is implicated, along with a range of other factors (e.g. habitat degradation, lowered water quality and alien species), in causing a reduction in native fish levels to ~10% of their pre European levels (Barrett 2004). Golden perch (*Macquaria ambigua*, Richardson, 1845; Percichthyidae) is a large bodied (up to 76 cm in total length, TL) potamodromous fish that is widespread in the inland rivers of Australia (Allen *et al.* 2002). Subspecies are recognised in the MDB (*Macquaria ambigua ambigua*), the Dawson and Fitzroy Rivers (*Macquaria ambigua oriens*) and potentially the Lake Eyre Basin (Musyl and Keenan 1992; Faulks *et al.* 2010). Golden perch (*Macquaria ambigua ambigua*) is an iconic fish in the MDB; it is a major target species for recreational anglers and once formed the primary component of a commercial fishery in the River Murray (Kailola *et al.* 1993). Golden perch has undergone a reduction in range and abundance in the MDB, which has primarily been attributed to anthropogenically altered flow regimes, cold water pollution and barriers to fish movement (Cadwallader 1978; Gehrke *et al.* 1995; Mallen Cooper 1996).

Golden perch has traditionally been described as a flood cued spawner, with a life history consistent with the flood pulse concept described by Junk *et al.* (1989). That is, fish spawn in association with spring floods that inundate floodplains, stimulating the production of abundant food such as zooplankton and facilitating high rates of survival of larval fish (Lake 1967; Harris and Gehrke 1993; Schiller and Harris 2001). This model, however, has been questioned in recent years, with spawning and recruitment found to occur also in association with increases in flow contained within the river channel or with no increase in flow (Mallen-Cooper and Stuart 2003; King *et al.* 2005; Balcombe *et al.* 2006; Roberts *et al.* 2008; Kerezsy *et al.* 2011).

Numerous studies have collected the drifting eggs or larvae of golden perch, and related the abundance of these to environmental conditions, but the success of subsequent recruitment in these studies remains unclear (Gilligan and Schiller 2003; King *et al.* 2005; King *et al.* 2009). Understanding recruitment and the demographics of populations, however, is essential for the conservation and restoration of freshwater fishes (Minckley *et al.* 2003). In the MDB, several studies have investigated the age or size structure of golden perch populations and related recruitment to antecedent flow conditions (Mallen-Cooper and Stuart 2003; Balcombe *et al.* 2006; Ebner *et al.* 2009). Using the age structure of golden perch in the mid-reaches of the River Murray, Mallen-Cooper and Stuart (2003) demonstrated a positive association between strong year classes and spring flows contained within the river channel. These findings support the proposition of Humphries *et al.* (1999) of a potential over-emphasis on the importance of flooding and floodplains in the biology of native fish in the MDB and that in-channel environments may also be important for spawning and rearing of native fish. Overall, our knowledge on how hydrology influences the population dynamics of golden perch is increasing; nevertheless, long-term studies that integrate investigations of larval abundance, survival, recruitment and the influence of flow have been lacking (King *et al.* 2005; Brown and Wooden 2007).

The objective of the present study was to investigate golden perch spawning and recruitment at a site within the lower River Murray. We expected that golden perch spawning and recruitment would be reliant on within-channel and overbank rises in flow and, consequently, golden perch recruitment would be episodic because of the highly altered flow regime of the lower River Murray. Specifically, we aimed to (1) investigate spawning and recruitment in relation to flow over a 3-year period in the lower River Murray, (2) verify the annual nature and seasonality of otolith increment formation for golden perch in the lower River Murray, (3) investigate the age structure of the golden perch population and relate back-calculated spawning dates to the antecedent flow regime and (4) inform the potential restoration of ecologically relevant components of the flow regime of the lower River Murray.

## Materials and methods

### *Study area*

The MDB drains an area of 1 073 000 km$^2$, or 17%, of the Australian continent. The combined length of the two major rivers, the Murray and the Darling, is $\sim$5500 km. The Murray and Darling Rivers flow through predominantly semiarid or arid landscapes. As such, in their natural states, they experienced highly variable flow regimes (Walker *et al.* 1995; Puckridge *et al.* 1998). River regulation in the form of large headwater storages, weirs, floodplain levees and tidal barrages, and consumptive use for irrigation and domestic supply, have had a profound impact on total discharge and discharge variability in the lower River Murray (Maheshwari *et al.* 1995). The seasonality of flows is retained, with flows peaking in spring/summer, but their magnitude is much reduced (Walker and Thoms 1993; Maheshwari *et al.* 1995). Mean annual discharge to the sea (4915 GL) is now $\sim$36% of the natural mean (12 300 GL). On the basis of modelled natural (i.e. preregulation) and current (i.e. regulated) flow data (MDBA, unpubl. data), median flow has decreased from $\sim$27 000 ML day$^{-1}$ to 8000 ML day$^{-1}$ and the frequency of within-channel pulses has been greatly reduced (e.g. flows of 20 000 ML day$^{-1}$ were equalled or exceeded 62% of the time under preregulation conditions, compared with 26% under current conditions). Large overbank flood flows (e.g. 100 000 ML day$^{-1}$) still occur, but their frequency has also been reduced such that they now occur $<$2% of the time compared to 4% historically (MDBA, unpubl. data).

The present study was conducted in the lower River Murray where a series of 10 low-level ($\sim$3 m) weirs fragment 830 km of river into a series of contiguous weir pools, transforming a historically highly dynamic lotic system into a homogenous series of lentic environments under low flows (Walker 2006). Spawning and recruitment of golden perch were investigated in the River Murray main channel and Chowilla Anabranch system, a complex of anabranches on the northern floodplain of the River Murray that circumvent Lock and Weir No. 6, $\sim$620 km from the river mouth (Fig. 1). As a result of the head differential created by Lock and Weir No. 6, flow diverted through the anabranches creates permanent lotic habitats in a region where such habitats are now rare in the main river channel.

### *Environmental data*

Daily mean flow (ML day$^{-1}$) for the period January 1980 to December 2008 for the River Murray at the South Australian border and daily water temperature (°C) data for the period July 2005 to February 2009 for the River Murray adjacent to the Chowilla system were obtained from the South Australian Department of Environment, Water and Natural Resources (DEWNR) surface water monitoring archive (DEWNR, unpubl. data). Long-term historical flow data for the lower River Murray in its unregulated state are unavailable; therefore, modelled 'natural' daily flow data were obtained from the Murray–Darling Basin Authority (MDBA, unpubl. data). These data are derived from the MSM–Bigmod model that employs a water balance approach and integrates hydrological, climatic and consumptive (e.g. irrigation diversions and losses) data, and storage and water-sharing operating rules (Close 1990). A modelled data series from 1891 to 2008 was utilised.

### *Collection of golden perch*

Golden perch larvae were sampled using drift nets and light traps at eight sites in the Chowilla Anabranch system and adjacent River Murray (Fig. 1). Sites were sampled fortnightly from October to January in 2004–05 and from September to

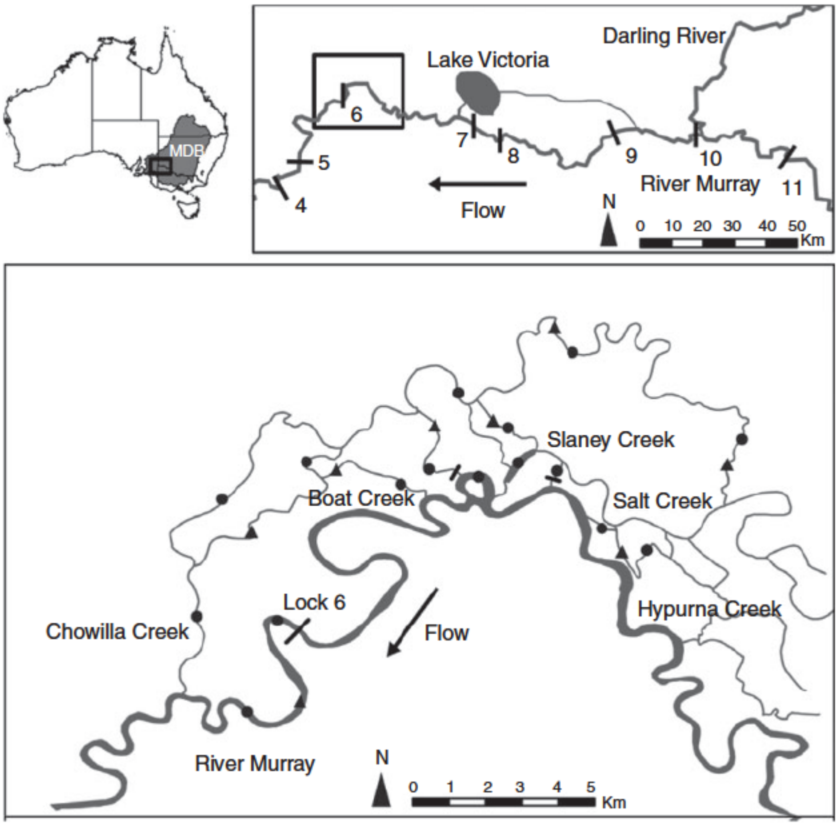

**Fig. 1.** Map of the Murray Darling Basin and lower River Murray, showing the numbered Locks and Weirs, Lake Victoria (an offstream storage used to regulate flows in the lower river) and detail of the Chowilla Anabranch system bypassing Lock and Weir No. 6, showing larval sampling sites (solid triangles) and electrofishing sites (solid circles).

February in 2005 06 and 2006 07. At each site, three drift nets (500 µm mesh, 0.5 m diameter opening, 1.5 m length) and three modified quatrefoil light traps (Floyd *et al.* 1984) were set concurrently. Drift nets were set to actively fish flowing water and light traps were set adjacent to available littoral habitats (e.g. submerged and emergent macrophytes and large wood). A Cyalume$^{TM}$ (Cyalume Technologies, West Springfield, MA, USA) light stick (yellow) was placed in each light trap to attract larvae with a positive phototactic response to light (Gehrke 1994) and mesh (5 mm stretched) was used to cover each light trap to prevent predation by larger fish (Vilizzi *et al.* 2008). Additional light traps were set in Chowilla Creek in December 2005, to collect supplementary golden perch larvae for ageing. These methods have been used to successfully sample Murray Darling fish larvae in several studies (Humphries *et al.* 2002; King *et al.* 2005; Vilizzi *et al.* 2008).

On retrieval, the contents of each drift net or light trap were rinsed into a sample jar and preserved in 95% ethanol. Drift net samples required larval fish to be separated from detritus and debris under a magnification lamp (×2). Samples from light traps did not require sorting. Fish were identified under a dissecting microscope using descriptions from Serafini and Humphries (2004). We have used the term larvae to describe all developmental stages between birth and the point when a fish attains its full complement and position of adult characters (e.g. scales, finrays and spines), after which we defined fish as juveniles (Serafini and Humphries 2004).

Golden perch juveniles and adults were collected in March over three consecutive years (2005 07), using a boat mounted 5 kW Smith Root Model GPP 5.0 electrofishing unit. Boat electrofishing has been shown to be the least selective fish sampling methodology for both species and size of fish in lowland rivers in south eastern Australia (Faragher and Rodgers 1997). Golden perch was collected during standardised quantitative surveys of fish assemblages at 16 sites representing all available meso (e.g. lentic and lotic waters) and micro (e.g. open water, aquatic macrophytes and woody debris) habitats in the Chowilla system and adjacent River Murray (Fig. 1). Supplementary fish were collected during *ad hoc* electrofishing operations in the Chowilla system and adjacent River Murray throughout the study period. All fish were measured to the nearest mm (TL) and a subsample ($n = 31$ 77 fish year$^{-1}$) representing the length frequency of fish collected each year (2005 07) was retained for ageing.

To validate the annual nature and seasonality of otolith increment formation, additional golden perch individuals were collected from a fishway at Lock and Weir No. 6 on the River Murray, adjacent to the Chowilla Anabranch system. Fish were collected monthly from August 2005 to July 2006 ($n = 8$ 15 fish month$^{-1}$).

### Ageing of golden perch

Under a dissecting microscope (×40), golden perch larvae were measured to the nearest millimetre and otoliths were removed. An earlier validation of daily increment formation of known age larvae identified that the sagittae were preferred to lapilli because they were easier to prepare, revealed an easily interpretable microstructure and provided higher and more confident increment counts (B. P. Zampatti and S. J. Leigh, unpubl. data). Furthermore, transverse sections provided better resolution and regularity of microstructural patterns than did other sectioning planes. For preparation of transverse sections, sagittae were embedded in Crystal Bond$^{TM}$ (Aremco Products Inc., Valley Cottage, NY, USA) and ground from both anterior and posterior surfaces to the primordium with 9 μm imperial lapping film and polished using 0.3 μm alumina slurry to produce sections between 50 and 100 μm thick.

Sections were examined using a compound microscope (×600) fitted with a digital camera and the *Optimas* image analysis software (version 6.5, Media Cybernetics, Rockville, MD, USA). A drop of immersion oil was used to enhance the clarity of sections. Increments were counted blind with respect to fish length and capture date. Estimates of age were determined by counting the number of increments from the primordium to the otolith edge. Three successive counts were made by one reader for one otolith from each fish. If these differed by more than 5%, the otolith was rejected, but if not, the mean was used as an estimate of the number of increments.

Increment counts were considered to represent the true age of golden perch larvae and juveniles from analysis of otoliths from known age larvae supplied by Narrandera Fisheries Centre, New South Wales Department of Primary Industries. Egg development and hatching occur within the first 24 h post spawning (Brown and Wooden 2007) and increment counts of known age larvae exceeded the known age at hatch by one increment, which incorporates egg development before hatch. Spawn dates were determined by subtracting the estimated age from the capture date.

Transverse sections of adult golden perch sagittae display a clear incremental pattern of opaque and translucent zones that form annually (Anderson *et al.* 1992; Mallen Cooper and Stuart 2003). Whole sagittae dissected from juvenile and adult fish were embedded in clear casting resin and a single 400 600 μm transverse section, incorporating the primordium, was prepared using a Gemmasta$^{TM}$ diamond cutting saw (Shelleys Lapidary Supplies Pty. Ltd., Mile End, South Australia). Sections of sagittae were examined using a dissecting microscope (×25) under transmitted light. Estimates of age were determined by counting the number of complete or clearly discernable opaque zones from the primordium to the otolith edge. Where the otolith was recorded as having an opaque edge, it was noted whether this marginal increment was included in the estimate of age. Otoliths were interpreted independently by three readers. Discrepancies in otolith age by one or two readers were due in all instances to the inclusion of a marginal increment (opaque zone at the otolith edge) and were adjusted accordingly to reflect the age with reference to the capture date and the estimated birth date. A suitable birth date was assigned by considering the timing of the formation of a new annulus (opaque zone) and the back calculated spawning dates estimated for larval fish.

Prepared transverse sections of sagittae from golden perch collected monthly in 2005 06 at the Lock and Weir No. 6 fishway were used to determine the seasonality (month) of annulus (opaque zone) formation. The margin of each otolith was first categorised as either being opaque or translucent. Second, where the margin was described as translucent, the distance between the last completed increment (opaque zone) and the outer edge of the otolith was further described as being thin or wide. The change in relative frequency of each of these three margin categories (i.e. opaque, translucent and thin, and translucent and wide) in each monthly sample was plotted across a 12 month period (Campana 2001).

## Results

### Hydrology

The maximum known age of golden perch is 26 years (Stuart 2006); hence, a 25 year flow record is considered adequate for an investigation of age structure of golden perch populations in the Chowilla region. Over the past 25 years, discharge in the River Murray at the South Australian border has varied considerably; maximum flows of $>110\,000$ ML day$^{-1}$ were recorded in the summer of 1993 94 and minimum flows of $<1000$ ML day$^{-1}$ were recorded in the winter of 2007 (Fig. 2). The 3 year study investigating the spawning and recruitment of golden perch was conducted during an unprecedented period (since river regulation in the 1930s) of low flow. Maximum daily discharges during the study period were $\sim$8500 ML day$^{-1}$, 15 000 ML day$^{-1}$ and 7000 ML day$^{-1}$ in December 2005, November 2006 and February 2007, respectively.

Modelled 'natural' discharge data demonstrated the profound effect river regulation and water extraction have had on the hydrology of the lower River Murray (Fig. 3). During a period of intensively regulated and low flows from 2000 to 2008, natural flows would have been characterised by several overbank flood events and substantial annual within channel rises in flow (Fig. 3).

### Temporal and spatial variation in occurrence of larvae

No golden perch larvae were collected in the 2004 05 sampling season, 14 golden perch larvae were sampled in 2005 06 (between 29 November and 14 December 2005) and no larvae were collected in 2006 07 (Fig. 4). Golden perch larvae collected in 2005 had a mean length of 11.2 mm (range 8 14 mm) and were collected in both light traps ($n = 13$) and drift nets ($n = 1$) from five creeks in the Chowilla system, namely Boat, Chowilla, Hypurna, Salt and Slaney Creeks.

### Length frequency structure

The size distribution of juvenile and adult golden perch ranged between 50 and 500 mm in TL for samples collected between 2005 and 2007. In 2005, the length frequency was unimodal, with fish ranging in length from 240 to 440 mm (Fig. 5). A bimodal distribution was observed in 2006, with a small mode of fish ranging from 50 to 80 mm and a mode of larger individuals ranging from 240 to 450 mm. In 2007, these modes progressed to 120 300 mm and 340 500 mm, respectively (Fig. 5).

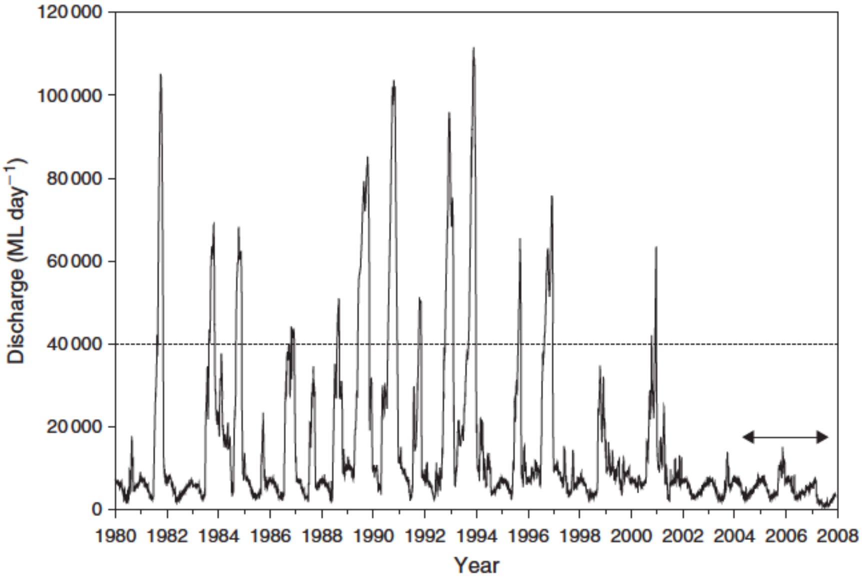

**Fig. 2.** River Murray flow (discharge into South Australia, ML day $^{1}$) from 1980 to 2007. Black arrow represents the study period and dotted line represents the approximate discharge at which overbank flows occur in the Chowilla region.

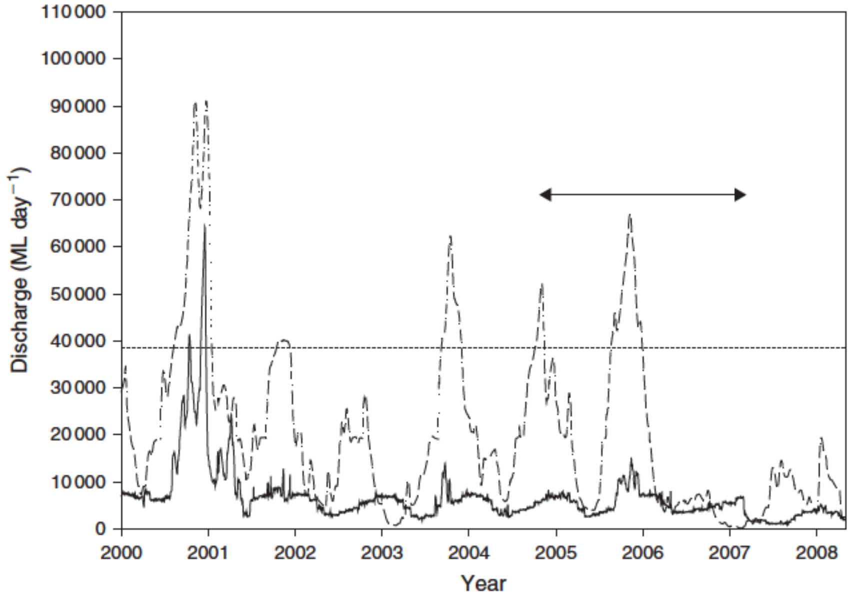

**Fig. 3.** Actual (solid line) and modelled 'natural' (dashed line) River Murray discharge into South Australia from 2000 to 2008. Dotted line represents approximate discharge at which overbank flows occur in the Chowilla region. Black arrow represents the study period. Modelled natural discharge from the Murray Darling Basin Authority (unpubl. data).

### *Age structure*

The mean age of golden perch larvae captured during the 2005 06 sampling season was 27 days (range 22 38 days). Back calculated spawning dates indicated that these fish were spawned in late October/early November 2005. Spawning at this time coincided with a water temperature of ~21 23°C and a small (5000 15 000 ML day$^{-1}$), but prolonged (~3 months) increase in discharge in the River Murray (Fig. 4).

The ages of three juvenile fish (0+) collected on the 25 January, 26 January and 4 March 2006, were 52, 78 and 147 days, respectively. With the exception of the 52 day old fish (spawned early in December), this corresponds to the

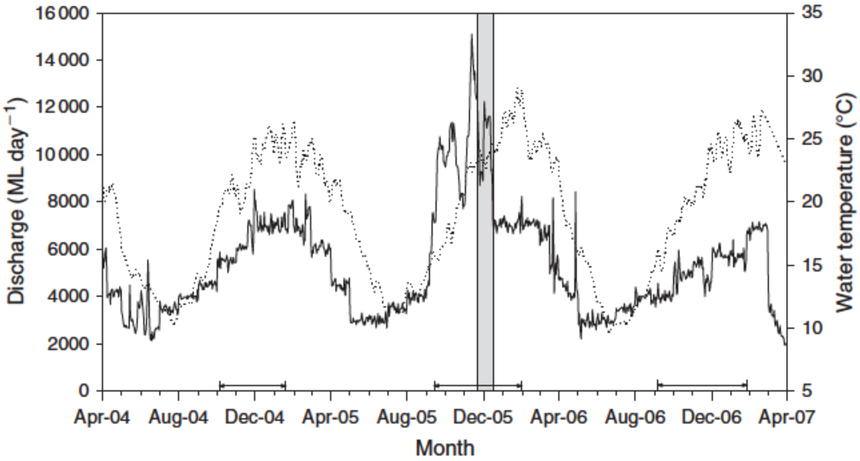

**Fig. 4.** Presence of golden perch larvae (grey bar) plotted against River Murray discharge (ML day $^{1}$) (solid line) and water temperature (°C) (dotted line) over the period from April 2004 to April 2007. Black arrows indicate the period over which fortnightly larval sampling was conducted in each year.

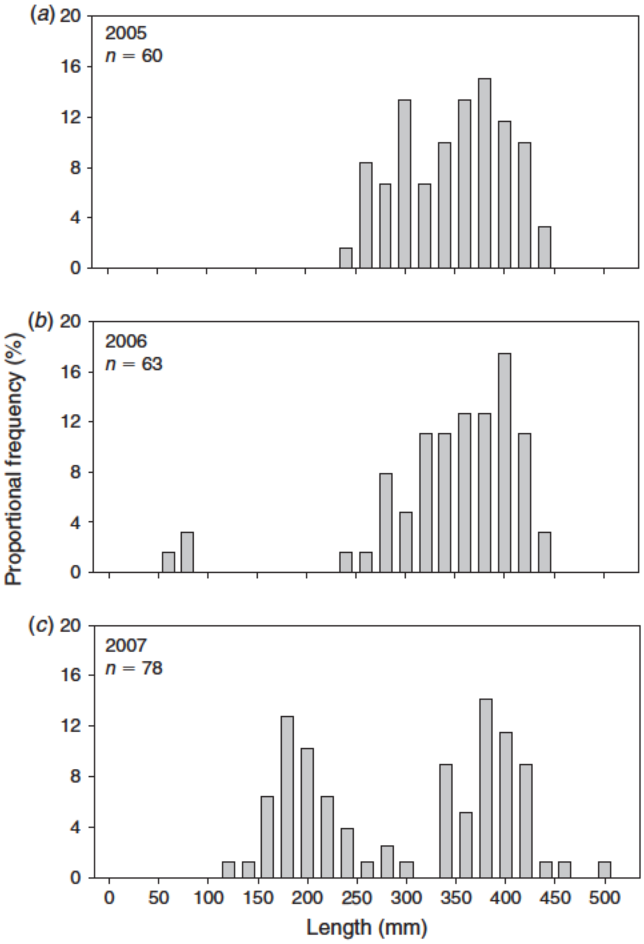

**Fig. 5.** Length frequency distribution of golden perch captured from the Chowilla region (including River Murray) in March/April (*a*) 2005, (*b*) 2006 and (*c*) 2007.

estimated spawning period (late October/early November) for all larvae collected in 2005 (Fig. 6).

The formation of a new opaque zone at the margins of adult golden perch otoliths collected between August 2005 and July 2006 displayed an annual sinusoidal cycle when plotted against season. Opaque zones were evident in samples from October December 2005, indicating spring and early summer formation (Fig. 7). During November and December 2005, ≥50% of otolith margins were classified as translucent and thin, indicating that the opaque zone had been recently completed. By February 2006, all opaque zones had been completely deposited. From August to September 2005 and February to July 2006, all otoliths were classified as having translucent margins. After considering the timing of the formation of a new annulus (opaque zone) and the back calculated spawning dates of post larval fish, we assigned a theoretical birth date for golden perch of 1 November.

The age frequency data for fish collected in 2005 showed three strong age classes, namely, 4, 6 and 8 year olds (Fig. 8). A clear annual progression is evident in the age structure from 2005 to 2007 where strong age classes remain dominant. The proportion that the 6 and 8 year old cohorts in 2005 contributed to the age structure declined substantially over the sampling period, whereas the 4 year olds remained relatively stable. In 2007, a new strong age class is present as 1 year olds, suggesting successful recruitment (to Age 1+) of fish spawned in 2005. Backdated birth years of fish sampled in 2005 07 showed that the three dominant year classes were spawned in association with increased discharge in years 2000, 1998 and 1996 (Fig. 9*a c*). The additional strong age class of 1 year old fish collected in 2007 was spawned in association with increased flow in spring/summer 2005 06 (Fig. 9*c*).

## Discussion

Understanding the recruitment ecology of freshwater biota, including fish, is imperative to the restoration of ecologically important features of the natural flow regime (Bunn and

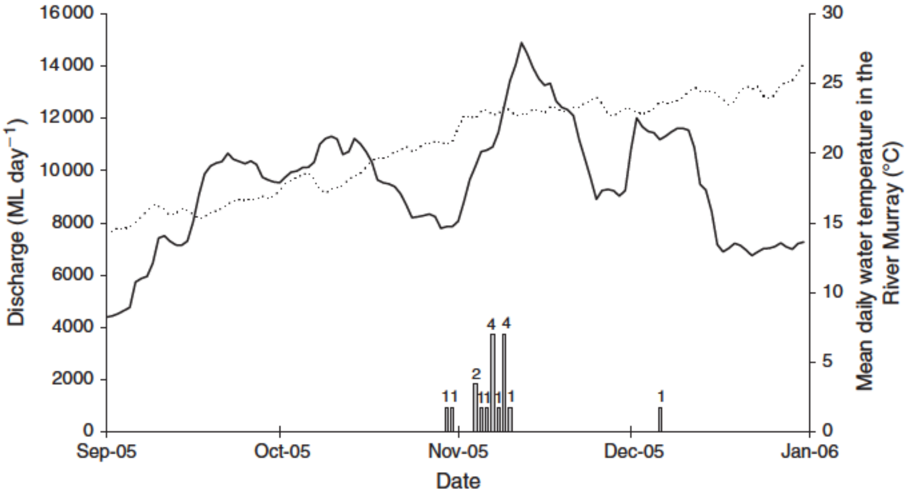

**Fig. 6.** Back-calculated spawning dates for larval and young-of-year golden perch golden perch (*n* = 17) captured in the Chowilla region during the 2005–06 sampling season, plotted against discharge (ML day$^{-1}$) (solid line) and water temperature (°C) (dotted line) in the River Murray. Numbers above bars indicate number of fish back calculated as spawning on that day.

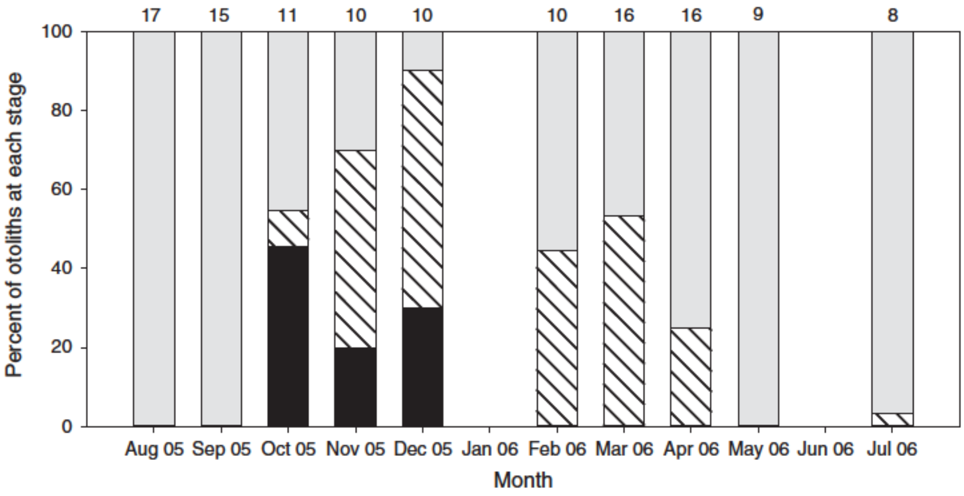

**Fig. 7.** Proportion of golden perch otoliths in each of the following three otolith-margin categories: (1) translucent and wide (grey), (2) translucent and thin (hatched) and 3) opaque (black). Otoliths were collected monthly from August 2005 to July 2006 from golden perch migrating through a fishway at Lock 6 on the River Murray. No samples were collected in January and June 2006. Numbers above bars indicate the sample size.

Arthington 2002). In the present study, we incorporated early life history data with population age structure data, to elucidate patterns in recruitment in relation to river flow. Golden perch larvae were collected only during a small but prolonged within channel rise in discharge in spring/summer 2005, and not in years characterised by low stable discharge (2004 and 2006). Young of year (YOY) fish were subsequently collected in 2006 but not in 2005 or 2007. The back calculated spawning dates of the YOY fish collected in 2006 corresponded with the spawning period determined for golden perch larvae collected in late November and December 2005. As such, these YOY fish had recruited from the Spring 2005 spawning event.

In the current study, it was not possible to determine whether the golden perch larvae and YOY collected from the Chowilla system and adjacent River Murray were spawned in the region. Nevertheless, the age of fish at collection and the habitats they were collected in (i.e. large woody debris in the littoral zone) indicated that the Chowilla region provides a nursery area for juvenile golden perch, as suggested by Lloyd (1990) and Pierce (1990). This was further supported by the Age 1+ fish that were subsequently collected in the region in 2007. YOY and 1+ fish were collected both in Chowilla Creek and the main stem of the River Murray, thus demonstrating that river channels provide suitable rearing habitats for juvenile golden perch that are

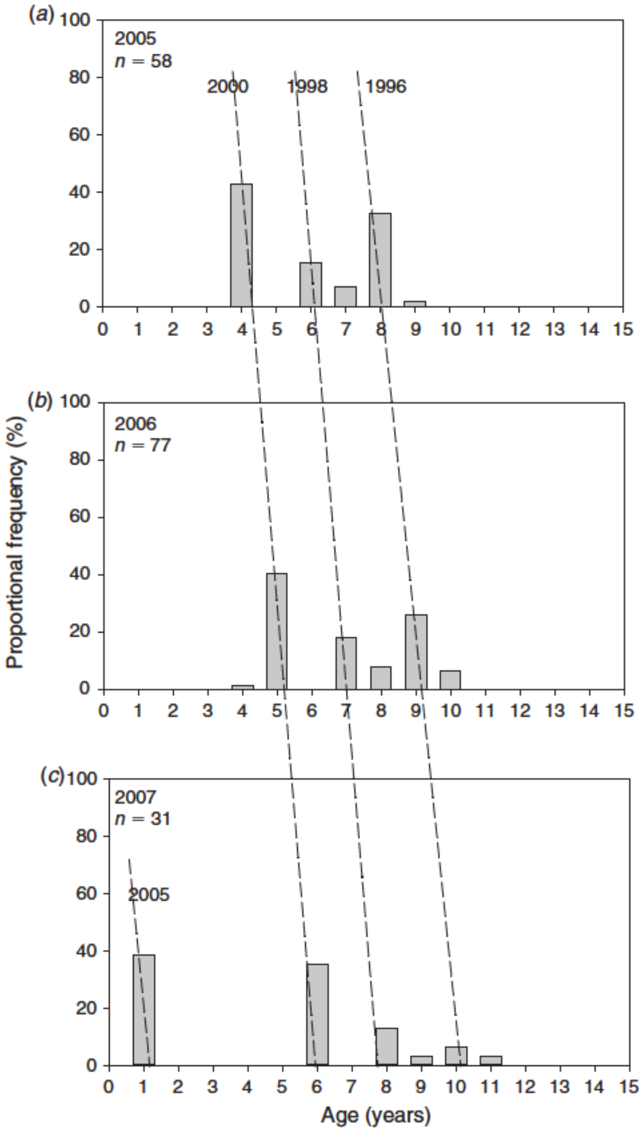

**Fig. 8.** Age frequency distributions of golden perch captured in the Chowilla region (including River Murray) in March/April of (*a*) 2005, (*b*) 2006 and (*c*) 2007. Dashed lines track progression of dominant year classes. Numbers in dashed lines represent year of birth.

spawned during within channel flows (Mallen Cooper and Stuart 2003).

Determining the natal origin of golden perch would enable investigation of the specific environmental factors that influence spawning. A promising method that could facilitate the retrospective determination of source environments of golden perch is the elemental or isotopic analysis of otoliths by using laser ablation inductively coupled plasma mass spectrometry (LA ICPMS) (Elsdon *et al.* 2008; Macdonald *et al.* 2008). Isotopic ratios in particular (e.g. strontium) can provide a precise geochemical signature that is not physiologically regulated (Hobbs *et al.* 2005) and we suggest that such an approach could be used to better understand the provenance of golden perch in the lower River Murray.

Back calculation of spawning dates of larval and YOY golden perch using daily growth increments in otolith microstructure revealed that spawning occurred in late October/early November 2005. Most fish were spawned on the ascending limb of the second flow peak of the September to December flow event. A few fish, however, were spawned during a small decrease in discharge between two flow peaks. Water temperatures during this period ranged from 21°C to 23°C. These discharge and water temperature conditions are consistent with those proposed for golden perch spawning by Lake (1967) and field observations made by J. O. Langtry in the River Murray in 1949 50, where golden perch spawned on predominantly rising but also falling river levels (Cadwallader 1977). Furthermore, spawning in the lower River Murray in late October/early November 2005 coincided with an early November 2005 spawning event ~1100 km upstream that also occurred on the second peak of a flow event and at similar water temperatures (King *et al.* 2009). These data support the notion that golden perch in the River Murray is indeed a flow cued spawner. Spawning occurred both during a rise and fall in the hydrograph; hence, some variation in the magnitude of flows rather than a sustained increase in flow may be important when recommending flow regimes that stimulate the spawning of golden perch. Using our data and that of King *et al.* (2009), the delivery in late spring/summer of at least two sequential but not necessarily equivalent peaks of ≥15 000 ML $\text{day}^{-1}$ would constitute an appropriate trial environmental flow.

A temperature threshold may also interact with flow and this may be integral in elucidating positive responses from environmental flow regimes that target fish spawning and recruitment (King *et al.* 1998; Roberts *et al.* 2008). For example, a trial flow release to stimulate Clanwilliam yellowfish (*Barbus capensis*) spawning in the Oliphants River, South Africa, failed because of the release of cold hypolimnetic water, even though the size, duration and timing of the release was the same as those previously linked to successful spawning (Cambray *et al.* 1997; King *et al.* 1998). The importance of the combination of water temperature and increased flow has also been shown for golden perch (*Macquaria ambigua oriens*) in the Fitzroy Basin, Australia, where recruitment is strongest when flow events coincide with water temperatures >23°C (Roberts *et al.* 2008). The gonads of golden perch (*Macquaria ambugua ambigua*) in the MDB develop regardless of environmental conditions and female gonadosomatic index (GSI) is maximised from November to January (Mackay, 1973) when water temperatures in the lower River Murray generally range between 20°C and 27°C. In line with this, and the results from the current study, the temperature threshold for golden perch spawning in the lower River Murray appears to be ~20°C.

Length frequency data collected from 2005 to 2007 provided some indication of recruitment but offered little accurate information on the actual age structure of the population. Precise age determination is essential to accurately investigate the relationship between recruitment success and environmental variables (Campana 2001). Thin sectioned otoliths provide a reliable means of determining the age of golden perch (Anderson *et al.* 1992). We used thin sectioned otoliths to validate that golden

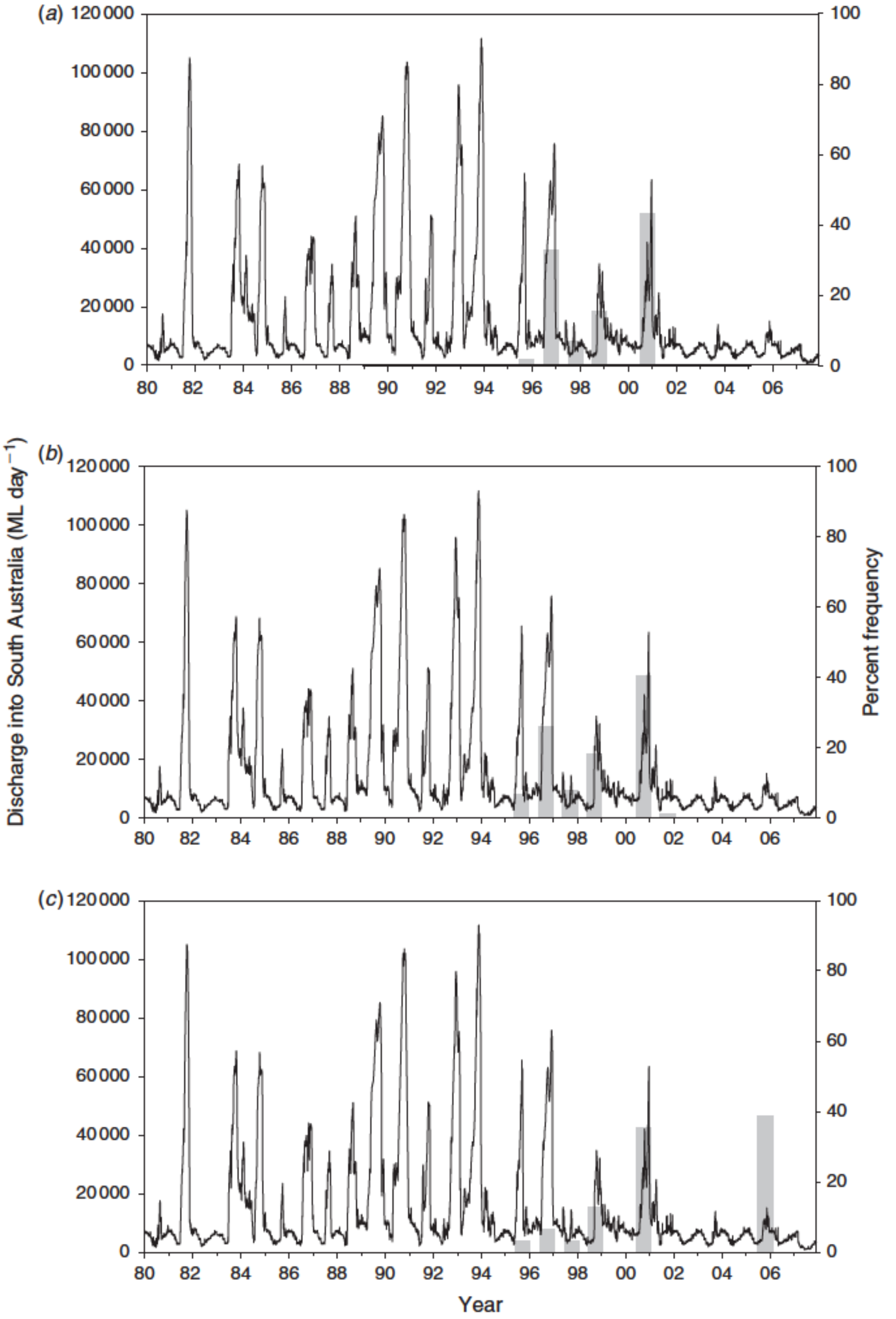

**Fig. 9.** Mean daily River Murray discharge (ML day $^{1}$) (solid line) and back-calculated birth years of golden perch (grey bars) shown as the percentage frequency each cohort contributed to the age structure in (*a*) 2005, (*b*) 2006 and (*c*) 2007.

perch in the lower River Murray forms an annual band in the otolith from October to December (data were unavailable for January). This technique, however, does not enable the determination of an actual birth date. Consequently, age estimates using daily increments in otolith microstructure of larval and/or YOY fish are required to be temporally accurate in relating environmental parameters to spawning.

In 2005, the golden perch population in Chowilla and the adjacent River Murray was dominated by three strong year classes (i.e. 4 , 6 and 8 year olds) spawned in 2000, 1998 and 1996, respectively. In each of these years, substantial within channel or overbank discharge occurred during the spawning period for golden perch (October January). The dominant year classes observed in 2005 progressed to 5 , 7 and 9 year olds in

2006, with no addition of further year classes. In 2007, an additional strong year class of 1 year old fish appeared, following successful spawning and recruitment of golden perch during a small but prolonged within channel increase in discharge in spring/summer 2005.

Age structure data also indicated that the number of older fish in the Chowilla region decreased over time. Golden perch is known to live up to 26 years (Stuart 2006); nevertheless, no fish older than 11 years was collected in the Chowilla region or adjacent River Murray during our study. The fate of these older fish is unknown but potential causes of the truncation of the age structure may include fishing pressure or emigration of older fish from the region (B. P. Zampatti and S. J. Leigh unpubl. data). Importantly, however, from a conservation perspective, selective removal or emigration of large, old individuals may ultimately contribute to serious population depletion for species with variable recruitment (Longhurst 2002).

Overall, our data supported the proposition of Mallen Cooper and Stuart (2003) that golden perch recruitment in the MDB is not reliant on flood flows (i.e. overbank) and that even relatively small within channel flow events may support significant recruitment. Nevertheless, golden perch recruitment in the lower River Murray appears to be absent or minimal during periods of stable low flow and regulated 'entitlement' flows (i.e. flow delivered for consumptive use). This is in contrast to golden perch in the more arid northern regions of the MDB, and the adjacent Lake Eyre Basin, where, on the basis of length frequency data, recruitment is proposed to occur during periods of zero flow and irrespective of antecedent flow conditions and season (Balcombe *et al.* 2006; Kerezsy *et al.* 2011). Consequently, there appears to be considerable variation in the life histories of golden perch throughout the species geographic range. Such regional variation in life histories is well acknowledged for northern hemisphere salmonids (e.g. Beechie *et al.* 2006; Malcolm *et al.* 2012) and is becoming increasingly recognised for golden perch (Balcombe *et al.* 2006; Roberts *et al.* 2008; Ebner *et al.* 2009; Kerezsy *et al.* 2011). Accordingly, regional differences in life histories should form an important consideration when determining management and conservation actions for golden perch, including the maintenance or restoration of components of the natural flow regime.

There still exists considerable conjecture on the role of overbank flows in golden perch recruitment (Mallen Cooper and Stuart 2003; King *et al.* 2009; Ebner *et al.* 2009). Although it appears that there is consensus that spawning and recruitment may occur during within channel and overbank flows, some authors have suggested that spawning intensity and recruitment may be strongest during overbank floods (King *et al.* 2009). Our data concurred with that of Roberts *et al.* (2008) for *Macquaria ambigua oriens* in the Fitzroy Basin indicating that dominant year classes may be associated with high flows (overbank) and within channel rises in flow. Nevertheless, to test the premise that spawning intensity increases during overbank floods, data on golden perch spawning during a major overbank flow in the MDB (e.g. $>90\,000$ ML day$^{-1}$ in the lower River Murray) are required.

There were two successful recruitment events for golden perch in the lower River Murray region in the period 2000 07, namely 2000 and 2005. In these years, spawning and recruitment corresponded with maximum discharges of ~60 000 and 15 000 ML day$^{-1}$, respectively. Recruitment appears negligible in all other years when flows were relatively low and stable. There was one flow event in 2003 of ~15 000 ML day$^{-1}$ that was not accompanied by significant recruitment; however, this was of a relatively short duration and occurred in late winter/early spring when water temperatures would have been <20°C.

Although overbank flooding may be important, particularly from a perspective of primary productivity (Junk *et al.* 1989), the fact that within channel flows can support strong golden perch recruitment has important implications for flow management in the lower River Murray. Medium sized flow events are the component of the flow regime that has been most significantly altered by river regulation in the lower Murray River (Walker 2006). Furthermore, it is these size events (e.g. 15 25 000 ML day$^{-1}$) that could practically be restored within the current constraints of system operation. Our results indicate that restoration of these within channel flow events may lead to more frequent golden perch recruitment.

Discharge data for the River Murray at the South Australian border indicated that since 2000, flows of a magnitude potentially suitable for golden perch spawning and recruitment (i.e. $>14\,000$ ML day$^{-1}$) occurred in 2 years out of the past 8 years (Fig. 3). In comparison, modelled 'natural' flow data indicated that, under unregulated conditions, flows of such magnitude would have occurred in 7 of the past 8 years. Golden perch is long lived (>20 years) and hence adapted to coping with a highly variable environment that may lead to variable recruitment. Nevertheless, golden perch (*Macquaria ambigua oriens*) recruitment in coastal rivers in eastern Australia is more variable (i.e. low numbers of dominant year classes) in rivers with higher levels of regulation than it is in less regulated rivers (Roberts *et al.* 2008). This is also evident in the lower River Murray where episodic recruitment results in only a few strong year classes dominating the population. Modelled flow data, however, indicated that discharges of the magnitude potentially conducive to spawning and recruitment may have been more frequent in the unregulated River Murray and hence may have resulted in more consistent recruitment and a golden perch population more resilient to environmental perturbations.

## Conclusions and management recommendations

Conceptual models of ecological response to flow alteration are useful tools to inform the delivery of environmental flows, but increasingly, water and natural resource managers require quantitative data to justify decisions regarding the allocation of finite water resources. The findings of the present study provide an empirical, testable basis for the formulation of flow ecology relationships that are necessary to underpin contemporary approaches to developing and testing environmental flow regimes (e.g. Poff *et al.* 2010) that will ultimately assist in the re establishment of native fish populations in the MDB. Although such approaches are often proposed, examples are generally rare (although see Cambray *et al.* 1997; King *et al.* 2010; Bradford *et. al.* 2011).

Our data and recent studies in the mid reaches of the River Murray (e.g. King *et al.* 2009) provide sufficient evidence for a trial flow manipulation in the lower River Murray to promote spawning and recruitment of golden perch. The acquisition by the Australian

Government Commonwealth Environmental Water Holder of >800 GL of environmental water in the southern MDB (CEWO 2012) provides an opportunity to increase the frequency of within channel flows in the lower River Murray. We suggest that flows of ≥15 000 ML $\text{day}^{-1}$ may promote spawning and recruitment of golden perch and confer resilience to regional populations. Water temperature at the time of flow augmentation needs to be considered, with flows being delivered in late spring through summer when water temperatures have reached at least 20°C. Such an approach could utilise active adaptive management principles (Souchon *et al.* 2008; King *et al.* 2010) which would incorporate a hypothesis driven, rigorously designed monitoring program to assess the effectiveness of delivering environmental flows for golden perch and inform future management (Murchie *et al.* 2008; Poff and Zimmerman 2010).

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# CHAPTER 3: Effects of flooding on recruitment and abundance of golden perch in the lower River Murray.

Juvenile golden perch post flooding in the lower River Murray

# Statement of Authorship

| | |
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| Title of Paper | Effects of flooding on recruitment and abundance of Golden Perch (*Macquaria ambigua ambigua*) in the lower River Murray |
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| Name of Principal Author (Candidate) | Brenton Zampatti | | |
| Contribution to the Paper | Designed study, collected and interpreted data, wrote manuscript and acted as lead and corresponding author | | |
| Overall percentage (%) | 80% | | |
| Certification: | This paper reports on original research I conducted during the period of my Higher Degree by Research candidature and is not subject to any obligations or contractual agreements with a third party that would constrain its inclusion in this thesis. I am the primary author of this paper. | | |
| Signature | | Date | 12/7/2019 |

## Co-Author Contributions

By signing the Statement of Authorship, each author certifies that:

i. the candidate's stated contribution to the publication is accurate (as detailed above);

ii. permission is granted for the candidate in include the publication in the thesis; and

iii. the sum of all co-author contributions is equal to 100% less the candidate's stated contribution.

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RESEARCH REPORT

# Effects of flooding on recruitment and abundance of Golden Perch (*Macquaria ambigua ambigua*) in the lower River Murray

### By Brenton Zampatti and Sandra Leigh

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**Summary** Flooding is often considered a stimulus for production of fish in floodplain rivers. In the southern Murray Darling Basin (MDB), Australia, however, few native fish species have been shown to use the floodplain for spawning, and recruitment has been positively and negatively associated with flooding. In 2010/11, extensive flooding in the lower River Murray provided an opportunity to investigate the recruitment response of Golden Perch (*Macquaria ambigua ambigua*) following 10 years of drought and floodplain isolation. Annual variation in Golden Perch abundance and recruitment were investigated in anabranch and main channel habitats at Chowilla in the floodplain geomorphic region of the lower River Murray over a 7 year period incorporating the flood and 6 years of in channel flow. Spatial variation in recruitment in the lower River Murray was also investigated by comparing the age structure of Golden Perch in the swamplands/lakes, gorge and floodplain geomorphic regions. Golden Perch abundance in the Chowilla region increased significantly postflooding compared with drought years. Age structures indicated that increased abundance was due predominantly to fish spawned during the flood (2010/11) and the previous year (2009/10), which was characterised by in channel flows. Age structure was similar in the nearby Katarapko Anabranch system indicating a uniform postflood recruitment response in the floodplain geomorphic region. Juvenile Golden Perch from the 2010/11 and 2009/10 cohorts were less apparent in the gorge and swamplands/lakes regions. Golden Perch have flexible life histories and will spawn and recruit in association with in channel rises in flow and overbank flows, but significant increases in abundance in the lower River Murray may result from overbank flooding. Contemporary approaches to flow restoration in the MDB emphasise overbank flows and floodplain processes. We suggest, however, that environmental flow management that incorporates floodplain and in channel processes, at appropriate spatiotemporal scales, will result in more robust populations of Golden Perch.

**Key words:** *floodplain, Murray Darling Basin, environmental flow, overbank, in channel.*

## Introduction

Throughout the world, the ecological integrity of floodplain rivers is threatened by river regulation and alteration of natural flow regimes (Bunn & Arthington 2002; Tockner & Stanford 2002). River regulation typically disrupts the natural disturbance regimes that maintain habitat heterogeneity in floodplain rivers (Ward *et al.* 1999; Poff *et al.* 2007) and alters connectivity, isolating main channel and floodplain habitats and reducing floodplain productivity (Sparks 1995; Jenkins & Boulton 2007). To redress the ecological impacts of river regulation, restoration of key components and variability of the natural hydrologic cycle is considered critical (Poff *et al.* 1997). However, to inform the restoration of ecologically important aspects of the hydrograph, it is first necessary to understand biotic responses to the various components of the flow regime (Walker *et al.* 1995; Arthington *et al.* 2006).

In the Murray Darling Basin (MDB), Australia, river regulation and water extraction have substantially altered the frequency and magnitude of flow events, decreasing floodplain inundation and disrupting river channel floodplain connectivity (Walker & Thoms 1993; Maheshwari *et al.* 1995). This hydrologic alteration is considered to have contributed to declines in native fish populations (Cadwallader 1978; Gehrke *et al.* 1995; Barrett 2004). Nevertheless, despite the perceived ecological importance of flooding, the role of floodplain inundation in the ecology of freshwater fish in the MDB remains unresolved (Humphries *et al.* 1999; Graham & Harris 2005).

In rivers of tropical and some temperate regions, predictable annual floodplain inundation is considered a primary driver of fish spawning and recruitment (Junk *et al.* 1989). In rivers in arid and semi arid regions, however, highly variable flow regimes may result in less predictable floodplain inundation and the evolution of biota with more plastic life histories (Humphries *et al.* 1999; Roberts *et al.* 2008). In the southern MDB, and specifically in the mid upper reaches of the River Murray, it appears that very few native fish species use the floodplain proper for spawning and recruitment (Humphries *et al.* 1999; King *et al.* 2003).

Golden Perch (*Macquaria ambigua ambigua*) is one of only two native fish species in the MDB, along with silver perch (*Bidyanus bidyanus*), that is considered to require increased discharge to initiate spawning (Humphries *et al.* 1999). Golden Perch is a large bodied (up to 76 cm total length) potamodromous fish that is widespread in the MDB, but has undergone a reduction in range and abundance in some regions due to altered natural flow regimes, cold water pollution and barriers to movement (Cadwallader 1978; Mallen Cooper 1996). Due to its recreational and commercial importance, Golden Perch is one of the most studied freshwater fish in the MDB. Investigations have included reproductive biology and early life history (Mackay 1973; Gehrke 1991), spawning and recruitment (Lake 1967; Mallen Cooper & Stuart 2003; Ebner *et al.* 2009) and movement (Reynolds 1983; Crook 2004; O'Connor *et al.* 2005).

Early studies suggested Golden Perch spawned in association with floodplain inundation (Lake 1967), which was considered to improve survival of larval fish by stimulating the production of zooplankton (Harris & Gehrke 1993; Schiller & Harris 2001). Recent research, however, indicates that spawning and recruitment may also occur in association with increases in flow contained within the river channel (Mallen Cooper & Stuart 2003; King *et al.* 2005; Zampatti & Leigh 2013). Nonetheless, investigation of Golden Perch recruitment in association with overbank flows and floodplain inundation has been confined to the mid reaches of the River Murray during relatively minor flooding (i.e. 25 000 35 000 ML/day) (King *et al.* 2009).

The mid reaches of the River Murray are hydrologically and hydraulically distinct from the lower river (Maheshwari *et al.* 1995; Walker 2006). Furthermore, whilst much of the mid River Murray has a broad (10 20 km) floodplain, the lower Murray is characterised by distinct floodplain and gorge geomorphic regions (Walker 2006). A series of 10 weirs also fragments and disrupts the natural hydrology and hydrodynamics of the lower River Murray, particularly under low medium flows (i.e. <50 000 ML/day). River regulation and fragmentation can have profound effects on pelagic spawning, potamodromous fish, such as Golden Perch, by interrupting upstream and downstream movements of all life stages and compromising larval survival (Dudley & Platania 2007). If flooding and floodplains are important for Golden Perch recruitment, inter and intra regional variation in geomorphology and connectivity may have consequences for the movement and recruitment of Golden Perch leading to regional variation in population dynamics.

In 2010/11, high flows (>90 000 ML/day) and extensive flooding in the lower River Murray provided an opportunity to investigate the recruitment of Golden Perch following 10 years of drought, low flows (<15 000 ML/day) and floodplain isolation. The objective of this study was to investigate the recruitment and abundance of Golden Perch in response to an overbank flow in the lower River Murray. We expected that increased discharge and floodplain inundation would promote Golden Perch recruitment (to at least age 0+) and augment Golden Perch abundance in the lower River Murray. We also sought to explore variation in recruitment between the distinct geomorphic regions of the lower River Murray.

## Study Area

This study was conducted in the lower River Murray, downstream of the South Australian border (Fig. 1). In this region, a series of 10 low level (~3 m) weirs regulate flow released by upstream dams and diverted by irrigation and fragment 830 km of river into a series of contiguous weir pools. Unlike the regulated but free flowing mid reaches of the River Murray, the weirs in the lower River Murray transform a historically highly dynamic lotic system into a homogenous series of lentic environments under low flows (Walker 2006).

To investigate the association between flooding and Golden Perch population structure, we surveyed a total of 128 sites in the River Murray main channel, the Chowilla and Katarapko Anabranch systems and the littoral zones of Lake Alexandrina (Fig. 1). Sites were sampled in three distinct geomorphic regions (Walker & Thoms 1993): (i) swamplands and lakes (downstream of Mannum), (ii) gorge (Mannum Lock 3) and (iii) floodplain (Lock 3 Lock 6) (Fig. 1).

## Materials and Methods

To investigate abundance and recruitment (to at least age 0+) of Golden Perch in association with the 2010/11 overbank flow, we examined annual variation in the catch per unit effort (CPUE) and length/age structure of Golden Perch collected in the Chowilla Anabranch system and adjacent River Murray using a 7 year dataset. Golden Perch were sampled in March/April 2005 2010 and May/June 2011 (following recession of floodwaters) during quantitative electrofishing surveys of fish assemblages at 16 22 sites representing all available meso (e.g. lentic and lotic waters) and microhabitats (e.g. open water, aquatic macrophytes and woody debris) in the region (Fig. 1). At each site, 12 × 90 s (power on time) electrofishing shots were conducted by boat electrofishing using a 5 kW Smith Root Model GPP 5.0 electrofishing unit. All fish were measured to the nearest mm (total length, TL), and a subsample (*n* = 31 78 fish/year), proportionally representing the length frequency of Golden Perch collected from each year, was retained for ageing. In April 2011, we used the same electrofishing technique to sample 18 sites in the Katarapko Anabranch system and three sites in the adjacent River Murray (Fig. 1) to compare recruitment of Golden Perch between the two main anabranch systems in the floodplain geomorphic region of the lower River Murray in South Australia.

To investigate whether age structure and hence recruitment of Golden Perch postflood varied spatially along the length of the lower River Murray (i.e. between the three geomorphic zones), we sampled 88 sites in the River Murray main channel in November/December 2011. This comprised 24, 41 and 23 sites in the swamplands and lakes, gorge and floodplain geomorphic regions, respectively (Fig. 1). Sampling was conducted by boat electrofishing using a 7.5 kW Smith Root Model GPP 7.5 electrofishing unit. Electrofishing was conducted during daylight hours, and all available littoral habitats were fished. All fish were measured to the nearest mm (total length, TL), and a subsample (*n* = 31 119 fish), proportionally repre

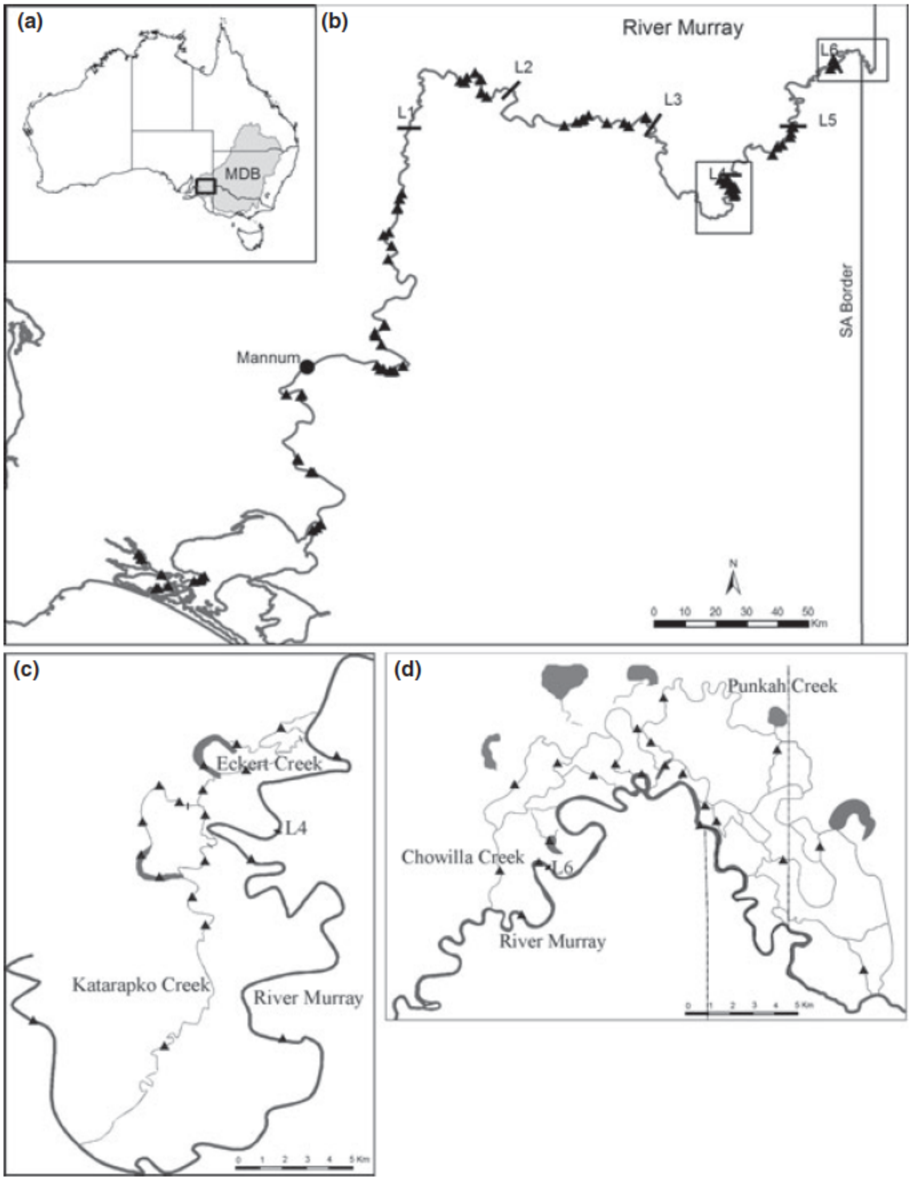

**Figure 1.** (a) Map of the Murray–Darling Basin and (b) lower River Murray showing the numbered locks and weirs up to the South Australian border, geomorphic regions defined as floodplain (L6–L3), gorge (L3–Mannum) and swamplands and lakes (downstream of Mannum) and detail of the (c) Katarapko and (d) Chowilla Anabranch systems bypassing lock and weir No. 4 and 6, respectively. The confluence of the Darling River is 212 km upstream from lock 6. Solid triangles represent electrofishing sites sampled in April–June or November/December 2011.

senting the length frequency of Golden Perch collected from each geomorphic region, was retained for ageing.

Golden Perch exhibit considerable variation in length at age in the MDB (Anderson *et al.* 1992). Therefore, to accurately assess the age structure of Golden Perch, we investigated both length and age frequency distributions. Fish retained for ageing were euthanized using AQUI-S® (Aqui-S, Lower Hutt, New Zealand), and sagittal otoliths were removed. Whole sagittae were embedded in clear casting resin, and a single 400–600 μm transverse section was prepared. Sections of sagittae 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. Young of year (YOY, <1 year old) fish were defined as individuals lacking clearly discernible annuli. These methods have been used to accurately age Golden Perch in the River Murray in a number of studies (Anderson *et al.* 1992; Mallen-Cooper & Stuart 2003; Zampatti & Leigh 2013).

## Results

### Hydrology

From 2001–2010, the MDB experienced its most severe drought on record (Potter *et al.* 2010) resulting in a prolonged period of highly regulated, low volume (<15 000 ML/day) in channel flows in the lower River Murray (Fig. 2a). The drought was broken in late 2010 by the largest overbank flow since 1993, peaking at 93 000 ML/day in February 2011 (Fig. 2a). During the period of highest flow in January–February 2011, approximately 80% of flow in the lower River Murray was derived from the River Murray catchment upstream of the Darling confluence and 20% from the Darling River (Fig. 2b).

### Abundance and recruitment

Over the 7 year period (2005–2011), 1440 Golden Perch were collected from anabranch and main river channel habitats in the Chowilla region with 56% ($n = 802$) of these fish collected postflooding in May 2011 (Fig. 3). There was a significant difference in the CPUE of Golden Perch between years (2005–2011) (univariate single factor PERMANOVA, Pseudo $F = 13.88$, df $= 6126$, $P = 0.001$) with abundance in 2011, 5–6 times greater than in all preceding years (Fig. 3). Pairwise comparisons indicated that the abundance of Golden Perch in 2011 was significantly greater than all other years ($P < 0.001$ for all comparisons; Bonferroni corrected $\alpha = 0.002$), but there was no significant difference in abundance between sampling years from 2005 to 2010.

From 2005 to 2009, the age structure of Golden Perch collected in the Chowilla region was dominated by fish spawned in 2005, 2000, 1998 and 1996 (Fig. 4a). The cohort of fish spawned in 2005

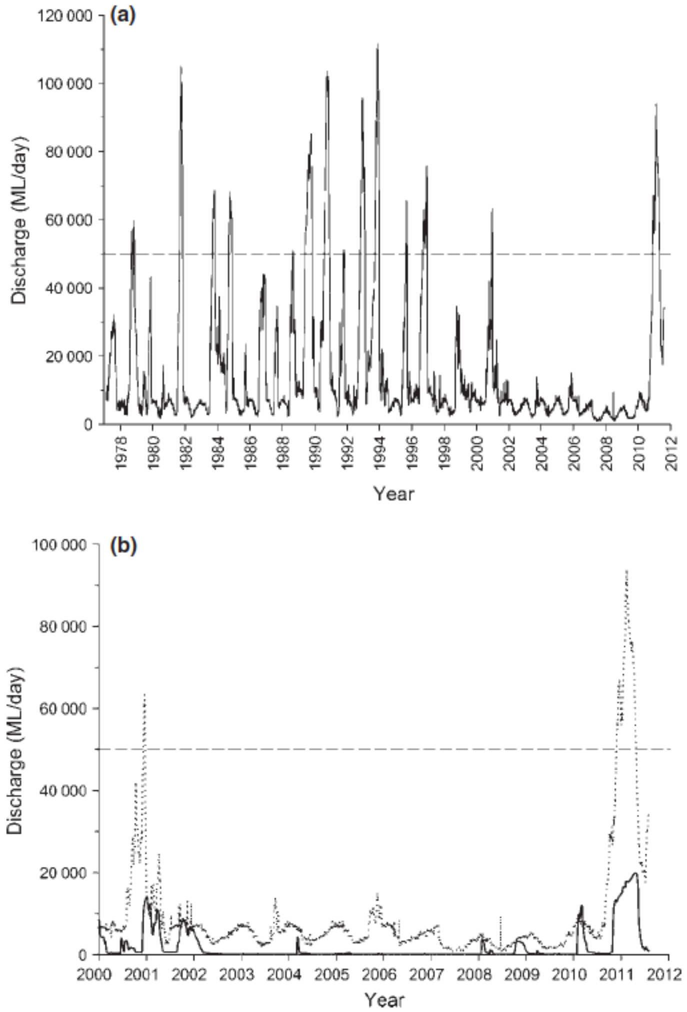

**Figure 2.** (a) River Murray flow (ML/day) at the South Australian border from 1977 to 2011 and (b) River Murray flow (ML/day) at the South Australian border (dotted line) and Darling River flow (ML/day) at Burtundy (solid line) from 2000 to 2011. Burtundy is the lowest gauging station on the Darling River. Dashed line represents approximate bank-full flow in the lower River Murray.

was apparent as fish <100 mm TL in 2006, but became relatively indiscernible in the length frequency data by 2009. The cohorts spawned in 2000, 1998 and 1996 decreased in abundance over time, but the 2005 spawned cohort remained strong, representing ~70% of the sampled population in 2009 and 2010. In 2010, a new cohort of 0+ fish appeared represented by fish $\leq$ 100 mm TL (Fig. 4a).

In 2011, three distinct but broad size classes of Golden Perch were collected at sites in the Chowilla region (Fig. 4a). The modes of these size classes were 110 mm, 200 210 mm and 410 mm with approximately 90% of the Golden Perch collected being represented by the two smaller size classes. The age frequency of Golden Perch was dominated (83%) by age 0+ and 1+ fish, with 0+ (spawned in 2010/11) and 1+ (spawned in 2009/10) Golden Perch comprising 29% and 54% of the age structure, respectively (Fig. 4a). Only low proportions of 3 older cohorts of fish (5, 10 and 12 year olds) were collected. Similar patterns in length and age structure were evident in the Katarapko region, although the age 0+ cohort comprised 50% of the age structure and the 1+ cohort 33% (Fig. 4b).

In November/December 2011, length frequency distributions of Golden Perch differed significantly between the floodplain and gorge regions of the lower River Murray (Kolmogorov Smirnov, large sample, two tailed test, $D_{265,463}$ 0.119, *P* 0.015) (Fig. 5), but differences between the swampland/lakes region and gorge and floodplain regions could not be analysed due to a low sample size. Two distinct size classes of Golden Perch were collected in the floodplain region (100 300 mm and 350 500 mm fish), whilst Golden Perch in the gorge and swampland/lower lakes were predominantly >300 mm (Fig. 5).

By November/December 2011, Golden Perch had deposited an additional annual otolith increment, hence were a year older than those fish sampled in April June 2011. In November/December 2011, the dominant age classes in the floodplain region were 1 (10%), 2 (25%), 6 (20%), 11(19%) and 15 (17%) year olds (Fig. 5). In the gorge region, the same age classes were present but 1 and 2 year old fish were collected in lower frequencies (5 and 10%, respectively) and the 11 and 15 year old age classes dominated (37 and 45%, respectively). Correspondingly, the 11 and 15 year old age classes dominated (19 and 42%, respectively) in the swamplands/lakes region and 1 year old fish comprised just 3% of fish collected. Two year old fish were absent from the swampland/lakes sample. Low numbers of 19 22 year old fish were present in the swampland/lakes region, and these age classes were absent from the floodplain region and rare in the gorge region (Fig. 5).

## Discussion

The importance of floodplains and flooding in the life cycles of native fish in the Murray Darling Basin has received considerable attention in recent years (Humphries *et al.* 1999; King *et al.* 2003; Mallen Cooper & Stuart 2003; Graham & Harris 2005; Ebner *et al.* 2009). Nevertheless, only a few studies have shown that overbank flows and flooding either stimulate fish to spawn or enhance recruitment (Tonkin *et al.* 2008; King *et al.* 2009). Furthermore, regional variations in the role of the floodplain in the MDB remain unresolved, particularly between the hydrologically and hydraulically distinct mid and lower reaches of the River Murray.

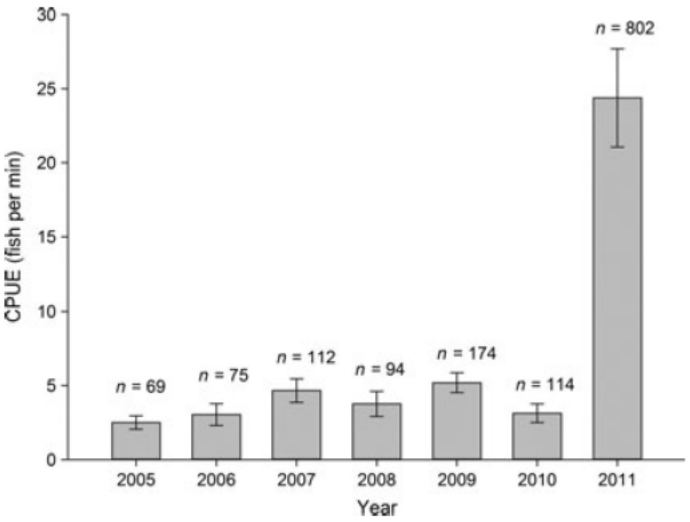

**Figure 3.** Mean (±S.E.M.) catch-per-unit-effort (fish/min) of Golden Perch collected annually during standardised electrofishing surveys from 2005 to 2011 at sites in the Chowilla Anabranch system and adjacent River Murray.

Following extensive flooding in the lower River Murray in 2010/11, Golden Perch abundance at sites in the Chowilla region was significantly greater than in the six previous years of generally low in channel flows. Age structure analysis revealed that the increased abundance was due to high numbers of age 0+ and 1+ fish spawned during the overbank flood in 2010/11 and during in channel flows in 2009/10. Age structures collected prior to flooding (2005 2010) indicate episodic recruitment in the lower River Murray with strong cohorts spawned in 2005, 2000, 1998 and 1996 and little or no recruitment in intervening years. These dominant cohorts were spawned in association with overbank floods (1996 and 2000) or increases in flow contained within the river channel (1998 and 2005) (Zampatti & Leigh, 2013). Our study was not a manipulative experiment hence demonstrating causality is difficult; nevertheless, our data do show a clear association between flooding and recruitment.

In the mid reaches of the River Murray at Barmah, flooding has been suggested to increase the spawning activity of Golden Perch, but survival to YOY could not be assessed (King *et al.* 2009). Studies using retrospective age determination of Golden Perch populations, however, have shown that strong recruitment may be associated with in channel flow pulses and overbank flows (Mallen Cooper & Stuart 2003; Zampatti & Leigh 2013). In the Lake Eyre Basin, Australia, high juvenile Golden Perch abundance and greater recruitment success have been observed following both large floods and smaller flow pulses (Balcombe & Arthington 2009). In conjunction with these studies, our study supports the notion that Golden Perch have flexible life histories and will spawn and recruit in conjunction with rises in flow contained within the river channel and overbank flows.

A large proportion of the juvenile Golden Perch collected postflooding in 2011 were spawned in 2009/10. This cohort of Golden Perch contributed to the significant increase in abundance of Golden Perch in the floodplain region of the lower River Murray in 2011, but was spawned during a period of largely regulated entitlement flow (5000 10 000 ML/day). Regulated flows of this magnitude have not previously been related to Golden Perch spawning and recruitment in the lower River Murray (Zampatti & Leigh 2013). It is possible that the 2009/10 cohort was not spawned in the lower River Murray in South Australia but instead originated in the lower Darling River, and downstream displacement was mediated by larval drift and/or the movement of juveniles. In early 2010, a substantial rise in discharge (0 11 000 ML/day) occurred in the lower Darling River (Fig. 2b) and this may have initiated spawning. In 2010, low abundances of 0+ fish were present in the Chowilla region, but it was not until 2011 that these fish, as 1 year olds, contributed to a significant increase in Golden Perch abundance in the region. If these fish were spawned in the Darling River, there is potential that high flows (>20 000 ML/day) in the Darling in early 2011 (Fig. 2b) caused further displacement and/or active movement of age 1+ fish into the lower River Murray.

Otolith geochemical signatures could prove a useful technique to retrospectively determine the natal origin and movement history of Golden Perch in the lower River Murray (Elsdon *et al.* 2008). Elemental isotope ratios have been used to successfully identify source environments and elucidate movement patterns of predominantly salmonids but also other species in North America (Gillanders 2005; Hayden *et al.* 2012). Strontium isotopic ratios in water reflect catchment geology, and in the MDB, strontium isotopic ratios differ significantly between the Murray and Darling catchments (Douglas *et al.* 1995). Consequently, analysis of strontium isotopic ratios in Golden Perch otoliths shows considerable promise in reconstructing the environmental history of all life stages and may subsequently assist in understanding the spatial factors that influence population dynamics (Campana & Thorrold 2001).

The timing of floods may have a substantial effect on the recruitment response of Golden Perch. Humphries *et al.* (1999) suggest that in the southern Mediterranean climatic region of the MDB, flooding and warm temperatures do not normally coincide, and thus, fish are unable to exploit the high levels of productivity (e.g. zooplankton abundance) than typically occur when such conditions correspond. This may be true for the mid reaches of the River Murray where flow is influenced by winter rain and spring snow melt, but in the lower River Murray, downstream of the Darling River junction, summer floods also occur as a result of summer rainfall in the Darling catchment (Maheshwari *et al.* 1995). Indeed, the

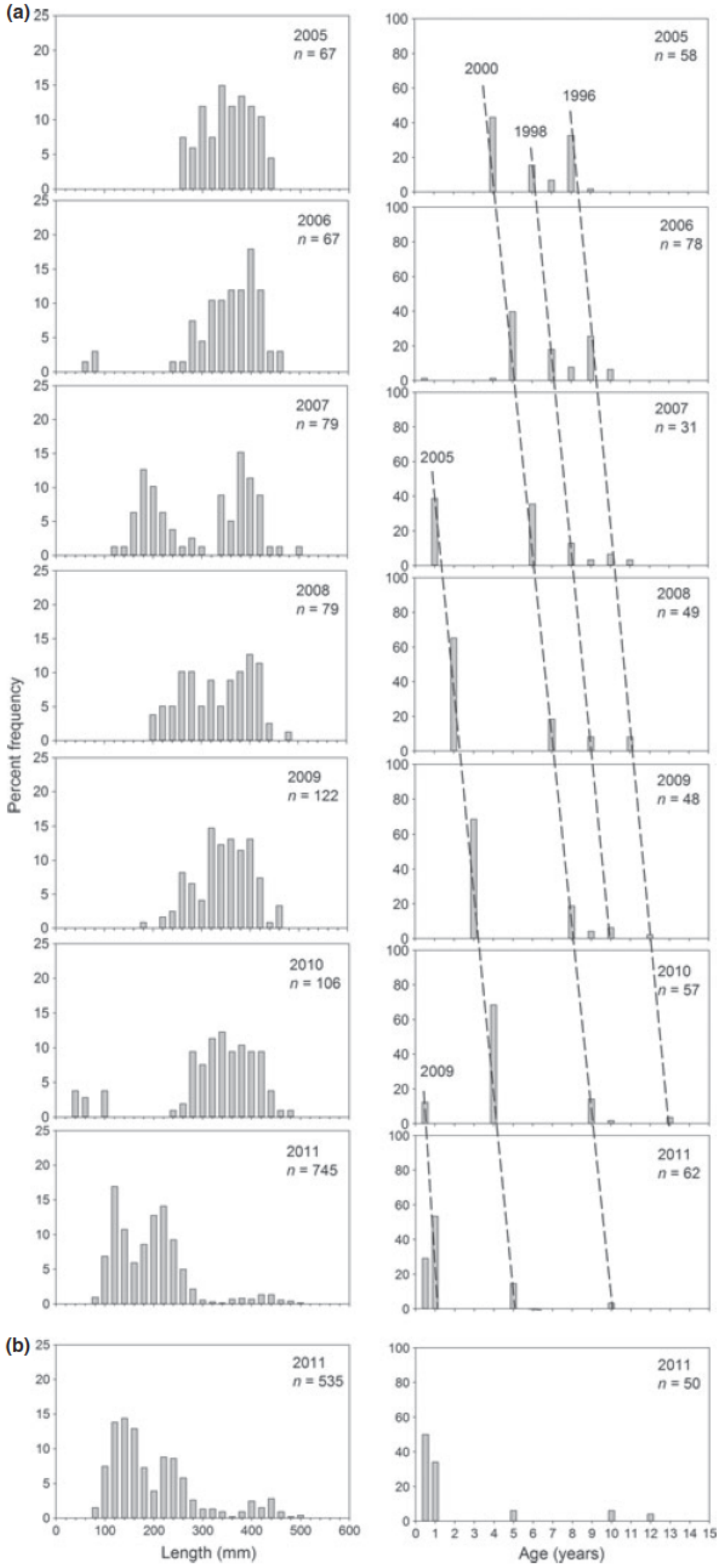

**Figure 4.** Length (left column) and age (right column) structure of Golden Perch collected during standardised electrofishing surveys from sites in the (a) Chowilla Anabranch system and adjacent River Murray in March/April 2005 2010 and May/June 2011 and (b) Katarapko Anabranch system and adjacent River Murray in April 2011. Dashed lines track progression of dominant year classes. Numbers above dashed lines represent birth year.

2010/11 floods in the lower River Murray peaked in late summer and contrary to observations in the mid Murray (Humphries *et al.* 1999; King *et al.* 2003), young of year Golden Perch were widespread and abundant in inundated ephemeral floodplain billabongs, anabranches and lakes (B. Zampatti, unpublished data). Similarly, in the northern MDB, Rolls and Wilson (2010) consistently sampled young of year Golden Perch on the floodplain of the Narran River during summer flooding. These results do not necessarily imply that Golden Perch were spawned on the floodplain but that inundated floodplains in the lower River Murray and northern MDB provide suitable rearing habitat for juvenile Golden Perch.

Not all flooding in the lower River Murray may be beneficial to Golden Perch spawning and recruitment. For example, reduced commercial catches of Golden Perch have been related to preceding years where floods have occurred prior to water temperatures that promote Golden Perch spawning (nominally 20°C) (Reynolds 1976). Where flooding has not corresponded with increased abundances of juvenile Golden Perch or a strong retrospectively determined age class (e.g. Mallen Cooper & Stuart 2003), flooding may have occurred in late winter/spring in conjunction with water temperatures unsuitable to initiate spawning or stimulate the production of food resources (i.e. zooplankton) for larvae (Humphries *et al.* 1999; Roberts *et al.* 2008).

In the gorge region of the lower River Murray in November/December 2011, the cohorts of fish spawned in 2009/10 and 2010/11 were present but less conspicuous and in the swamplands/lakes region, only 3% of fish collected were spawned in 2010/11 and none in 2009/

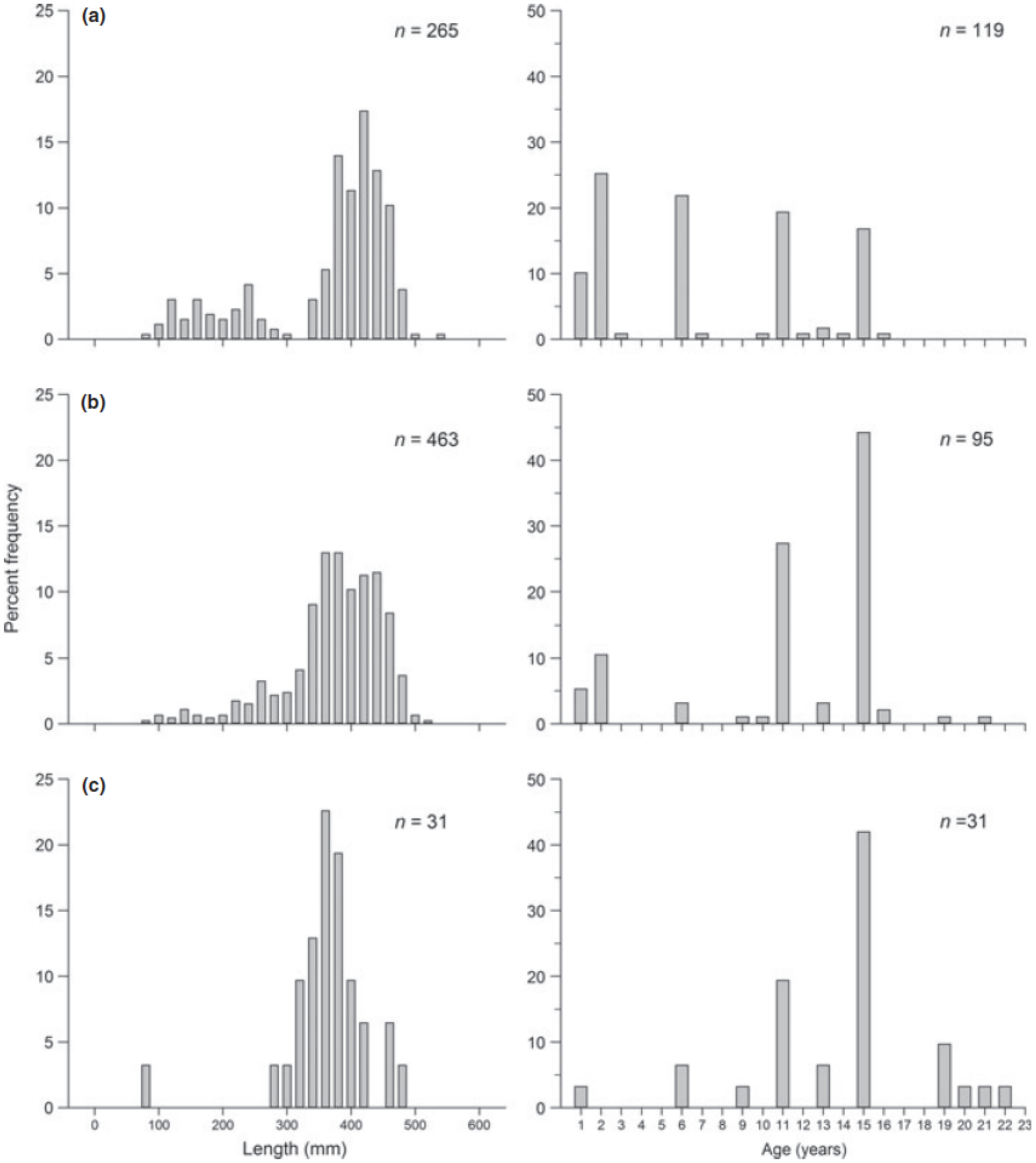

**Figure 5.** Length (left column) and age (right column) structure of Golden Perch collected from the River Murray in Nov/Dec 2011: (a) floodplain section (L6 L3), (b) gorge section (L3 Mannum), (c) swamplands and lakes (downstream of Mannum).

10. Nevertheless, over 3000 YOY Golden Perch were collected attempting to ascend fishways at the interface between the Coorong Estuary and the lower lakes of the River Murray in 2010/11 (Zampatti *et al.* 2012). Unfortunately, the small sample size of fish collected in this region in our study does not assist in determining the fate of the juvenile fish collected by Zampatti *et al.* (2012).

The potential restriction of the downstream movement of larvae, and upstream and downstream movements of juveniles and adults, may explain some of the differences observed in age structure between the floodplain, gorge and swamplands/lakes regions of the lower River Murray. The lower River Murray is fragmented by 10 weirs which significantly impact longitudinal connectivity and impede flow until the weirs are removed at approximately 50 000 ML/day. The weirs have transformed a free flowing river into a series of stepped pools characterised by lentic habitats at low flows (Walker 2006). Loss of lotic habitats and altered longitudinal connectivity are global issues for the conservation of freshwater fish (Nilsson *et al.* 2005; Dudley & Platania 2007) and certainly affect Golden Perch populations in the lower River Murray. Weirs impede the upstream and downstream movement of juvenile and adult Golden Perch (O'Connor *et al.* 2006) and potentially impact the downstream drift of larvae. Fishways are currently being constructed at all weirs on the main stream of the River Murray to facilitate the upstream movement of juvenile and adult fish (Barrett & Mallen Cooper 2006), but facilitating downstream passage and determining the fate of larvae in weir pools remain important questions for future research.

Postflooding in 2011, 11 and 15 year old fish, spawned during overbank floods in 2000 and 1996, respectively (Zampatti & Leigh 2013), formed strong cohorts across all geomorphic regions of the lower River Murray. Historically, cohorts spawned in flood years were a dominant feature of the age structure of Golden Perch populations in the lower River Murray and contributed significantly to commercial catches (Reynolds 1976; Ye 2004). During a period of drought from 2005 to 2010, older age classes of Golden Perch in the floodplain geomorphic region of the lower River Murray diminished, as adults potentially migrated upstream or were caught by anglers. Despite this, abundances of Golden Perch remained relatively constant due to a strong recruitment event in 2005 associated with an in channel rise in discharge (Zampatti & Leigh 2013). In 2010/11, strong recruitment (to at least age 0+) was associated with a substantial overbank flow (~93 000 ML/day) and, unlike the within channel flow event in 2005, the flood had a major influence on abundance. Consequently, overbank flows may be particularly important for enhancing Golden Perch populations in the lower River Murray by facilitating local spawning and recruitment and/or redistributing larvae and juveniles from upstream.

## Implications for Managers

Reallocation of water to the environment has become a central tenet of water resource management in the Murray Darling Basin (Murray Darling Basin Authority 2012a). To inform effective environmental water delivery, an understanding of biotic response to components of the flow regime is essential (Arthington *et al.* 2006). Contemporary approaches to flow restoration in the Murray Darling Basin propose the life cycle, and habitat requirements of native fish will be met by providing overbank flows that inundate floodplains for the primary objective of restoring the health of floodplain eucalypts (Murray Darling Basin Authority 2012b). Overbanks flows and inundation of the floodplain are undoubtedly important in the ecological functioning of floodplain rivers. Nevertheless, there are other aspects of the flow regime, such as increases in discharge that remain in channel, which may support substantial recruitment of Golden Perch and other native fish (Mallen Cooper & Stuart 2003).

There has been a general lack of recognition of the importance in channel habitats and processes, including the significance of in channel flow pulses (Humphries *et al.* 1999; Mallen Cooper & Stuart 2006). For native fish such as Golden Perch, these intermediate flows may be as important as conspicuous overbank events. Floods do indeed facilitate recruitment and substantially augment abundance, but infrequent flooding interspersed with in channel increases in discharge may result in more frequent spawning and recruitment and more robust native fish populations. The life histories of some large bodied fish species such as Golden Perch may also operate at spatial scales of thousands of kilometres, and environmental factors at spawning sites may be significantly different from those at receiving habitats for juvenile fish. The spatio temporal scales of life history processes that influence the population dynamics of Golden Perch require further consideration and flow restoration in the MDB ultimately needs to be undertaken at scales that are relevant to the life histories of the organisms of concern.

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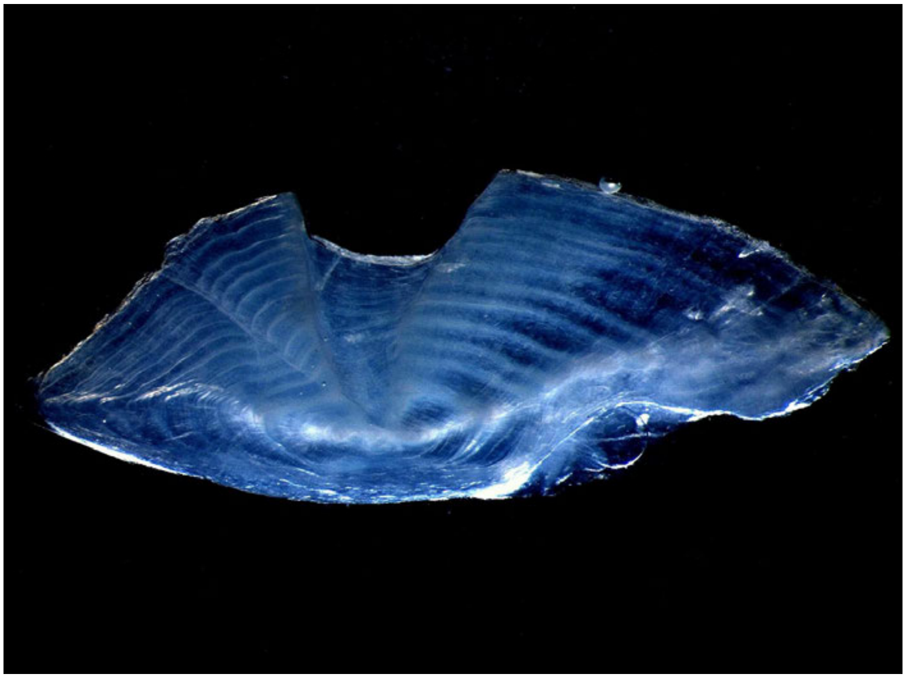
# CHAPTER 4: Otolith chemistry delineates the influence of provenance and dispersal on the population dynamics of golden perch in a regulated river.



A cross-section of a golden perch otolith

# Statement of Authorship

| | |
|---|---|
| Title of Paper | Otolith chemistry delineates the influence of provenance and dispersal on the population dynamics of golden perch (*Macquaria ambigua*) in a regulated river. |
| Publication Status | ☐ Published ☐ Accepted for Publication<br>☐ Submitted for Publication ☑ Unpublished and Unsubmitted work written in manuscript style |
| Publication Details | This manuscript will be submitted to *Marine and Freshwater Research*. Authorship is as follows: Brenton P. Zampatti, Sandra, J. Leigh, Phillipa J. Wilson, David Crook, Bronwyn M. Gillanders, Roland Maas, Jed I. Macdonald and Jon Woodhead. |

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| Overall percentage (%) | 80% | | |
| Certification: | This paper reports on original research I conducted during the period of my Higher Degree by Research candidature and is not subject to any obligations or contractual agreements with a third party that would constrain its inclusion in this thesis. I am the primary author of this paper. | | |
| Signature | | Date | 12/7/2019 |

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i. the candidate's stated contribution to the publication is accurate (as detailed above);

ii. permission is granted for the candidate in include the publication in the thesis; and

iii. the sum of all co-author contributions is equal to 100% less the candidate's stated contribution.

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| Signature | | Date | 5/8/2019 |

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# Otolith chemistry delineates the influence of provenance and dispersal on the population dynamics of golden perch (*Macquaria ambigua*) in a regulated river.

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## Abstract

In regulated rivers globally, migratory fishes are threatened by fragmentation and flow modification. Effective management of these fishes requires a spatio-temporal context for the life history processes (spawning, recruitment and movement) that determine population dynamics. The structural and chemical properties of fish otoliths provide a unique means to recount a fish's life history in time and space. We investigated the age structure of the migratory, pelagophil golden perch (*Macquaria ambigua*) in the River Murray, Australia, and utilised water and otolith $^{87}Sr/^{86}Sr$ to delineate the provenance and movement of fish from discrete cohorts. Water $^{87}Sr/^{86}Sr$ was distinct among the Darling River (a major tributary), and lower and mid-River Murray. Otolith chemistry revealed golden perch collected in the lower River Murray were the progeny of spawning in either the River Murray or Darling River, during years characterised by within-channel rises in flow, or in both rivers in a year characterised by overbank flooding. Movement of juvenile fish from the Darling River substantially influenced population structure in the lower River Murray, whereby population growth post flooding was largely a result of immigration of age 1+ fish. This study demonstrates the potential importance of tributary recruitment sources and dispersal on main-stem population dynamics, and the utility of otolith chemistry for spatially reconciling population structure and the life history processes of freshwater fishes.

## Introduction

Globally, modification of riverine habitats and flow regimes alters ecosystem function, with related impacts on population resilience and biodiversity (Dudgeon *et al.* 2006; Poff *et al.* 2007). Freshwater fishes are particularly vulnerable to river regulation (Nilsson *et al*. 2005), and effective management requires a spatio-temporal context for the key life history processes (spawning, recruitment and movement) that determine population dynamics. Rivers are dendritic in nature and riverine fish may disperse among the branches of these networks (Fagan 2002; Koster *et al*. 2014). Ontogenetic variation in habitat use is also commonplace, with alternative locations potentially used for spawning, rearing and refuge (Amoros and Bornette 2002; King 2004). As such, dispersal and migration between disparate locations can be an important determinant of metapopulation structure and function (Jager *et al*. 2001).

In lotic ecosystems, migratory, pelagic-broadcast spawning fishes (pelagophils) are particularly impacted by fragmentation and flow modification (Hoagstrom and Turner 2013). Hydrologic cues and hydraulic habitats for spawning are altered by flow regulation, and spawning migrations and the obligate downstream drift of eggs and larvae, essential for the development of early life stages, are interrupted by physical barriers and the hydraulic impacts of dams and weirs (Welcomme *et al*. 2006; Perkin *et al*. 2015). Consequently, in regulated rivers, these fishes may demonstrate episodic recruitment and low demographic resilience (Zampatti and Leigh 2013a). Conservation and rehabilitation of pelagophils requires an understanding of habitat and hydrological requirements across a fish’s lifetime, including characterising natal, juvenile and adult habitats, and movement among these (Dudley and Platania 2007).

In Australia’s Murray Darling Basin (MDB), flow regulation has negatively impacted native fish populations (Barrett 2004). To redress this, fish form a primary objective for environmental water delivery under contemporary river rehabilitation programs (Koehn *et al*. 2014). Golden perch (*Macquaria ambigua*) is one of few species in the MDB that are migratory, pelagic-broadcast spawners, and where spawning, recruitment and movement have been explicitly associated with flow variability (Mallen-Cooper and Stuart 2003; Mallen-Cooper and Brand 2007; King *et al*. 2009; Zampatti and Leigh 2013a; Koster *et al*. 2014; 2017). Accordingly, these aspects of golden perch life history form a focus for environmental flow management in the MDB.

To inform flow restoration, knowledge regarding the spatial structure of populations and influence of flow on population processes is vital. Nevertheless, few investigations relating fish recruitment to flow have considered precisely *when* and *where* fish originated (although see Limburg *et al*. 2013, and Macdonald and Crook 2014). In the lower River Murray, golden perch spawning and recruitment (i.e. ≥ age 0+) are associated with in-channel and overbank rises in flow, nominally >15,000 ML day$^{-1}$ (Zampatti and Leigh 2013a). Following extensive flooding in the lower River Murray in 2010–11, golden perch abundance increased significantly, compared to six previous years of generally low, in-channel flows (Zampatti and Leigh 2013b). Age-structure analysis revealed that increased abundance was due to high numbers of age 0+ and 1+ fish born in the flood year and in the year prior, respectively. Indeed, ~50% of the juvenile golden perch collected post-flooding were age 1+ fish born during a period of low flow in the lower River Murray (<10,000 ML day$^{-1}$, 44th percentile exceedance flow, MDBA unpublished data). Zampatti and Leigh (2013b) speculated that the age 1+ cohort did not originate in the River Murray and instead originated in the Darling River, the major tributary of the River Murray, potentially in association with a substantial rise in discharge (0–11,000 ML day$^{-1}$) in the lower Darling River in early 2010. Confirming the provenance of golden perch in the lower River Murray and integrating this with migration history will improve understanding of the spatial ecology of golden perch in the MDB and relationships of flow with key life history processes and population dynamics.

The chemical composition of fish otoliths (earstones) can be used to study the origin and movement of fish (Elsdon *et al*. 2008). A fish's historical movement, including its place of birth and death, can potentially be determined by comparing geochemical signatures in otoliths with ambient signatures in water, if there is geographic variability in water chemistry. Stable isotopes of strontium (Sr) have been used successfully to discern the natal habitats and movements of numerous diadromous and freshwater fishes. (Kennedy *et al.* 2002; Crook *et al.* 2013; Brennan and Schindler 2017). Unlike metal:Ca ratios (e.g. Sr/Ca, Ba/Ca), Sr isotope ratios are not biologically fractionated; therefore, $^{87}$Sr/$^{86}$Sr values measured in otoliths directly reflect the ambient water $^{87}$Sr/$^{86}$Sr (Kennedy *et al*. 2000). As a result, spatio-temporal 'isoscapes' of dissolved $^{87}$Sr/$^{86}$Sr in water can provide a template for determining the spatial origin and movement history of fish (Barnett-Johnson *et al.* 2008; Muhlfeld *et al*. 2012).

The aims of this study were to characterise the age structure of golden perch populations in the lower River Murray and use water and otolith strontium isotope ratios to elucidate the natal origin and migration history of fish from discrete cohorts. Our specific objectives were to: 1) demonstrate the persistence of specific age-classes in the lower River Murray population associated with distinct flow events, 2) characterise spatio-temporal variability in water $^{87}Sr/^{86}Sr$ at sites in the Murray and Darling rivers, 3) determine otolith core $^{87}Sr/^{86}Sr$ in distinct cohorts of golden perch, 4) compare $^{87}Sr/^{86}Sr$ in otolith cores with water $^{87}Sr/^{86}Sr$ in the study region to elucidate fish provenance, and 5) measure $^{87}Sr/^{86}Sr$ along transects from otolith core to edge to investigate the migration history of golden perch from the specific age cohorts.

## Study Region

The Murray–Darling Basin (MDB) drains an area of 1 073 000 km$^2$. The combined length of the two major rivers, the Murray and the Darling, is ~5500 km and both flow through predominantly semi-arid or arid landscapes. River regulation, in the form of large headwater storages, weirs, floodplain levees and tidal barrages, and consumptive use for irrigation and domestic supply, has had a profound impact on the magnitude and variability of discharge in the River Murray (Maheshwari *et al*. 1995) and many of its tributaries (Kingsford 2003).

This study was conducted in the lower and mid reaches of the River Murray, and the lower Darling River. The lower River Murray extends downstream from the Darling junction to the river mouth (Figure 1). In this region, 10 low-level (~3 m) weirs fragment 830 km of river into a series of contiguous weir pools. Under low flows, the weirs transform a historically dynamic lotic system into a homogenous series of lentic environments (Walker 2006; Mallen-Cooper and Zampatti 2018). The mid Murray extends upstream for 1155 km, from the Darling River junction to Yarrawonga (Figure 1). This region is less fragmented by weirs and retains long reaches (100s km) of lotic habitat (Mallen-Cooper and Zampatti 2018); nevertheless, it is impacted by regulated discharge and, in some reaches, seasonal inversion of flow (Maheshwari *et al*. 1995). The lower Darling River extends for 510 km upstream from the junction with the River Murray to the Menindee Lakes, an extensive series of off-channel lakes (457 km$^2$; 1731 GL capacity) used to regulate and store Darling River flows for consumptive use.

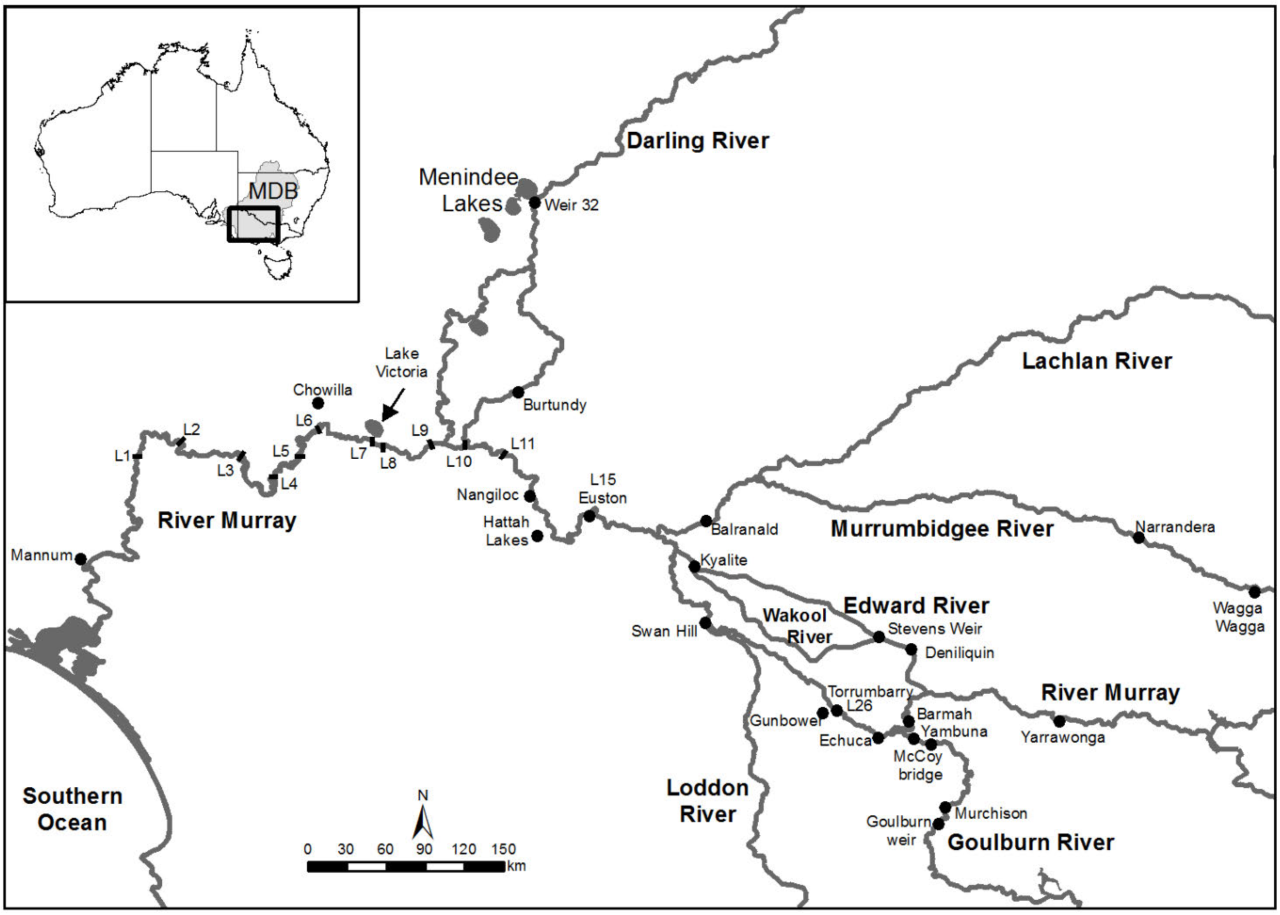

Figure 1. Map showing the location of the River Murray, Darling River and other major tributaries in the southern Murray–Darling Basin, including the numbered Locks and Weirs (up to Lock 26, Torrumbarry).

## Methods

*Fish collection and ageing*

Sampling of golden perch occurred annually from 2010 to 2014 in main-channel and anabranch habitats between Lock 3 and 6 in the lower River Murray. In each year, golden perch were sampled in March–May by boat electrofishing using either a 5 kW or 7.5 kW Smith Root (Model GPP 5 or 7.5) electrofishing unit. At each site, electrofishing was conducted during daylight hours and all available littoral habitats were fished. All fish were measured to the nearest mm (total length, TL) and a sub-sample of fish (*n* = 50–70) proportionally representative of the length-structure was retained for ageing. Fish were euthanized in the field by overdose of AQUI-S® (Aqui-s, Lower Hutt, New Zealand) prior to the removal of sagittal otoliths.

Whole sagittae were embedded in clear resin and sectioned transversely through the primordium (400 to 600 μm). Sections were mounted on microscope slides and examined using a dissecting microscope (x 25) under transmitted light. Annual increment formation in golden perch otoliths has been validated (Anderson *et al.* 1992; Mallen-Cooper and Stuart 2003; Zampatti and Leigh 2013a). Independent estimates of age were made by three readers by counting the number of opaque zones (annuli) from the primordium to the otolith edge. Young-of-year (YOY, < 1 year old) fish were defined as individuals lacking clearly discernible annuli.

*Water collection and Sr isotope analysis*

To investigate spatio-temporal variability in dissolved $^{87}Sr/^{86}Sr$ in water, surface water samples were collected at a range of intervals (fortnightly to monthly) over a four-year period from December 2011–December 2014 in the River Murray upstream of the Darling River confluence (Mildura, Lock 11), the River Murray downstream of the Darling River confluence (Lock 6), and the lower Darling River (Lock 32). One water sample was also collected in the Darling River at Pomona (immediately upstream of Wentworth) in December 2011 (Figure 1). Water samples were collected in new polypropylene 114 x 44 mm sample containers (SARSTEDT, Nümbrecht, Germany) and refrigerated.

An aliquot (20 ml) of each water sample was filtered through a 0.2 µm Acrodisc syringe-mounted filter into a clean polystyrene beaker and dried overnight in a HEPA-filtered fume cupboard. Previous analyses have shown that filtering after transfer to the laboratory, rather than after sample collection in the field, has no influence on measurement of $^{87}$Sr/$^{86}$Sr (Palmer and Edmond 1989). Strontium was extracted using a single pass over 0.15 ml (4 x 12 mm) beds of EICHROMTM Sr resin (50–100 µm). Following Pin *et al*. (1994), matrix elements were washed off the resin with 2M and 7M nitric acid, followed by elution of clean Sr in 0.05M nitric acid. The total blank, including syringe-filtering, is ≤0.1 ng, implying sample to blank ratios of ≥4000; no blank corrections were therefore deemed necessary. Strontium isotope analyses were carried out on a *Nu Plasma* multi-collector Inductively Coupled Plasma Mass Spectrophotometer (ICPMS) (Nu Instruments, Wrexham, UK) interfaced with an ARIDUS desolvating nebulizer, operated at an uptake rate of ~40 µL min$^{-1}$. Mass bias was corrected by normalizing to $^{87}$Sr/$^{86}$Sr = 8.37521 and results reported relative to a value of 0.710230 for the SRM987 Sr isotope standard. Internal precisions (2SE) based on at least 30 ten-second integrations averaged ± 0.00002 and average reproducibility (2SD) was ± 0.00004.

*Otolith preparation and Sr isotope analysis*

Otoliths for Sr isotope analysis were obtained from golden perch collected for age determination and prior collections (2005–2010) of golden perch juveniles and adults sampled by electrofishing in main channel and anabranch habitats in the lower River Murray between Lock 3 and Lock 6 (Table S1, Supplementary material). Post larval fish (age 0+) were collected in riverine and anabranch habitats in 2005, using the methods outlined in Zampatti and Leigh 2013a. Briefly, drift nets (500-µm mesh, 0.5-m-diameter opening, 1.5-m length) and modified quatrefoil light traps (Floyd et al. 1984) were set concurrently, overnight.

Sagittal otoliths were dissected and retained whole (age 0+ fish) or embedded in clear casting resin (≥ age 1+ fish) and sectioned transversely (400 to 600 µm). Whole otoliths and sections were then mounted on acid-washed glass slides using Crystalbond™. Whole otoliths were mounted proximal surface downwards and polished to the primordium using a graded series of wetted lapping films (9, 5 and, 3 µm), whilst transverse sections were polished using wetted lapping film (9 µm). Slides were then reheated and the polished otolith/section transferred to a 'master' slide, on which otoliths from all collection sites were arranged randomly to remove any potential for systematic bias during analysis. The samples were rinsed in ultrapure water (Millipore) and air-dried overnight in a class 100 laminar flow cabinet at room temperature.

Laser ablation – inductively coupled plasma mass spectrometry (LA-ICPMS) was used to measure $^{87}Sr/^{86}Sr$ in the otoliths of juvenile and adult fish. The experimental system consisted of a Nu Plasma multi-collector LA-ICPMS (Nu Instruments, Wrexham, UK), coupled to a HelEx laser ablation system (Laurin Technic, Canberra, Australia, and the Australian National University) constructed around a Compex 110 excimer laser (Lambda Physik, Gottingen, 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 v6.14 software (Resonetics, USA). For YOY fish collected in 2010, a single 55 µm ablation spot was used to measure $^{87}Sr/^{86}Sr$ in the region of the otolith core (area incorporating early life history information i.e. first few days of a fish's life) and edge (area incorporating information from the capture location). The laser was operated at 80mJ and pulsed at 10 Hz.

For all other samples, otoliths were ablated along a transect from the primordium to the dorsal margin using a 6 × 100 µm rectangular laser slit. The laser was operated at 90 mJ, pulsed at 10 Hz and scanned at 5 or 10 µm sec$^{-1}$ (depending on the size of the otolith) across the sample. Ablation was performed under pure He to minimise the re-deposition of ablated material, and the sample was then rapidly entrained into the Ar carrier gas flow. Each otolith transect was pre-ablated using reduced energy (50 mJ) was conducted along each transect to remove any surface contaminants and a 20–30 sec background was measured prior to acquiring data for each sample. Corrections for Kr and Rb interferences were made following the procedures of Woodhead *et al*. (2005) and mass bias was then corrected by reference to an $^{86}Sr/^{88}Sr$ ratio of 0.1194. Iolite Version 2.13 (Paton *et al*. 2011) that operates within IGOR Pro Version 6.2.2.2 (WaveMetrics, Inc., Oregon) was used to process data offline, with data corrected for potential Ca argide/dimer interferences.

A modern marine carbonate standard composed of mollusc shells ($^{87}Sr/^{86}Sr$ value of 0.70916 according to long-term laboratory measurements, identical to the accepted modern seawater value of 0.709160, MacArthur and Howarth 2004) was analysed after every 10 otolith samples to allow for calculation of external precision. Mean (±1 SD) values of $^{87}Sr/^{86}Sr$ values in the modern marine carbonate standard (n = 24) run throughout the analyses were 0.70918 ±

0.00017, with external precision (expressed as ± 2 SE) calculated as ± 0.00006. Mean within-run precision, measured as ± 2 SE, was ± 0.00005.

## Results

### *Golden perch age demographics 2010–2014*

From 2010–2014, three distinct cohorts of golden perch were present in the lower River Murray, corresponding with birth years of 2005–06, 2009–2010 and 2010–11 (Figure 2). In 2010, age 4+ fish, from the 2005–06 cohort, comprised ~70% of population, but this cohort diminished in 2011, to represent <20% of population as age 5+ fish (Figure 2) and by 2014 was absent (Figure 2). In 2011, age 0+ and 1+ fish from the 2010–11 and 2009–10 cohorts, respectively, comprised >70% of the population, and continued to dominate through 2012–2014 (Figure 2). The most prominent cohort in the lower River Murray from 2010–2014, was 2009–10 recruits which comprised at least 50% of the population from 2011–2014, as age 1+–4+ fish, respectively (Figure 2).

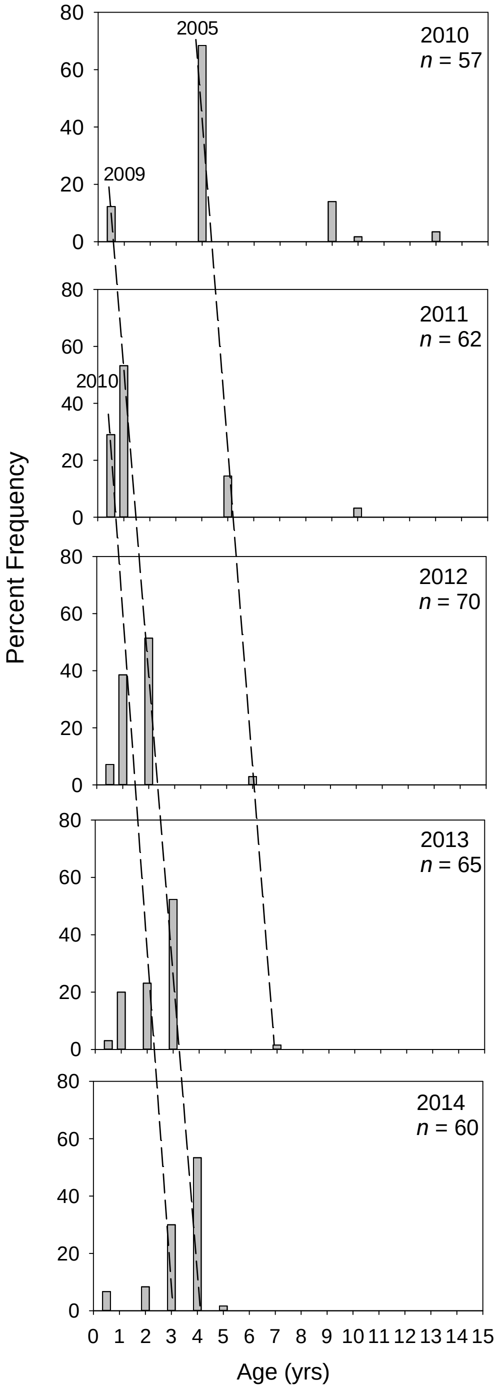

Figure 2. Age-frequency distributions of golden perch collected in the lower River Murray annually in March–May 2010–2014. Dashed lines track progression of cohorts originating in 2005–6, 2009–10 and 2010–11.

### *Spatio-temporal variation in water $^{87}Sr/^{86}Sr$*

Water $^{87}Sr/^{86}Sr$ showed substantial variation both among years and among regions. In the lower Darling River, $^{87}Sr/^{86}Sr$ values ranged from 0.707434–0.707592 and exhibited considerable intra and inter-annual stability (Table 1 and Figure 3). Water $^{87}Sr/^{86}Sr$ values in the lower Darling River were considerably lower and clearly distinct from the mid-Murray and lower Murray, which ranged from 0.715954–0.717482 and 0.708619–0.714719, respectively (Table 1 and Figure 3). Water $^{87}Sr/^{86}Sr$ values in the lower River Murray reflected mixed water sources and variability in contribution of discharge from the River Murray and Darling River catchments (Table 1 and Figure 3). For example, in February 2012, flow from the Darling River comprised >95% of flow to the lower River Murray, and water $^{87}Sr/^{86}Sr$ in this region (0.708619) approached that of the Darling River (~0.7075) (Table 1 and Figure 3). In contrast, in November 2014, flow from the Darling River was negligible and water $^{87}Sr/^{86}Sr$ in the lower River Murray (Lock 6, 0.714130) more closely resembled that in the mid River Murray (Lock 11, 0.716920) (Table 1 and Figure 3).

Table 1. Site location, dates, $^{87}Sr/^{86}Sr$, and internal precision (2SE) for water samples collected from the River Murray and Darling River from December 2011–December 2014.

| Site | Date | $^{87}Sr/^{86}Sr$ | Internal Precision |
|---|---|---|---|
| River Murray at Lock 11 | Dec 2011 | 0.716295 | 0.000017 |
| | 19 Nov. 2012 | 0.716434 | 0.000015 |
| | 12 Dec. 2012 | 0.715954 | 0.000010 |
| | 7 Jan. 2013 | 0.716214 | 0.000015 |
| | 23 Sept. 2013 | 0.717318 | 0.000015 |
| | 7 Oct. 2013 | 0.717334 | 0.000017 |
| | 4 Nov.2013 | 0.717482 | 0.000017 |
| | 2 Dec. 2013 | 0.717399 | 0.000017 |
| | 6 Jan. 2014 | 0.716988 | 0.000018 |
| | 3 Feb. 2014 | 0.716424 | 0.000017 |
| | 17 Sept. 2014 | 0.716694 | 0.000020 |
| | 2 Oct. 2014 | 0.716482 | 0.000019 |
| | 8 Nov. 2014 | 0.716920 | 0.000019 |
| | 8 Dec. 2014 | 0.716872 | 0.000028 |
| Darling River upstream of Wentworth | Dec. 2011 | 0.707434 | 0.000015 |
| Darling River downstream Weir 32 | 6 Nov. 2012 | 0.707592 | 0.000022 |
| | 8 Oct. 2013 | 0.707509 | 0.000016 |
| | 4 Nov. 2013 | 0.707542 | 0.000022 |
| | 2 Dec. 2013 | 0.707486 | 0.000017 |
| | 3 Jan. 2014 | 0.707498 | 0.000016 |
| | 26 Feb. 2014 | 0.707458 | 0.000017 |
| | 9 Sept. 2014 | 0.707481 | 0.000019 |
| | 7 Oct. 2014 | 0.707486 | 0.000017 |
| | 3 Nov. 2014 | 0.707462 | 0.000014 |
| | 11 Dec. 2014 | 0.707490 | 0.000014 |
| River Murray at Lock 6 | Dec. 2011 | 0.712042 | 0.000022 |
| | 18 Jan. 2012 | 0.708715 | 0.000017 |
| | 6 Feb. 2012 | 0.708619 | 0.000016 |
| | 23 Mar. 2012 | 0.710413 | 0.000016 |
| | 10 Apr. 2012 | 0.711247 | 0.000016 |
| | 13 Nov. 2012 | 0.709700 | 0.000015 |
| | 11 Dec. 2012 | 0.710338 | 0.000014 |
| | 16 Sept. 2014 | 0.713774 | 0.000024 |
| | 14 Oct. 2014 | 0.713254 | 0.000026 |
| | 11 Nov. 2014 | 0.714130 | 0.000020 |
| | 9 Dec. 2014 | 0.714719 | 0.000019 |

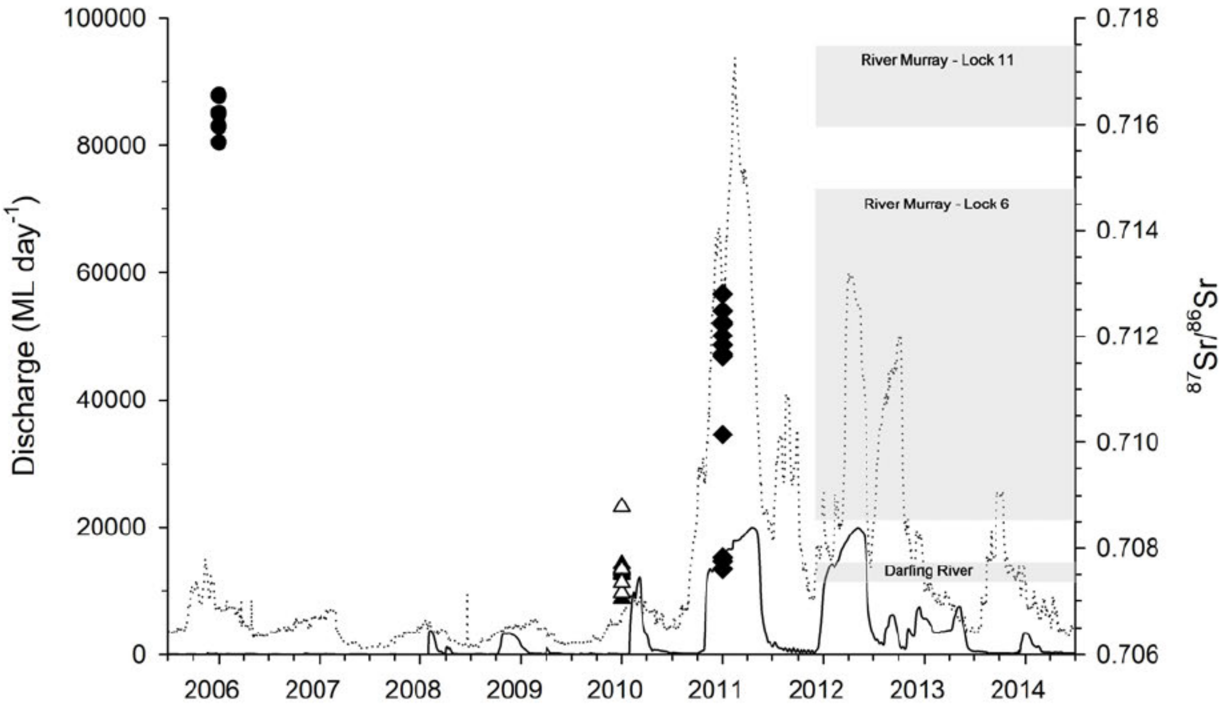

Figure 3. River Murray (discharge into South Australia, ML day$^{-1}$, dotted line) and Darling River flow (solid line) from July 2005 to July 2014. Symbols represent otolith core $^{87}Sr/^{86}Sr$ for golden perch from the 2005–06 (closed black circle, age 1+ collected in 2007), 2009–10 (closed black triangle, age 0+ collected in 2010 and open triangle, age 4+ collected in 2014), and 2010–11 (closed black diamond, age 0+ collected in 2011) cohorts. Grey boxes represent range of measured $^{87}Sr/^{86}Sr$ in water between December 2011 and December 2014 in the River Murray at Lock 11 (upstream of the Darling junction) and Lock 6 (downstream of the Darling junction), and the Darling River at Weir 32.

*Provenance of golden perch*

Golden perch from the 2005–06 cohort exhibited otolith core $^{87}Sr/^{86}Sr$ ranging from 0.71651–0.71741 and 0.71566–0.71655 for age 0+ and age 1+ fish, respectively (Figure 3 and Table 2). These otolith $^{87}Sr/^{86}Sr$ correspond with water $^{87}Sr/^{86}Sr$ in the mid River Murray at Lock 11 (Figure 3 and Table 1), indicating a River Murray natal origin for the 2005–06 cohort of golden perch. In contrast, golden perch from the 2009–10 cohort exhibited otolith core $^{87}Sr/^{86}Sr$ ranging 0.70704–0.70878 for age 0+ and age 4+ fish (Figure 3 and Table 2) suggesting that the majority of fish had originated in the Darling River (Figure 3 and Table 1). Of the fish from the 2010–11 cohort, 75% (*n* = 9) had otolith core $^{87}Sr/^{86}Sr$ values ranging from 0.71163–0.71280 and the remaining 25% (*n* = 3) from 0.70760–0.70783 (Figure 3 and Table 2), corresponding with water $^{87}Sr/^{86}Sr$ in the lower River Murray and Darling River, respectively (Figure 3 and Table 1). As such, the 2010–11 cohort of golden perch differed from the 2005–06 (River Murray origin) and 2009–10 (Darling River origin) cohorts in that fish originated from both the lower River Murray and Darling River.

Table 2. Otolith core and edge $^{87}Sr/^{86}Sr$ for golden perch from three prominent cohorts: 1) 2005–06 (collected as age 0+ in 2005 and age 1+ in 2007), 2009–10 (collected as age 0+ in 2010 and age 4+ in 2014), and 2010–11 (collected as age 0+ in 2011).

| Year collected | Age | Year of birth | Core $^{87}Sr/^{86}Sr$ | Edge $^{87}Sr/^{86}Sr$ |
|---|---|---|---|---|
| 2005 | 0+ | 2005–06 | 0.71652 | 0.71559 |
| | 0+ | 2005–06 | 0.71741 | 0.71555 |
| | 0+ | 2005–06 | 0.71651 | 0.71455 |
| | 0+ | 2005–06 | 0.71667 | 0.71573 |
| | 0+ | 2005–06 | 0.71678 | 0.71576 |
| 2007 | 1+ | 2005–06 | 0.71622 | 0.71448 |
| | 1+ | 2005–06 | 0.71597 | 0.71572 |
| | 1+ | 2005–06 | 0.71655 | 0.71473 |
| | 1+ | 2005–06 | 0.71566 | 0.71476 |
| | 1+ | 2005–06 | 0.71620 | 0.71532 |
| 2010 | 0+ | 2009–10 | 0.70704 | 0.70854 |
| | 0+ | 2009–10 | 0.70770 | 0.71010 |
| | 0+ | 2009–10 | 0.70750 | 0.70866 |
| | 0+ | 2009–10 | 0.70757 | 0.70957 |
| | 0+ | 2009–10 | 0.70762 | 0.70918 |
| | 0+ | 2009–10 | 0.70758 | 0.70923 |
| | 0+ | 2009–10 | 0.70757 | 0.70770 |
| | 0+ | 2009–10 | 0.70752 | 0.70857 |
| 2014 | 4+ | 2009–10 | 0.70717 | 0.71117 |
| | 4+ | 2009–10 | 0.70759 | 0.71155 |
| | 4+ | 2009–10 | 0.70760 | 0.71176 |
| | 4+ | 2009–10 | 0.70878 | 0.71144 |
| | 4+ | 2009–10 | 0.70735 | 0.71132 |
| 2011 | 0+ | 2010–11 | 0.71184 | 0.71316 |
| | 0+ | 2010–11 | 0.71202 | 0.71260 |
| | 0+ | 2010–11 | 0.70776 | 0.71307 |
| | 0+ | 2010–11 | 0.71167 | 0.71253 |
| | 0+ | 2010–11 | 0.71227 | 0.71325 |
| | 0+ | 2010–11 | 0.71248 | 0.71220 |
| | 0+ | 2010–11 | 0.70783 | 0.71133 |
| | 0+ | 2010–11 | 0.71014 | 0.71215 |
| | 0+ | 2010–11 | 0.71163 | 0.71191 |
| | 0+ | 2010–11 | 0.70760 | 0.71262 |
| | 0+ | 2010–11 | 0.71223 | 0.71189 |
| | 0+ | 2010–11 | 0.71280 | 0.71203 |

### *Migration history of fish*

To investigate the migration history of golden perch we analysed $^{87}Sr/^{86}Sr$ profiles from otolith core to edge, thus elucidating lifetime variability in $^{87}Sr/^{86}Sr$. Age 1+ golden perch from the 2005–06 cohort exhibited otolith $^{87}Sr/^{86}Sr$ transects indicative of spawning and residence in the River Murray. At a finer spatial scale, early in their lives,these fish displayed otolith $^{87}Sr/^{86}Sr$ comparable to water $^{87}Sr/^{86}Sr$ in the mid River Murray early in their lives prior to transition to a lower River Murray $^{87}Sr/^{86}Sr$ (Figure 4a). Age 4+ golden perch from the 2009–10 cohort exhibited otolith $^{87}Sr/^{86}Sr$ transects indicative of a Darling River origin and subsequent transition into the River Murray as age 1+ fish (Figure 4b). Of the 12, age 0+ golden perch from the 2010–11 cohort, 75% exhibited otolith $^{87}Sr/^{86}Sr$ indicative of a lower River Murray spawning origin and continued residence in the lower River Murray until capture (Figure 4c). The remaining 25% exhibited otolith core $^{87}Sr/^{86}Sr$ values comparable to that of water in the Darling River, but rapid transition to values representative of water $^{87}Sr/^{86}Sr$ in the lower River Murray early in the fish's lives (Figure 4d), indicating a lower Darling River natal origin and subsequent dispersal into the lower River Murray as larvae.

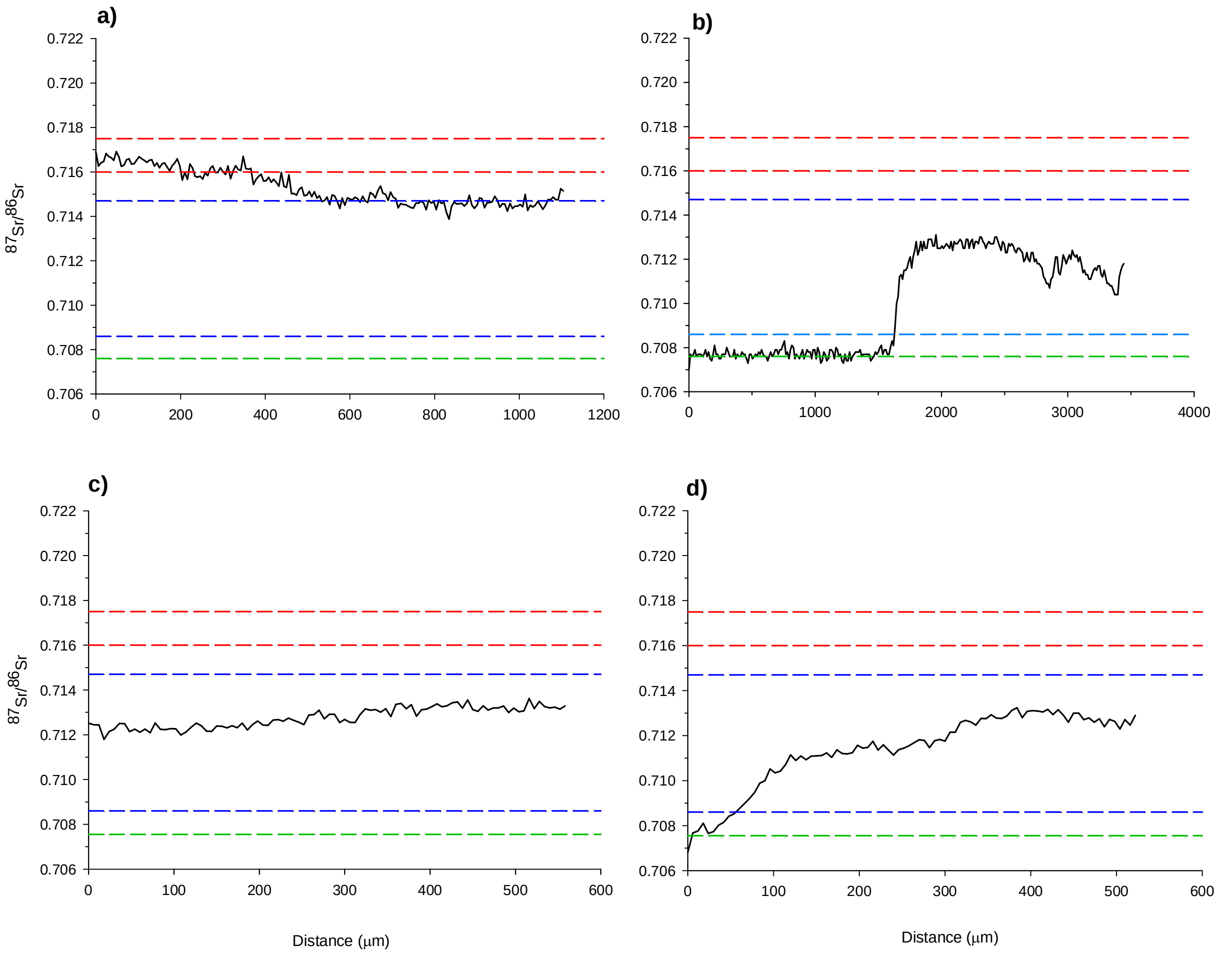

Figure 4. Individual life history profiles based on transect analysis of $^{87}$Sr/$^{86}$Sr from core to edge of otoliths from a) an age 1+, 2005–06 cohort, golden perch, b) an age 4+, 2009–10 cohort, golden perch, c) an age 0+, 2010–11 cohort, golden perch and d) an age 0+, 2010–11 cohort, golden perch. Green dashed line indicates the $^{87}$Sr/$^{86}$Sr of the lower Darling River water(~0.7075–0.7076), blue dashed lines represent the range of $^{87}$Sr/$^{86}$Sr in the lower River Murray water (~0.7086–0.7147) and red dashed lines represent the range of $^{87}$Sr/$^{86}$Sr in the mid River Murray water (Lock 11 ~0.7160–0.7175).

## Discussion

### *Population demographics*

Data on population age structure are fundamental for fisheries management, including understanding how interventions, such as flow augmentation, influence populations (Berkley *et al*. 2004; Cowx and Van Zyll de Jong 2004). In 2010, the golden perch population in the lower River Murray was dominated (~70%) by a single age-class (4+ fish), That originated in association with a spring flow-pulse in the River Murray four years previously (late 2005). Although fish ranged in age from 0+ to 14+, the population was characterised by a depauperate age structure, with an absence of recruitment during an extended period (2001–2009) of drought (hereafter the 'Millennium Drought')(Van Djik *et al*. 2013; Zampatti and Leigh 2013a). Long-lived freshwater fishes with *periodic* life histories, like golden perch, characteristically demonstrate large inter-annual variation in recruitment, and distinct cohorts may dominate populations for many years (Winemiller 2005). In regulated rivers, hydrological alteration and fragmentation, can compromise the demographic resilience of species with periodic life history traits (Olden and Kennard 2010), and climate variability, including drought, may further exacerbate this impact (Bond *et al*. 2015). As such, the appearance of a cohort of age 0+ golden perch in early 2010, during the later stages of the Millennium Drought, and in association with unprecedented low flows in the River Murray, was unexpected and, at the time, the provenance of these fish was unclear (Zampatti and Leigh 2013a).

In subsequent years, several cohorts that emanated from years characterised by drought and overbank flooding, dominated the population (Zampatti and Leigh 2013b). Concurrently, older age classes declined and were absent by 2014. The mechanisms for this decline may include mortality and emigration. Golden perch can live for >20 years (Stuart 2006), so age-related mortality is unlikely, but anoxic blackwater during flooding in 2011 may have affected survival (Leigh and Zampatti 2013; Thiem *et al*. 2017). Recreational fishing mortality also occurs but has not been quantified in the River Murray. Reproductively mature golden perch migrate upstream in the River Murray and Darling River (Reynolds 1983; Mallen-Cooper 1999; Zampatti *et al*. 2018), and movement rates of freshwater fish may increase in association with higher flows (Albanese *et al*. 2004). Indeed, investigations of the abundance and size-structure of golden perch populations in the mid–upper reaches of the River Murray have shown an influx of larger, adult fish, post-flooding (Lyon *et al*. 2019). In association with a decrease in reproductively mature age-classes in the lower River Murray, this suggests that upstream movement during floods may have substantial influence on population structure in donor and receiving populations. Given the fundamental roles of survival and movement in determining population structure, rates of mortality and movement for golden perch in the River Murray represent essential knowledge.

### *Integrating water and otolith chemistry*

Spatial heterogeneity in water chemistry among rivers allowed the spatial origin and migration histories of fish to be determined. Catchment lithology and geological variation was sufficient to distinguish river water $^{87}Sr/^{86}Sr$ (Douglas *et al*. 1995; Gingele and De Deckker 2005), although the lower River Murray showed substantial variation in water $^{87}Sr/^{86}Sr$ over 4 years. Temporal variation in water $^{87}Sr/^{86}Sr$ is expected in rivers that receive inputs from heterogeneous sub-catchments or groundwater (Crook *et al*. 2013; 2016); nevertheless, $^{87}Sr/^{86}Sr$ in the lower River Murray in 2011–2014 (~0.7086–0.7147) was distinctly lower than the mid River Murray, primarily due to the influence of low $^{87}Sr/^{86}Sr$ water from the Darling River. Consequently, the lower and mid River Murray, and Darling River, exhibited distinctive isotopic signatures, and fish originating in, or moving between, these regions, were discernible based on otolith $^{87}Sr/^{86}Sr$.

Otolith chemistry revealed that golden perch from the lower River Murray were the progeny of spawning in either the River Murray or Darling River. Recruitment occurred during years characterised by within-channel rises in flow, in either river, or by extensive overbank flooding, across both catchments. Fish from the 2005–06 year class, when there was an in-channel rise in discharge in the River Murray, originated in the mid River Murray before transitioning to the lower River Murray. Relatively low otolith $^{87}Sr/^{86}Sr$ observed early in the fish's lives suggests a natal origin in the lower reaches of the mid River Murray (i.e. the Lock 11 region) and drifted as early-stage juveniles into the lower River Murray. During the same period, flows in the lower Darling River were negligible and unlikely to promote spawning and recruitment of golden perch.

From 2010 to 2014, golden perch from the 2009–10 year class formed the dominant cohort in the lower River Murray and these fish exhibited otolith core $^{87}Sr/^{86}Sr$ commensurate with a Darling River natal origin. In 2009–10, the River Murray was in the latter stages of the Millennium Drought (VanDijk *et al*. 2013), and low flows in the river were unlikely to promote golden perch spawning and recruitment (Zampatti and Leigh 2013a). In the Darling River, however, golden perch spawning was associated with a substantial increase in discharge (0 to 11,000 ML.day$^{-1}$). In early 2010, low abundances of 0+ golden perch (2009–10 cohort) were collected in the lower River Murray, but it was not until 2011 that these fish, as 1 year olds, contributed to a significant increase in golden perch abundance in this region (Zampatti and Leigh 2013b). All otolith $^{87}Sr/^{86}Sr$ transects from age 4+ (2009–10 cohort, $n$ = 5) golden perch collected in the lower River Murray in 2014, demonstrated a distinct transition from the Darling River to the River Murray at age 1+, indicating movement between these rivers in association with wide-spread flooding in the River Murray and Darling River in 2010–11.

Flooding in 2010–11, was also associated with an additional cohort of golden perch, that like 2009–10 cohort, contributed substantially to the lower River Murray age structure over subsequent years (Zampatti and Leigh 2013b). Otolith $^{87}Sr/^{86}Sr$ analysis of this cohort indicated two potential natal origins, the Darling River and the lower River Murray. For fish with a Darling River origin, transects of otolith $^{87}Sr/^{86}Sr$ showed a transition in $^{87}Sr/^{86}Sr$ early in the fish's life, indicative of movement from the Darling River to the River Murray. This suggests a lower Darling River natal origin and subsequent larval drift into the lower River Murray. The presence and progression of this cohort, in association with overbank flooding, accords with: 1) contemporary models of golden perch spawning and recruitment, whereby both flooding and in-channel flows may promote strong cohorts (Mallen-Cooper and Stuart 2003; Zampatti and Leigh 2013b), and 2) concepts of increased productivity and ecosystem response in floodplain rivers, corresponding with flooding (Puckridge *et al*. 1998).

### *Dispersal and movement*

This study demonstrates that the Darling River is an important source of golden perch to the lower River Murray, with fish dispersing from natal habitats either in the year of birth, as eggs and early stage juveniles, or at age 1+, in association with high flows (flooding) in the Darling River and River Murray. The dispersal of eggs and early stage juveniles is mediated by the hydraulic characteristics of flowing water. Worldwide, fishes with pelagic early life stages are disadvantaged by fragmentation and flow regulation, with obligate downstream drift of early life stages interrupted by the physical and hydraulic impacts of dams and weirs (Dudley and Platania 2007; Perkin *et al*. 2015). The lower Darling River is unconstrained by weirs and characterised by lotic habitats for 100s of kilometres, even under low discharges (e.g. 200 ML.day$^{-1}$). These conditions may facilitate the development of golden perch eggs and larvae to a juvenile stage that can then tolerate the lentic, weir pool environments of the lower River Murray (Mallen-Cooper and Zampatti 2018). Comparative hydraulic conditions are re-established in the weir-pool constrained lower River Murray at discharges exceeding ~20,000 ML.day$^{-1}$, a discharge that has been shown to be a potential threshold for golden perch spawning and recruitment in this region (Zampatti and Leigh 2013a)

Interactions between mainstem rivers and tributary streams are increasingly recognised as important determinants of riverine ecological function, particularly in regulated rivers where tributaries may retain native habitats and hydrological characteristics (Kiffney *et al*. 2006; Rice *et al*. 2008; Pracheil *et al*. 2013). For native fish populations, tributary spawning and rearing habitats, and mainstem-tributary movements, may confer benefits to mainstem fish populations and, in some cases, be integral to population persistence (Pollux *et al.* 2006; Pracheil *et al*. 2009). Certainly, in the case of golden perch in the southern MDB, population demographics in the lower River Murray are substantially influenced by interaction with the Darling River. The hydrological and hydraulic characteristics of the Darling River, and connectivity between the Darling River and lower River Murray, promote greater demographic resilience to golden perch populations in the lower River Murray than would occur if populations were dependent wholly on the River Murray. Rehabilitation of flow-impacted rivers will benefit from considering mainstem-tributary interactions and their influence on to the spatial structuring and dynamics of fish populations (Galat and Zweimuller 2001; Koster *et al*. 2014).

Whilst the importance of drift for early life stages (eggs and larvae) of riverine fish is increasingly considered (Lechner *et al*. 2016), the downstream movement of juvenile fish (e.g. age 1+ and 2+) has received less attention; although the downstream migration of juvenile diadromous salmonids (smolts) has been extensively studied (e.g. McDonald 1960; McCormick *et al*. 1998). In this study, the flood-mediated downstream movement of age 1+ golden perch from the Darling River had a substantial influence on population structure in the lower River Murray. Flooding has been shown to displace juvenile and small-bodied freshwater fish, and increase active movement, with subsequent impacts on assemblage structure (Albanese *et al*. 2004; Walton *et al*. 2017). Nevertheless, for iteroparous, potamodromous, non-salmonid fishes, there is a paucity of studies considering the flood-associated downstream dispersal of juvenile fish and the influence of these movements on receiving population dynamics (Kraabol *et al*. 2009). This process, which may be a fundamental driver of riverine fish population dynamics in large floodplain rivers, warrants further investigation.

### *Management implications and conclusions*

Knowledge of the demographics of populations, including variability through space and time, is essential to understanding the stability and resilience of populations (Winemiller 2005; Kerr *et al*. 2010). For many of the world's riverine fish, however, basic age structure data are deficient, thus impeding conservation (Reynolds *et al*. 2005). In Australia's MDB, contemporary demographic data for most riverine fishes has been lacking, and despite a motivation to improve native fish populations (Barrett 2004), demographic targets have not, until recently (e.g. Commonwealth Environmental Water Office 2016), formed part of population monitoring or management.

Critical to managing fish populations, is an understanding of the processes that determine population structure. In this study, we used the chemistry of otoliths as a natural tag to investigate natal origin and trace the movements of larval, juvenile and adult fish, an ontological approach not possible with traditional mark-recapture or telemetric techniques (Gillanders 2005). The findings of this study support Zampatti and Leigh (2013b) who suggested that a dominant cohort of golden perch in the lower River Murray, spawned during a drought, actually originated in the Darling River. They also support the premise that spawning and recruitment of golden perch in the lower River Murray does not generally occur in low spring–summer flow years (e.g. <15,000 $ML.d^{-1}$; Zampatti and Leigh 2013a). Nevertheless, conspicuous cohorts of golden perch in the lower River Murray, may align with low-flow years, due to immigration from disparate regions that have experienced appropriate hydrological conditions to promote spawning and recruitment. This complex structuring of populations, that incorporates spatio-temporal variability in population processes and associated environmental drivers, highlights the importance of considering the range of factors that may influence population structure (e.g. spawning, recruitment and movement), to effectively manage riverine fish populations.

In the Murray-Darling Basin, the movement of reproductively mature golden perch between river catchments has long been recognised (Reynolds 1983), and contemporary genetic studies indicate high rates of dispersal and genetic diversity (Faulks *et al*. 2010). Nevertheless, golden perch are traditionally managed as individual jurisdictional stocks. In concert with previous studies, the results of this study suggest that golden perch, at least in the southern MDB, need to be managed holistically as one meta-population (stock) over a large spatial scale (1000s km). Furthermore, whilst within-channel flow pulses and overbank floods may both promote golden perch recruitment (Mallen-Cooper and Stuart 2003; Sharpe 2011; Zampatti and Leigh 2013a), it appears that large-scale flooding is an important driver of population growth, facilitated by: 1) localised spawning and recruitment, and 2) dispersal of early life stages and juvenile fish (e.g. age 1+), from disparate regions.

Concepts of provenance and migration form essential questions for understanding population dynamics and the management of freshwater fishes (Kennedy *et al*. 2002; Brennan *et al*. 2015). Ultimately, to promote population persistence, research and management need to be undertaken at scales commensurate with population processes. This study has shown that integrating water and otolith $^{87}Sr/^{86}Sr$ enables determination of spawning regions and the age-related movement of a migratory, pelagic-spawning fish. This approach has broad utility for understanding the ecology and population dynamics of riverine fishes, and providing insight into the processes that structure populations, the scales over which these operate and associated environmental conditions.

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## Supplementary Material

Table S1. Golden perch used for otolith Sr isotope analysis to establish the provenance and migration history of three distinct age cohorts collected in the lower River Murray.

| Year class | Collection date | Age | Sample size (*n*) |
|---|---|---|---|
| 2005–06 | Nov–Dec 2005 | 0+ | 5 |
| | May 2007 | 1+ | 5 |
| 2009–10 | Mar–Apr 2010 | 0+ | 8 |
| | March 2014 | 4+ | 5 |
| 2010–11 | May 2011 | 0+ | 12 |

# CHAPTER 5: Multiscale movements of golden perch in the River Murray, Australia

**Please return tagged callop to the water**

In order to monitor the movement of native fish in response to water management, a number of callop from the Chowilla Anabranch have been implanted with radio tags.

Radio-tagged callop can be recognised by a trailing wire antenna and a small external coloured tag.

This logging station is one of six erected within the Chowilla anabranch system. The antenna can detect the radio signals emitted by the tags, and allows researchers to monitor fish movement.

If you catch a callop with a trailing antenna (as shown on the picture), **please return it to the water**, note its location and the date of capture and contact SARDI Aquatic Sciences on 1800 119 194

This research is being conducted by SARDI Aquatic Sciences, and is managed by the SA Department of Water, Land and Biodiversity Conservation with assistance from the SA Department of Environment and Heritage. Funding for the project is provided by the Murray Darling Basin Commission's Living Murray Environmental Works and Measures Program.

Keeping the public informed about our research

# Statement of Authorship

| | |
|---|---|
| Title of Paper | Multiscale movements of golden perch (Percichthyidae: *Macquaria ambigua*) in the River Murray, Australia |
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## Principal Author

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| Name of Principal Author (Candidate) | Brenton Zampatti | | |
| Contribution to the Paper | Designed study, collected and interpreted data, wrote manuscript and acted as lead and corresponding author | | |
| Overall percentage (%) | 80% | | |
| Certification: | This paper reports on original research I conducted during the period of my Higher Degree by Research candidature and is not subject to any obligations or contractual agreements with a third party that would constrain its inclusion in this thesis. I am the primary author of this paper. | | |
| Signature | | Date | 12/7/2019 |

## Co-Author Contributions

By signing the Statement of Authorship, each author certifies that:

i. the candidate's stated contribution to the publication is accurate (as detailed above);

ii. permission is granted for the candidate in include the publication in the thesis; and

iii. the sum of all co-author contributions is equal to 100% less the candidate's stated contribution.

| | | | |
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| Name of Co-Author | Sandra Leigh | | |
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# Multiscale movements of golden perch (Percichthyidae: *Macquaria ambigua*) in the River Murray, Australia

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**Abstract** Understanding the spatio-temporal characteristics of animal movement is integral to effective conservation and management. Golden perch (*Macquaria ambigua*) is a potamodromous species known to undertake long-distance movements, putatively in response to elevated flow in spring and summer. In this study, 52 adult golden perch from the lower River Murray were surgically implanted with radio transmitters and passive integrated transponder (PIT) tags, and tracked for 2 years. Strong site fidelity was common, with 19 fish (~36%) remaining at the site of capture throughout the study. This included a spawning season (spring-summer) and a period of elevated flow. Eighteen fish (35%) made small- to medium-scale (2 22 km) movements that included the establishment of new home sites. Fifteen fish (29%) migrated long distances (33 270 km) upstream in spring summer, coincident with steady, falling and rising flows. These movements were correlated with seasonal variation in mean daily water temperature, and to a lesser extent, short-term (10-day) flow variability, and did not coincide with spawning or recruitment during the year of migration. This contrasts previous studies that have associated long-distance movements of golden perch with increased flows and spawning. Upstream migration continued until passage was blocked by a weir, or fish were captured by anglers. Our results highlight the need for a broad spatio-temporal perspective when investigating the movement of long-lived potamodromous fishes, to integrate the range of behaviours exhibited by individuals and population contingents. We advocate that life history models that incorporate behavioural plasticity and a river-scale perspective will advance conservation.

**Key words:** fishway, freshwater fish, Murray Darling Basin, partial migration, PIT tag, radio-telemetry, river regulation.

## INTRODUCTION

Management and conservation of fishes require an understanding of life history and spatial ecology, including habitat use and patterns of movement (e.g. Nestler *et al.* 2008; Kraabøl *et al.* 2009; Cooke *et al.* 2016). Fish movements may range from small scales (e.g. tens to hundreds of metres) for habitat selection, accessing food resources and predator avoidance (Gowan & Fausch 2002; Koster *et al.* 2015), to basin-scale migrations (e.g. thousands of kilometres) for spawning and other life history processes (Schlosser 1991; Fausch *et al.* 2002). The spatio-temporal characteristics of movement may vary between individuals, contingents within a population (e.g. 'partial migration') and populations within a species (Leggett & Carscadden 1978; Kynard 1997; Secor 1999; Chapman *et al.* 2012). Consequently, conservation strategies will be most effective when informed by life history and population models that integrate knowledge obtained across a continuum of scales that are relevant to fish life histories (Fausch *et al.* 2002; Durance *et al.* 2006).

Golden perch, *Macquaria ambigua* (Richardson), is a large-bodied (up to 75 cm total length), long-lived (>25 years), iteroparous and potamodromous Percichthyid, native to the Murray Darling Basin (MDB), south-eastern Australia (McDowall 1996; Stuart 2006). Golden perch historically supported an extensive commercial fishery and continue to be a primary target for recreational fishers (Kaiola *et al.* 1993). In the last century, the range and abundance of the species have declined (Cadwallader 1978; Walker 1979; Brumley 1987), largely due to altered hydrological regimes and instream barriers to movement (Gehrke *et al.* 1995; Mallen-Cooper & Brand 2007). As such, golden perch represents a primary target species for contemporary environmental water management and fish passage restoration that aim to promote recruitment and movement to rehabilitate populations (Stuart *et al.* 2008; King *et al.* 2009; Koster *et al.* 2017). To be successful, such actions require knowledge of the movement ecology of this species across its range.

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Movements of golden perch are known to vary from strong home-range fidelity (Crook 2004a; Koehn & Nicol 2016) to large-scale up- and downstream migrations of thousands of kilometres (Reynolds 1983; O'Connor *et al.* 2005). The migratory nature of golden perch is well recognized (Allen *et al.* 2002; Barrett & Mallen-Cooper 2006), particularly the occurrence of long-distance upstream migrations in association with elevated river flow (Reynolds 1983). Nevertheless, data from the tag-recapture study of Reynolds (1983) indicate only 5% of recaptured fish moved >200 km upstream and 1% moved >1000 km. Furthermore, although long-distance movements in spring and early summer are proposed to be associated with spawning, and early life-stages of golden perch are collected in the river channel, data linking spawning with movement are rare (Reynolds 1983; O'Connor *et al.* 2005). More recently, however, Koster *et al.* (2017) associated golden perch movement with the spatio-temporal presence of eggs and larvae in a tributary of the River Murray.

Previous telemetric studies of the movement and habitat use of golden perch have been conducted in the lotic mid-reaches or tributaries of the River Murray and Darling River (e.g. Crook 2004a,b; O'Connor *et al.* 2005, 2006; Koster *et al.* 2014; Koehn & Nicol 2016; Marshall *et al.* 2016). None have been undertaken in the hydrodynamically distinct lower River Murray, where 10 low-level (3 m) weirs and five tidal barrages form serial impoundments over 830 km of river, from the Darling River confluence to the River Murray mouth (Walker 2006). These hydraulically distinct and fragmented reaches of the lower River Murray may modify fish behaviour and impede movement.

Telemetry is a useful method for monitoring fish movements (Lucas & Baras 2000; Jellyman 2009), but it can be logistically difficult and costly when applied at broad scales (Lucas & Baras 2001), thus may limit the spatial and temporal scope of a study. Combinations of techniques may provide more extensive coverage and yield more accurate data to inform models of population dynamics (Bridger *et al.* 2001; Lowe 2003; Gilroy *et al.* 2010). This study employed radio-telemetry and PIT tags to investigate the movements of adult golden perch in anabranch and main channel habitats of the lower River Murray. The objectives of the study were to (i) describe the movement patterns of golden perch in relation to flow and season in the serially impounded lower River Murray, and (ii) contrast these to movement patterns observed in previous studies in the lotic reaches of the mid River Murray. We expected that golden perch would display individual variability in movement behaviours ranging from site fidelity to long-distance migration. When long-distance movements did occur (upstream and/or downstream), we expected that this behaviour would be associated with increased river flow in spring/summer.

## Study area

The Murray Darling Basin (MDB) extends over 1 073 000 km$^2$ and the combined length of the two major rivers is ~5500 km. The Basin is largely arid to semi-arid, and in a global context, runoff and discharge generally are low, but highly variable (Puckridge *et al.* 1998). Flows in the system are regulated by diversions and headwater dams, weirs, offstream regulators, floodplain levees and river-mouth barrages, and on average only ~36% (4915 GL) of the natural mean annual discharge (12 300 GL) now reaches the sea (Walker 2006). The lower River Murray extends from the Darling River confluence to the river mouth and is dominated by a series of 10 low-level (3 m) weirs, constructed in 1922 1936, that form contiguous lentic weir pools (29 88 km long) (Walker 2006) (Fig. 1). Each weir incorporates a lock to facilitate boat passage, and the lock and weir structures in combination are generally referred to as 'Locks'. Since 2002, the weirs have progressively been retrofitted with fishways that effectively facilitate the upstream passage of the whole migratory fish community, including golden perch (Barrett & Mallen-Cooper 2006; Stuart *et al.* 2008).

Golden perch movement was investigated in the River Murray channel and in the Chowilla Anabranch system (hereafter 'Chowilla'), adjacent to Lock 6, about 620 river-km from the river mouth (Fig. 1). Chowilla is a diverse complex of creeks, backwaters, billabongs and lakes situated in the 'floodplain' geomorphic region of the lower River Murray, South Australia (O'Malley & Sheldon 1990). Due to the 3-m head differential created by the weir at Lock 6, up to 90% of low flows (<10 000 ML day$^{-1}$) are diverted through Chowilla, maintaining permanent lotic habitats in a region where these have become rare. Chowilla is part of a *Wetland of International Importance* under the 1971 Ramsar Convention and is recognized as an *Icon Site* under the Murray Darling Basin Authority's (MDBA) *The Living Murray Program* (TLM) (MDBA 2016). Nevertheless, the region has been degraded by changes to the river flow regime, salinization, overgrazing and drought. Management interventions including environmental watering, offstream weir construction to aid artificial floodplain inundation, and mitigation of barriers to fish movement, have been implemented to address declines in native fish species in the region (MDBC 2016).

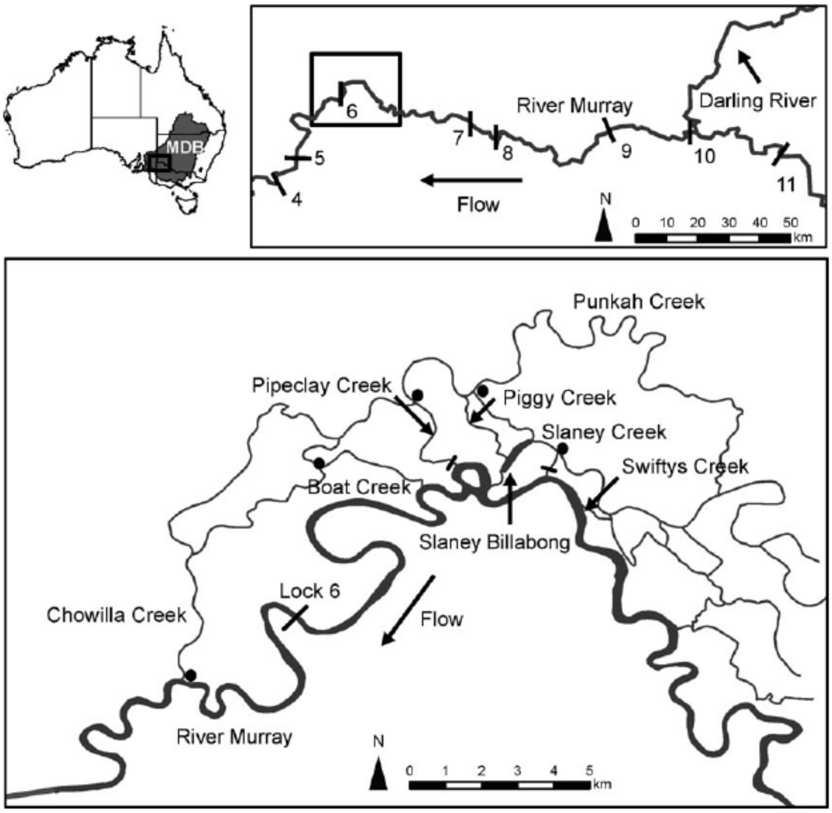

**Fig. 1.** The Murray Darling Basin (MDB), the lower River Murray (downstream of the Darling River junction) and Lock 4 11. Inset depicts the Chowilla Anabranch system bypassing Lock 6. Closed black circles indicate the locations of the fixed radio telemetry logging stations.

## MATERIALS AND METHODS

### Transmitters and PIT tags

Radio transmitters implanted into golden perch were cylindrical, 150 MHz, with a 30 cm (0.7 mm diameter) trailing antenna (Advanced Telemetry Systems (ATS), Insanti, MN, USA). Two transmitters were used: models F1840 and F1845, weighing 14 and 21 g, respectively, in air, with warranted battery lives of 260 and 300 days respectively. Model selection was based on maintaining a transmitter to fish weight ratio of 2% (Jepsen *et al.* 2002). Battery lives were maximized by incorporating a 43% duty cycle of 9 s 'on' and 12 s 'off'. Transmitters were fitted with a 'mortality' circuit, activated if the transmitter (fish) did not move for >8 h.

Unlike battery powered radio transmitters, passive integrated transponder (PIT) tags are not limited by battery life and are a complementary means for monitoring fish movements, particularly passage at fishways. Thus, combined use of battery powered radio transmitters and PIT tag technology was applied in this study to investigate fish movement and behaviour over broad spatial and temporal scales. PIT tags were Texas Instruments RI TRP REHP half duplex eco line glass transponders (23.1 mm long, 3.85 mm in diameter, 0.6 g in air).

### Fish capture and tag implantation

A total of 52 mature golden perch (395 ± 29 mm TL, 874 ± 219 g [mean ± SD], 6.4:1 [female:male]) were captured in August 2005 ($n = 38$) and May July 2006 ($n = 14$) using a Smith Root® 7.5 kVA boat mounted electrofishing unit. Fish were collected from the lower reaches of Chowilla Creek between the Murray confluence and Pipeclay Creek, a distance of about 12 km (Fig. 1).

The fish were anaesthetized using 0.75 mL of Alfaxan (Jurox, Rutherford, NSW, Australia) per 10 L of river water. The length ($L_T$, mm) and weight (g) of individuals was measured before fish were inverted onto a V shaped cradle and the gills irrigated with a 50% solution of Alfaxan. A 2 3 cm incision was made through the ventral wall, slightly above the mid ventral line, beginning adjacent to the pelvic fin and extending towards the anus. The sex of the fish was determined by visual examination of the gonads and a transmitter inserted into the abdominal cavity. A shielded needle technique (Adams *et al.* 1998) or plastic catheter was used to guide the trailing antenna through the lateral body wall posterior to the incision, and the incision was closed with two internal and three external sutures. The dorsal musculature was then injected with 0.1 mL kg$^{-1}$ of antibiotic (Baytril®: Bayer Australia, Pymble, NSW, Australia). A PIT tag was inserted in the dorsal

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musculature forward of the dorsal fin and a dart tag (PDL or PDXL: Hallprint, Victor Harbor, SA, Australia) was positioned between the dorsal pterygiophores to enable external visual identification and reporting by anglers. Following recovery, fish were released at their capture location.

### Fish tracking

Five fixed logging stations (ATS radio receiver/loggers) were installed on major tributaries of Chowilla Creek and its junction with the River Murray (Fig. 1). Each fixed logging station constantly scanned preprogrammed radio tag frequencies. Three Yagi antennas were positioned on each station: one upstream, one downstream and one in the direction of the tributary. The presence of a tagged fish in the vicinity of an antenna was recorded automatically as a frequency (Fish ID), antenna number, date and time, and signal strength, indicating the direction of movement.

Golden perch were also tracked manually by boat every 2 4 weeks between August 2005 and August 2007, using a three element Yagi antenna and an ATS radio receiver/logger (model RC4500C). Regular tracking was undertaken throughout the Chowilla anabranch system and up to 20 km upstream and downstream of Lock 6 in the River Murray. On occasion, individuals were manually tracked as far as 83 km upstream of Lock 6 (i.e. Lock 7). Radio signals could be detected from approximately 600 m, and once a fish was detected, the area of greatest signal strength was located and recorded by GPS. Trials with hidden transmitters indicated that they could be located consistently to within 2 $m^2$.

Broader upstream movements of fish that exited Chowilla were identified by interrogating data from PIT tag reader systems on fishways at Lock 7 10 on the River Murray (Barrett & Mallen Cooper 2006; Fig. 1). At the time of the study, Lock 11 did not include a fishway and was impassable to golden perch (other than via the navigation lock itself).

Movements were categorized based on the total linear range (i.e. distance (river km) between the most upstream and downstream locations for each individual fish) and macrohabitats (i.e. main river channel, anabranch creeks or backwaters) occupied during the 24 month study.

### Data analysis

To test the premise that emigration from Chowilla and long distance movement would be associated with increasing flow in spring/summer, relationships between the initiation of long distance movement and potential environmental drivers were assessed using Generalized Linear Mixed Models and Template Model Builder (glmmTMB, October 26, 2017) (Brooks *et al.* 2017) in R version 3.4.2 (2017 09 28). Individuals were deemed to have initiated a 'long distance movement' when they were detected moving from home ranges and exiting Chowilla by remote logging stations, and were subsequently detected upstream in the River Murray by manual tracking and/or on PIT readers at Locks 7 10.

The GLMMs were fitted using maximum likelihood and the Laplace approximation, and a binomial distribution with a log link. Individual tagged Fish ID was assigned as a random effect to account for behavioural variability between tagged individuals. Explanatory variables included in the GLMMs were: (i) day of year (Julien day); (ii) season; (iii) mean daily Chowilla Creek water temperature (°C); and (iv) flow, which was represented in the GLMMs in four different ways. Firstly, parameters were included for River Murray and Chowilla Creek flow. Secondly, flow at each location was represented as mean daily flow and per cent change in daily flow (i.e. average daily flow over the previous 5 days as a percentage of the average daily flow over the previous 10 days). Flow and water temperature data for analyses were sourced from hydrographic monitoring stations in Chowilla Creek (A4260535 and A4261091) and the River Murray (A4261001) www.waterconnect.sa.gov.au).

Candidate models, including the dependent variable of initiation of movement (emigration) were fitted with combinations of explanatory variables, ranging from the full model with all predictors included, to single term fits. Model fits and their Akaike information criteria (AIC) were compared to those of the null model, for example, $\sim 1 + 1 \mid$ Fish ID. Final model selections (eight candidate models) were based on the magnitude of differences ($\Delta$AIC) between the null model and the best model fit with the smallest AIC (Burnham & Anderson 2002; Zuur *et al.* 2009).

## RESULTS

### Movement patterns

Data on the individual movement patterns of the 52 tagged fish were collected over 96 680 days (mean ± SD: 418 ± 145 days) between August 2005 and August 2007. There was no evidence of mortality immediately post-tagging, but the tags of two fish commenced emitting mortality signals at 246 and 392 days post-tagging (Table 1). Given the time that had elapsed since tagging, we suggest this was most likely due to tag rejection, or potentially natural mortality.

Movements by golden perch over the study period could generally be grouped into three distinct categories:

1. Site fidelity within Chowilla (total linear range 0 2 km),
2. Small- to medium-scale movements within Chowilla and the adjacent River Murray (total linear range 2 22 km), and
3. Long-distance unidirectional movements upstream in the River Murray (total linear range 33 270 km).

Most (94%, $n = 49$) golden perch exhibited site fidelity and limited movements for periods of 2

**Table 1.** Biological and movement details for the 52 golden perch tracked in this study. Fish are grouped into three movement types: 1) site fidelity (F), 2) small medium distance (S M), and 3) long distance (L D). Sex: male (M), female (F). Fate at the end of the study: living (L), captured by an angler (A), mortality signal (M), missing (MI)

| Movement type (F, S M, L D) | Total linear range (km) | Length (mm) | Weight (g) | Sex | Time at liberty (days) | Fate (L, A, M, MI) |
|---|---|---|---|---|---|---|
| F | 0.00 | 432 | 1168 | M | 336 | L |
| F | 0.00 | 364 | 658 | F | 605 | L |
| F | 0.00 | 362 | 572 | F | 680 | L |
| F | 0.11 | 429 | 959 | F | 393 | L |
| F | 0.12 | 379 | 700 | F | 420 | L |
| F | 0.13 | 387 | 732 | F | 510 | L |
| F | 0.14 | 415 | 1014 | F | 337 | L |
| F | 0.28 | 446 | 1299 | F | 540 | L |
| F | 0.50 | 397 | 742 | F | 392 | M |
| F | 0.55 | 355 | 570 | F | 420 | L |
| F | 0.60 | 449 | 1206 | F | 359 | L |
| F | 0.62 | 420 | 1015 | F | 671 | L |
| F | 0.66 | 407 | 901 | F | 143 | MI |
| F | 1.00 | 351 | 648 | F | 360 | L |
| F | 1.00 | 409 | 940 | M | 603 | L |
| F | 1.10 | 384 | 818 | F | 622 | L |
| F | 1.16 | 376 | 780 | F | 483 | L |
| F | 1.25 | 370 | 780 | F | 358 | L |
| F | 1.40 | 450 | 1308 | F | 246 | M |
| S M | 2.28 | 410 | 950 | M | 673 | L |
| S M | 2.40 | 380 | 735 | F | 392 | L |
| S M | 3.00 | 390 | 745 | F | 533 | L |
| S M | 3.47 | 400 | 873 | F | 358 | L |
| S M | 4.85 | 387 | 813 | F | 393 | L |
| S M | 5.17 | 367 | 669 | F | 510 | L |
| S M | 7.35 | 373 | 724 | F | 121 | A |
| S M | 7.60 | 360 | 591 | F | 547 | L |
| S M | 7.80 | 485 | 1754 | M | 358 | L |
| S M | 8.20 | 381 | 749 | F | 426 | L |
| S M | 10.22 | 365 | 659 | F | 536 | L |
| S M | 10.70 | 367 | 865 | F | 154 | L |
| S M | 13.07 | 395 | 828 | F | 545 | L |
| S M | 14.47 | 393 | 822 | F | 515 | L |
| S M | 16.10 | 394 | 897 | F | 220 | MI |
| S M | 18.10 | 385 | 824 | M | 547 | L |
| S M | 21.20 | 396 | 1031 | F | 186 | L |
| S M | 21.50 | 397 | 947 | F | 467 | A |
| L D | 33.20 | 357 | 641 | F | 551 | A |
| L D | 81.75 | 408 | 941 | F | 464 | L |
| L D | 92.80 | 354 | 634 | F | 402 | L |
| L D | 149.15 | 396 | 915 | F | 414 | L |
| L D | 150.30 | 360 | 666 | F | 474 | L |
| L D | 151.35 | 382 | 786 | F | 96 | L |
| L D | 153.85 | 381 | 835 | F | 452 | L |
| L D | 155.00 | 397 | 769 | F | 468 | L |
| L D | 191.30 | 400 | 895 | F | 402 | L |
| L D | 199.40 | 400 | 930 | F | 302 | L |
| L D | 208.60 | 423 | 1025 | | 307 | L |
| L D | 214.26 | 422 | 1081 | M | 359 | A |
| L D | 264.50 | 380 | 790 | F | 496 | A |
| L D | 266.00 | 421 | 1041 | M | | A |
| L D | 271.60 | 438 | 1216 | F | 173 | A |

24 months. Continued site fidelity (i.e. residency) was exhibited by 19 golden perch, which moved <2 km from their release location throughout the study period (Table 1 and Fig. 2a). Site fidelity was also characteristic of fish prior to and/or following small- to medium-scale movements within Chowilla

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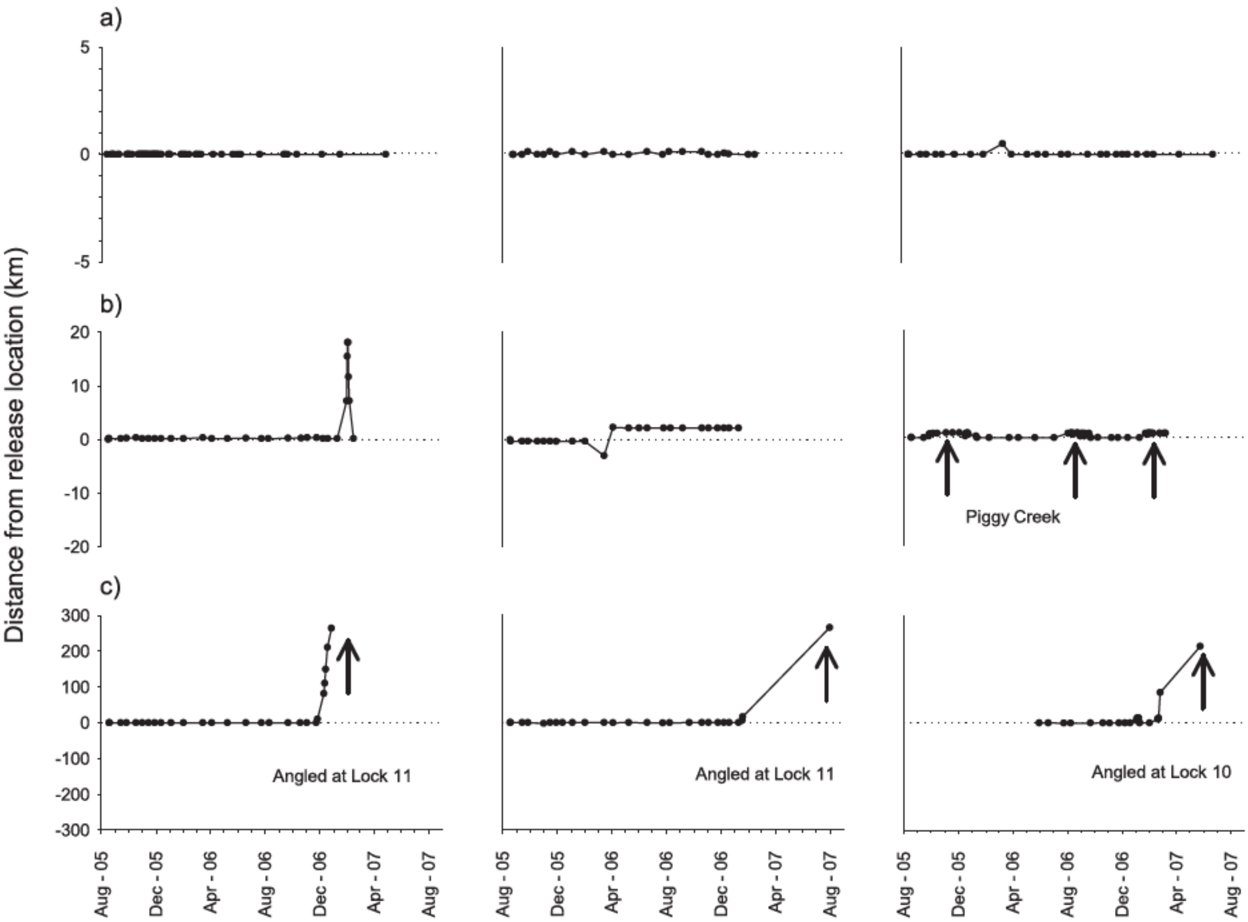

**Fig. 2.** Examples of radio and PIT tagged golden perch movements within the Chowilla Anabranch system and lower River Murray from August 2005 August 2007. The nine examples characterize three patterns: (a) site fidelity/residency to capture sites in Chowilla Creek, (b) small (2 10 river km) and medium scale (10 22 river km) exploratory/ranging movements within the Chowilla Creek system and the River Murray, and (c) long distance (33 270 river km) unidirectional migration out of the Chowilla Anabranch system and up the River Murray.

or between Chowilla and the River Murray, and prior to long-distance movements upstream in the River Murray (e.g. Fig. 2b,c).

Eighteen fish made small-scale (2 10 km) movements within Chowilla or medium-scale (10 22 km) movements between Chowilla and the River Murray (Table 1 and Fig. 2b). Small-scale movements (*n* = 10) often occurred on single occasions and followed residency at a site in Chowilla Creek, and either a return to this site (*n* = 5) or new residency elsewhere in Chowilla Creek or its tributaries (*n* = 5) (e.g. Fig. 2b). Medium-scale movements (*n* = 8) involved fish moving down Chowilla Creek into the River Murray downstream of Lock 6 (Fig. 1). These fish either moved upstream in the River Murray and ascended an old submerged-orifice fishway at Lock 6 (the new vertical-slot fishway was yet to be constructed) or returned to Chowilla Creek before then moving upstream though the anabranch system and into the River Murray above Lock 6.

Four fish moved into two tributaries of Chowilla Creek (Boat and Piggy creeks) and a backwater (Slaney Billabong) during a sustained 3-month increase in discharge (5000 14 000 ML day$^{-1}$) and river stage (+0.7 m) in spring summer 2005. Following the recession of flow, these four fish continued to move between these habitats and Chowilla Creek (e.g. Fig. 2b).

## Long-distance movements

Fifteen golden perch moved out of Chowilla (via Chowilla and Slaney creeks) and up the River Murray, above Lock 6 (Fig. 1). These fish continued to move upstream until they were caught by anglers (*n* = 5), predominantly in the tailwater of Lock 10 or 11 (e.g. Fig. 2c), or their passage was blocked at Lock 11 located at Mildura, Victoria. Lock 11 is 265 river-km upstream of Lock 6 and at the time of this investigation, lacked a fishway. The mean speed of upstream movement was 0.50 ± 0.19 km h$^{-1}$ (*n* = 13). No return downstream movements were detected by remote logging stations, manual radio-tracking or PIT readers on fishways during the period of this study.

There was no difference (Student's $t = 0.28$, df = 50, $P = 0.39$) between the mean sizes ($L_T$) of fish that undertook long-distance upstream movements and those that remained at Chowilla. Furthermore, the ratio of males to females that moved upstream (2:12) and those that remained at Chowilla (6:31) were similar.

The model best explaining initiation of long-distance upstream movement of radio-tagged golden perch ($\Delta$AIC = 11.3) included the explanatory variables, day of year (coeff = 0.005, $P = 0.031$) and mean daily Chowilla Creek water temperature (coeff = 0.264, $P = 0.005$) (Table 2). Movements out of Chowilla and upstream in the River Murray were undertaken by fish during the austral summer in 2005 2006 and through late spring summer in 2006 2007, and despite water temperature varying 10 27°C across the study, upstream movements only occurred at temperatures >17°C (Fig. 3). The next best model ($\Delta$AIC = 9.5) included day of year, mean daily water temperature in Chowilla Creek and per cent change in daily flow in Chowilla Creek indicating that short-term (days weeks) flow variability was also associated with migration. For those fish migrating from Chowilla, per cent change in flow ranged −6 +7% demonstrating movement in association with increasing, decreasing and relatively stable flow (Fig. 3).

## DISCUSSION

Adult golden perch displayed movement types that could be assigned to three categories: (i) site fidelity characterized by small-scale (<2 km) bidirectional activity, (ii) small- to medium-scale bidirectional movements (2 22 km) including potential exploratory behaviour and the establishment of new home ranges, and (iii) rapid, unidirectional, long-distance movements (33 270 km). These movements may correspond to *foraging*, *ranging* and *migration* (Dingle & Drake 2007) and during the course of our study some golden perch displayed all three behaviours. Importantly, the approach of using both radio transmitters and PIT tags enabled the elucidation of these multiscale movements that would have otherwise been unresolved with the use of single methods. We, therefore, advocate the use of multiple techniques, across appropriate temporal scales, to investigate the movement and population dynamics of fishes across riverscapes (Fausch *et al.* 2002).

Extended periods of site fidelity are common among freshwater fishes, even those that display long-distance spawning migrations (e.g. Colorado pikeminnow, *Ptychocheilus Lucius*) (Irving & Modde 2000). Limited movement and site fidelity are characteristic traits of golden perch in the mid-reaches of the River Murray and its tributaries (Crook 2004a; O'Connor *et al.* 2005; Koehn & Nicol 2016) and in the current study, nearly all golden perch exhibited site fidelity and limited movements for periods of 2 24 months. Indeed, 19 fish maintained their home site throughout the time their tags were active, which included a spawning season (spring summer) and a small flow pulse in spring/early summer (2005 2006).

Ten fish that initially exhibited site fidelity and occupied small home ranges undertook small- and medium-scale movements and subsequently returned to their original range or, alternatively, selected new sites. The movements of these fish were consistent with a 'home-range shift' (HRS) model (Crook 2004b), and

**Table 2.** Model selection results comparing the effects of explanatory environmental variables on the initiation of long distance movements (i.e. emigration from Chowilla) of individual golden perch (FISH ID). The top ranked model (lowest AIC compared to null model, greatest $\Delta$AIC) is shown in boldface. Variables in the models were represented by: DOY = day of year, SEAS = season, TEMP CHOW = mean daily water temperature in Chowilla Creek, %CHFLOW RM = percentage change in flow in River Murray (average daily flow over the previous 5 days as a percentage of the average daily flow over the previous 10 days), %CHFLOW CHOW = percentage change in flow in Chowilla Creek

| Model | AIC | ΔAIC | Deviance | Log likelihood |
|---|---|---|---|---|
| Null model | 182.1 | | 178.1 | −89.0 |
| **DOY* + TEMP-CHOW** + FISH-ID** | **170.8** | **11.3** | **162.8** | **−81.4** |
| DOY* + %CHFLOW CHOW + TEMP CHOW** + FISH ID | 172.6 | 9.5 | 162.6 | −81.3 |
| DOY* + %CHFLOW RM + TEMP CHOW** + FISH ID | 172.8 | 9.3 | 162.8 | −81.4 |
| SEAS + TEMP CHOW** + FISH ID | 173.3 | 8.8 | 165.3 | −82.7 |
| DOY + %CHFLOW RM* + %CHFLOW CHOW + TEMP CHOW** + FISH ID | 174.5 | 7.6 | 162.5 | −81.2 |
| SEAS + %CHFLOW RM + TEMP CHOW** + FISH ID | 175.1 | 7.0 | 165.1 | −82.6 |
| SEAS + %CHFLOW CHOW + TEMP CHOW** + FISH ID | 175.1 | 7.0 | 165.1 | −82.6 |
| SEAS + %CHFLOW RM + %CHFLOW CHOW + TEMP CHOW** + FISH ID | 177.1 | 5.0 | 165.1 | −82.5 |

*The significant variables in each model, where ** = $P < 0.01$ and * $P < 0.05$.

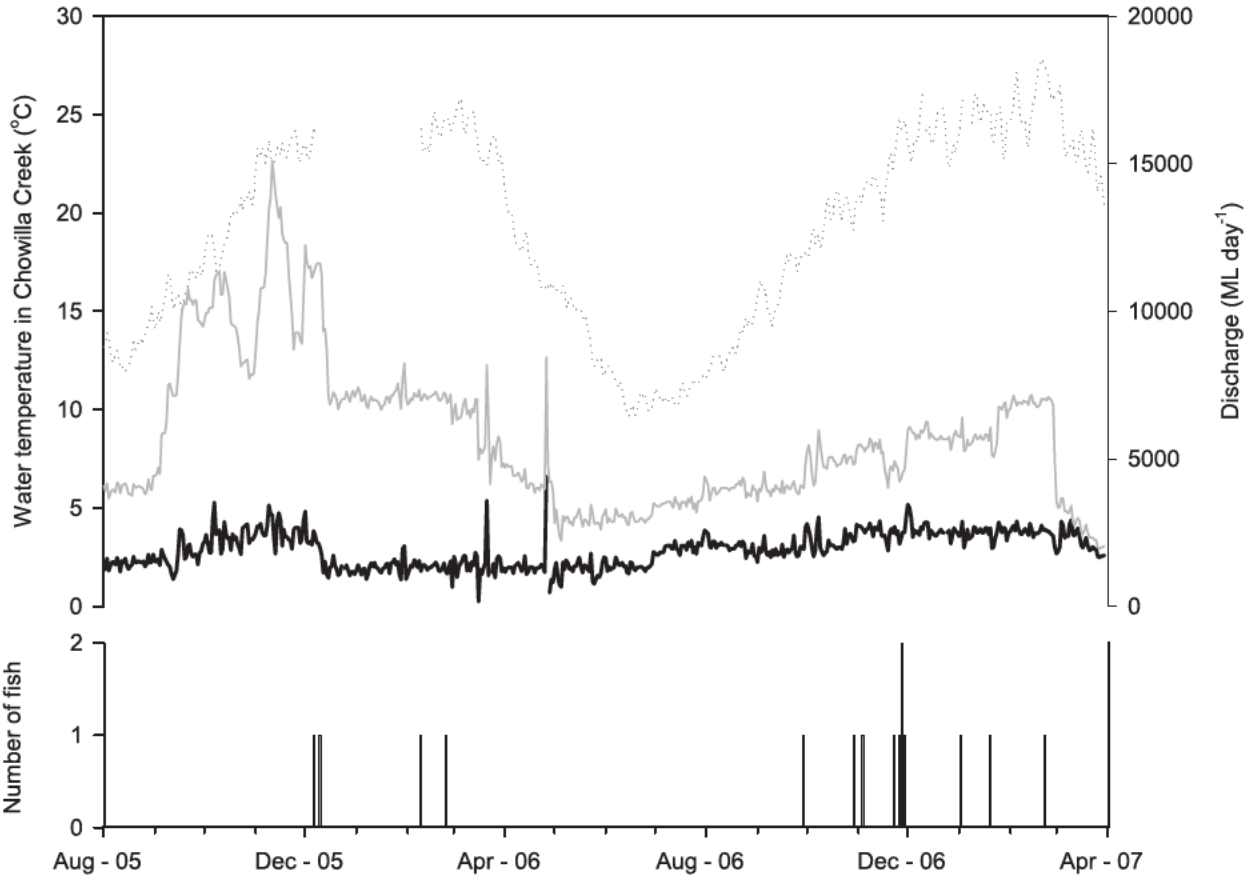

**Fig. 3.** Timing of upstream movement of golden perch out of the Chowilla Anabranch system and into the River Murray with mean daily water temperature (°C) in Chowilla Creek (dotted line), discharge (ML day$^{-1}$) in the Murray (grey line) and discharge in Chowilla Creek (black line) August 2005 April 2007.

were potentially driven by the 'profitability' of habitats encountered elsewhere.

A subset of these fish ($n = 4$) exhibited more complex movement behaviour, alternating between various locations within the Chowilla system (e.g. Piggy Creek and Slaney Billabong) at which they exhibited limited movement over periods of weeks to months. Such behaviour suggests that some golden perch may exhibit fidelity to a broad area comprised of a complex of distinct home sites among which they repeatedly move. Similar patterns have been documented for Macquarie perch (*Macquaria australasica*) in a lentic reservoir environment (Ebner *et al.* 2011). In concert with the results from our study, these observations potentially expand the HRS model to include cyclical movements among several distinct home ranges as opposed to unidirectional movement between two home ranges or return to the original home range. Alternatively, as suggested by Ebner *et al.* (2011), fish may not be *shifting* home ranges, but instead using a complex of core habitats within a broader home range. Regardless, the temporal scale of measurement is crucial to elucidating this behaviour (Hilderbrand & Kershner 2000; Crook 2004a). For example, short-term studies (i.e. months) may interpret this behaviour as a unidirectional shift between home ranges, whereas studies conducted over longer periods (i.e. years) may elucidate the presence of a complex of core habitats which constitute a broad 'home range'. Characterization of these patterns is essential for the spatial management of fishes.

Changing environmental conditions may stimulate exploratory behaviour (ranging), enabling fish to opportunistically discover more profitable locations in the riverscape (Barraquand & Benhamou 2008; Louca *et al.* 2008). Golden perch that ventured into fast-flowing secondary creeks (e.g. Boat Creek) and backwaters (e.g. Slaney Billabong) in late 2005 early 2006 did so in association with small increases in discharge and water level, making new habitats and resources accessible. Newly inundated littoral zones could provide alternative feeding opportunities including easier access to decapod crustaceans, an important prey for golden perch (Baumgartner 2007). Such movements, however, are not without

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risk, and accessing resources at novel sites may require individuals to trade-off the security of a known site with the potential risk of increased mortality (Brodersen *et al.* 2008). Consequently, changing environmental conditions and the availability of resources may contribute to heterogeneity in individual behavioural responses.

The high proportion of fish exhibiting localized movements, including site fidelity, home-range shift and ranging, appears unusual for a species that by reputation, is considered migratory. Previous studies with tags (Reynolds 1983) or in fishways (Mallen-Cooper 1999) have tended to highlight the migratory individuals, but contemporary movement models for golden perch suggest a range of behaviours (Koehn & Crook 2013). Individual variation in movement is a common characteristic of riverine fishes (Lucas & Baras 2001; Chapman *et al.* 2012), and like many other freshwater fishes, golden perch populations may also include less mobile or nonmigratory contingents. This is indicated by our results and has been demonstrated for golden perch in an intermittent dryland river in the northern MDB (Marshall *et al.* 2016).

All golden perch that exited Chowilla in an upstream direction and entered the River Murray (29% of tagged fish) did so following the same route, despite the presence of multiple alternative pathways. In varied hydrodynamic environments, migrating fish navigate using complex hydraulic cues (e.g. spatial velocity gradients; Nestler *et al.* 2008), and in the current study, the route chosen by out-migrating golden perch followed the path of greatest discharge and water velocity (DEWNR, unpublished data). Consequently, manipulation of discharge (e.g. by weir operations), through creeks in Chowilla and elsewhere in the MDB, may influence the route taken by migrating fish.

Golden perch undertaking long-distance upstream migrations moved as far upstream as possible in the River Murray before encountering Lock 11, which lacked a fishway at the time of this study. Rates of movement were rapid and comparable to those observed by O'Connor *et al.* (2005) in the middle reaches of the River Murray, suggesting that fish were undertaking a more purposeful movement than simple ranging. The fish accumulated in the tailwater at Lock 11 and were subject to substantial angling mortality (cf. Gehrke *et al.* 2002). Movement is inherently risky and may increase the incidence of individual mortality (Alerstam *et al.* 2003). In anthropogenically modified rivers, this risk is exacerbated by regulating structures (e.g. dams and weirs) that impede movement, thus delaying migration and increasing the incidence of angler-induced mortality. Impacts on the individual can have population level outcomes, and for golden perch, barriers to movement are considered a primary cause of population decline (Lintermans 2007). Effective fish passage that minimizes migratory delay may assist in mitigating these impacts and assist in rehabilitating fish populations (Castro-Santos & Haro 2003).

Radio-tagged golden perch in the middle reaches of the Murray undertake long-distance up- and downstream movements in spring, in association with within-channel increases in flow (5000 25 000 ML day$^{-1}$), while large numbers of adults commonly move upstream through fishways (Mallen-Cooper 1996; O'Connor *et al.* 2005). These movements are generally considered to be spawning related (Reynolds 1983; Mallen-Cooper 1996; O'Connor *et al.* 2005), as golden perch spawn pelagic eggs in the river that hatch as drifting larvae in spring summer, when there are warmer water temperatures and increased flow (Lake 1967; King *et al.* 2009; Zampatti & Leigh 2013).

While our modelling results support the notion of increased movement during spring/summer, when water temperatures are elevated, there was limited evidence of elevated discharge stimulating movement. Indeed, long-distance upstream movements were initiated during periods of both stable low flow and small in-channel flow pulses. Furthermore, these movements occurred post the collection of larval golden perch in the lower River Murray in 2005, and in 2006 when no larval golden perch were collected and recruitment of a young-of-year cohort was absent (Zampatti & Leigh 2013). Consequently, seasonal long-distance upstream movements of golden perch may not necessarily be associated with spawning, at least in the short term (i.e. the year of movement).

Stimuli for fish migration are diverse and often species-specific, and may include both external (i.e. environmental) and endogenous factors (cf. McMahon & Matter 2006). While our study suggests, in concurrence with others (e.g. O'Connor *et al.* 2005), that golden perch movements are more likely at certain times of year and at water temperatures above a threshold, this temporal period is broad (September February). Additionally, while there was some support for flow variability (not flow magnitude) contributing to initiation of migration, this was minor in the context of the overall hydrological regime (Puckridge *et al.* 1998). As such, we found little evidence of migrations being stimulated by fine temporal scale environmental cues. This does not preclude environmental factors being associated with migration, but raises the question of potential endogenous cues (e.g. sexual maturity/age). Both males and females undertook long-distance movements, and there was no difference in mean size ($L_T$) between migratory and nonmigratory individuals. This does not exclude possible age differences, however, as length is an unreliable indicator of age, and hence sexual maturity in

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golden perch (Anderson *et al.* 1992). The role of endogenous factors in promoting long-distance upstream migrations of golden perch awaits further research.

Long-distance upstream movements were not accompanied by corresponding downstream homing movements, unlike migratory golden perch in the free-flowing middle reaches of the Murray (O'Connor *et al.* 2005). While anglers caught five upstream migrants, the remaining 10 upstream migrants were not subsequently detected downstream during the course of the study. Low-level weirs (~3 8 m) can constitute an obstacle to the downstream homing movements of fishes (Ovidio & Philippart 2002), and has been demonstrated for golden perch in the mid River Murray (O'Connor *et al.* 2006). In the lower River Murray in particular, serial weirs may form a substantial impediment to the downstream movement of fishes, and while the construction of fishways on these weirs has facilitated the upstream movement of migrating fish (Barrett & Mallen-Cooper 2006), they provide limited downstream passage (Baumgartner *et al.* 2014). As such, the fate of downstream migrants and the facilitation of bidirectional fish passage warrant further investigation.

The River Murray is over 2500 km long and the impacts of river regulation vary along its length (Walker 1985, 2006). Our data and previous studies suggest that the movement patterns of golden perch may also vary within and among regions of the MDB. Flexible behaviour is common in freshwater fishes, and is well documented for northern hemisphere salmonids, pike (*Esox lucius*) and sturgeon (Lucas & Baras 2001; Hodder *et al.* 2007; Watry & Scarnecchia 2008). Indeed, *partial migration*, or the existence of contingents with various migration strategies, is recognized in many species of freshwater fishes (Chapman *et al.* 2012). Such strategies enable species and populations to persist in variable environments by buffering the effects of adverse environmental conditions and promoting resilience. In the highly regulated MDB, the occurrence of a range of migration strategies in golden perch populations may well promote some level of population maintenance in a hydrologically homogenized and anthropogenically fragmented environment.

To be effective, conservation strategies for golden perch should be underpinned by life history models that account for the spatio-temporal variability observed in behaviour, including site fidelity, exploratory movements and home-range shift, potential large-scale spawning migrations and homing behaviour, and large spatial-scale emigration. Of merit would be further research that investigates the abiotic and biotic drivers of movement behaviour. This knowledge would also strengthen the conceptual underpinnings of contemporary population dynamics models, a fundamental tool for conservation and management (Shenton *et al.* 2012; Bond *et al.* 2015)

Ultimately, species conservation relies on an understanding of the processes that drive population dynamics. As such, it is imperative to understand the spatio-temporal scale of the life history of fish, and design and implement management strategies at these scales (Fausch *et al.* 2002; Kraabøl *et al.* 2009). The high spatio-temporal variability in golden perch behaviour and movement emphasizes the potential need for river-scale approaches to the management of migratory fishes, at scales that are relevant to the life histories of fish and not constrained by human perspectives of artificially delineated sites or state boundaries.

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# CHAPTER 6: General Discussion

A new generation: age 0+ golden perch collected in the lower River Murray

# General Discussion

Striking a balance between water security for human needs and the maintenance of aquatic ecosystem integrity is one of the great challenges of modern society (Richter *et al*. 2003; Vorosmarty *et al*. 2010). Whether to restore facets of a river's native flow regime (Poff *et al*. 1997) or create novel ecosystems (Acreman *et al*. 2014), there remains a pressing need to understand the ecology and population dynamics of aquatic biota. Ultimately, this knowledge will inform trade-offs and aid planning for future scenarios (e.g. climate change) (Poff and Matthews 2013; Arthington *et al*. 2018).

Knowledge of population structure and dynamics is essential to understanding the stability and resilience of populations. Age demographic data form a basic premise of marine fisheries management (e.g. Hilborn and Walters 1992), yet are scarce for many of the world's riverine fishes (Reynolds 2005; Cooke *et al*. 2012). These data, along with autecological knowledge, are integral to progressing the management and conservation of riverine fishes (Shenton *et al*. 2012; Crook *et al*. 2015).

In Australia's Murray-Darling Basin, native fish populations have declined markedly (Barrett, 2004), but few studies have considered the age demographics and dynamics of populations (although see Anderson, *et al*. 1992; Rowland 1998; Mallen-Cooper and Stuart 2003; Crook *et al*. 2016) and demographic targets seldom form part of monitoring or fisheries management. An understanding of these factors, however, is critical to inform management and measure population response to conservation initiatives (e.g. environmental flows).

In this thesis, I have explored the population structure and dynamics of the migratory pelagophil, golden perch, in the flow regulated and fragmented River Murray, in an effort to understand how flow and connectivity influence population dynamics. Specifically, I characterised temporal variability in age demographics over a period of hydrological extremes (drought–flood), then to understand the processes promoting these temporal patterns, I investigated spawning, recruitment and movement. Here, I integrate and discuss the findings of my research, including their utility for the management and conservation of riverine fishes, and provide directions for future research.

### Spawning, recruitment and age-structure

From 2001 to 2010, the Murray-Darling Basin (MDB) experienced one of the most severe droughts in recorded history (van Dijk *et al*. 2013). From 2005–2010, flows in the River Murray system were approximately 40% below average and insufficient to inundate floodplains. In late 2010, the drought was broken with widespread flooding across the southern MDB. Chapters 2 and 3 of this thesis investigated the spawning, recruitment and age demographics of golden perch in the lower River Murray over this period.

Throughout the Millennium Drought, the age structure of golden perch in the lower River Murray was characterised by intermittent recruitment and the dominance of a few specific cohorts. These distinct cohorts were predominantly recruited prior to the drought in association with overbank floods or increased flow contained within the river channel. Episodic recruitment is a defining characteristic of fishes with *periodic* life histories, where extended periods of poor recruitment are punctuated by specific strong cohorts that persist in the population (Winemiller and Rose 1992; Kraus and Secor 2004). In flow-regulated rivers, this demographic pattern is exacerbated (Olden *et al*. 2006). For example, in the coastal river basins of north-eastern Australia, golden perch exhibit disparate recruitment patterns between regulated rivers and those retaining more natural flow regimes, whereby recruitment is more consistent in the later (Roberts *et al*. 2008). In extreme cases, extensive river regulation may preclude the recruitment of pelagic spawning fishes, leading to their demise (Copp 1990).

A broad age structure promotes resilience to environmental perturbations (Berkeley *et al*. 2004) and may improve spawning outcomes and future recruitment (Secor 2000). In marine ecosystems, overfishing can curtail age-structure diversity (Marteinsdottir and Thorarinsson 1998; Hsieh *et al*. 2010), and for riverine fishes, river regulation in its various forms may have a comparable effect (Winemiller 2005: Reynolds *et al*. 2005; Olden *et al*. 2006). During the decade-long Millennium Drought, only one cohort of golden perch entered the lower Murray population. This cohort was the product of spawning associated with a spring flow-pulse in 2005. In all other years, characterised by depressed flows and the absence of spring flow-pulse, recruitment was absent.

An annual spring flow-pulse was a predictable hydrological characteristic of the un-regulated River Murray, and is now one of the most impacted flow components in the regulated river (Maheshwari *et al*. 1995; Mallen-Cooper and Zampatti 2018; Chapter 2 this thesis). The loss of this annual characteristic of the hydrograph likely compromises the demographic resilience of golden perch and other riverine biota in the lower River Murray and as such, its re-establishment should be a priority for environmental water management (Mallen-Cooper and Zampatti 2018). Indeed, restoration of this distinct hydrological characteristic is within the realms of current environmental water availability and management (CEWO 2016).

Golden perch relative abundance in the lower River Murray was consistent throughout the Millennium Drought, but increased significantly post flooding (Chapter 3). Ecological extremes, such as floods and droughts, can exert a major influence on the structure and function of riverine ecosystems (Lake 2000). Low-flow events in rivers characteristically lead to the reduced survival, recruitment and abundance of freshwater fishes (Jowett *et al*. 2005; Poff and Zimmerman 2010). Golden perch abundances throughout the Millennium Drought were low, but relatively stable, potentially due to the recruitment event in 2005 offsetting mortality and emigration of older age classes.

Despite a depauperate age structure at the end of the Millennium Drought, population growth of golden perch in association with flooding in 2010 was rapid and substantial. This response superficially supports the *flood-pulse* model (Junk *et al*. 1989), where flooding promotes high abundances of biota in floodplain and riverine environments, due primarily to reproduction and recruitment driven by floodplain derived energy. This classic concept, however, may be more applicable to tropical rivers (e.g. Dutterer *et al*. 2012) than rivers in temperate regions (Humphries *et al*. 1999). In the lower River Murray, significant growth in the golden perch population was promoted by age 0+ and 1+ fish, recruited during the flood and in the year prior, respectively, thus in part supporting the flood pulse model. Yet approximately 50% of the population sampled post-flooding was age 1+ fish that were absent from the population as age 0+ the year prior (2009–10), indicating that immigration was also a substantial driver of population growth. In Chapter 3 of this thesis, I proposed that the age 1+ fish may have originated in the Darling River (the major tributary of the River Murray) in association with a high flow event in 2009–10, that was absent in the River Murray, and then dispersed to the lower Murray in association with widespread flooding in 2010-11. I explored this hypothesis in Chapter 4.

Flooding was associated with substantial recruitment of golden perch to age 0+, demonstrating the capacity of fishes with periodic life histories to respond to episodic events that promote high survival of early life stages. In the case of golden perch, this occurred even when the extant population was characterised by limited and ageing year classes. For periodic species, recruitment variability goes hand-in-hand with longevity, which enables populations to persist over long periods (multiple years) of poor recruitment and recruitment failure (Secor 2000; Winemiller 2005). A proposed mechanism for this is the *storage effect*, where stored egg production, across multiple age-classes of long-lived fishes, can promote rapid population growth when conditions are favourable for the survival of early life stages (Secor 2007). It is notable, however, that at the end of the Millennium Drought, the lower Murray golden perch population was dominated (~70%) by age 4+ fish, that had likely just entered reproductive maturity, and low proportions (<10%) of fish aged 9+ and greater. Consequently, even with what may be regarded as a population with low demographic resilience and potentially limited storage effect, population growth was rapid.

In this thesis, I have demonstrated that high abundances of a *periodic* fish species post flooding may be due to the combined effects of flood mediated: 1) recruitment and 2) immigration of juvenile fish spawned in an alternative location the year prior. Depending on the longevity of fishes, the influence of these processes may persist as distinct cohorts in the demographics of the broader metapopulation for many years (Winemiller 2005). In the case of golden perch in the lower River Murray, the cohorts that promoted population growth post flooding remained prominent for at least five years, at which point our study ceased, but have subsequently persisted much longer (Zampatti *et al*. 2018). This response is analogous to that of water birds in the arid Lake Eyre Basin of Central Australia where rare large floods may promote breeding events and recruitment, and maintain population abundance across landscapes for decades (Kingsford *et al*. 1999). Thus, such *boom* events are fundamental to the resilience of populations in highly variable environments.

### Provenance and movement

Variability in the age-structure and abundance of populations is a function of births, deaths, emigration and immigration, and an understanding of these processes is a prerequisite for management. Indeed, elucidating the mechanisms promoting population fluctuations has occupied fisheries science for over a century (e.g. Hjort 1914). Fundamental to this understanding is an appreciation of the spatial scale over which population processes occur, including how the spatial behaviour of individuals and contingents influence population dynamics (Cooke *et al*. 2016).

In the fourth and fifth chapters of this thesis, I investigated how the provenance and movement of fish influenced population structure. In particular, I used: 1) otolith chemistry to retrospectively determine the provenance and movement history of individuals from specific age cohorts, and 2) radio telemetry to investigate the movements of adult fish. These investigations provide knowledge on the spatial arrangement of recruitment sources, and the influence of immigration and emigration on the population structure of golden perch.

The structural and chemical properties of fish otoliths provide a unique means to recount a fish's life history in time and space. I used water and otolith $^{87}Sr/^{86}Sr$ to delineate the provenance and movement of golden perch from discrete cohorts. Water $^{87}Sr/^{86}Sr$ was distinct among the Darling River and lower and mid-River Murray. In turn, otolith chemistry revealed golden perch collected in the lower River Murray were spawned in either the River Murray or Darling River, during years characterised by within-channel rises in flow, or in both rivers in a year characterised by extensive overbank flooding. Movement of fish from the Darling River was a substantial driver of population structure in the lower River Murray, with fish dispersing from natal habitats in the Darling River either in the year of birth, as eggs and larvae, or at age 1+ in association with flooding in the River Murray and Darling River.

The downstream drift of early life stages is a defining trait of pelagic-spawning fishes and one that makes them particularly susceptible to river regulation. Riverine fishes with drifting early life stages rely on advection to promote suspension and in turn development and survival (Pavlov *et al*. 2008). For all pelagic-spawning fishes, this process will operate over some minimum time or length of river (Braaten *et al*. 2008). Whilst the hydrology of the Darling River has been grossly altered (Thoms and Sheldon 2000), the lotic characteristics of the lower Darling River remain intact, facilitating the downstream transport of eggs, larvae and early stage juveniles, and providing suitable developmental conditions for these life stages.

Dams and weirs exert two primary impacts on the downstream movement of fish: 1) the physical impediment of the structure itself and 2) the hydraulic obstacle created by upstream reservoirs or weir pools, which may affect behaviour and the passive downstream movement of fishes. Worldwide, there is growing recognition that restoration of longitudinal connectivity for riverine fishes is a *two-way street* (*sensu* Calles and Greenberg 2009) and that consideration of the upstream and downstream movement of all life stages is required to conserve fish populations (Agostinho et al. 2008; Baumgartner *et al*. 2014). Nevertheless, the impacts of weir pools and reservoirs on the downstream movements of all life stages of fish remains a major knowledge gap.

Preventing the downstream dispersal of fishes fragments populations and may ultimately influence survival and population resilience. In regulated rivers in South America, the mitigation of upstream passage through fishway construction, without recognition of the impacts of reservoirs on downstream movement, is considered to have little conservation value (Pelicice *et al*. 2015). For example, in the Amazon River Basin, fishways are constructed to cater for the upstream passage of adults, but for fishes with a drifting larval stage, the lentic environments created by reservoirs and weir pools subsequently prevent downstream dispersal and compromise survival (Pompeu *et al*. 2012).

Similarly, in the Murray-Darling Basin, the physical impediment of dams and weirs is dealt with via fishways (Barrett and Mallen-Cooper 2006) and consideration of weir configuration (i.e. overshot or undershot) on the early life stages of fish (Baumgartner *et al*. 2006). Yet, the impact of hydraulic alteration and the influence of reservoirs and weir pools on the downstream drift of early life stages, or the active downstream movement of juveniles (e.g. Tiffan *et al*. 2009), has received minimal consideration. These impacts form important avenues for future research, particularly the hydraulic conditions necessary for promoting the drift of eggs and larvae, and the active downstream movements of juveniles and adults.

In this study, the Darling River constituted a spawning location for golden perch when environmental conditions were unsuitable in the River Murray. Subsequently, fish emigrated into the River Murray during early development (eggs and larvae), likely via passive drift, or used the Darling River as a nursery habitat and emigrated as age 1+ juveniles in association with subsequent high flow events. Elsewhere in the Murray-Darling Basin, major tributaries with intact lotic habits (e.g. the Ovens and lower Goulburn rivers) have also been identified as potential recruitment sources for riverine fishes such as golden perch and Murray cod (*Maccullochella peelii*) (Koehn *et al*. 2009; Koster *et al*. 2017).

In regulated river systems worldwide, the ecological importance of tributaries and tributary-mainstem junctions is increasingly being recognised (Rice *et al*. 2006; Pracheil *et al*., 2013; Gualtieri *et al*. 2017). Tributaries may preserve hydrological and hydraulic conditions that promote fish spawning and recruitment, and in turn provide a source of juvenile recruits to main channel habitats (Pollux *et al*. 2006; Pracheil *et al*. 2009; Webber *et al*. 2013). Our results concur that: 1) tributaries may provide hydrological and hydraulic characteristics that are permanently or temporarily absent from regulated main river channels, and are important to fish recruitment, and 2) connectivity between tributary and mainstem habitats can be a substantial driver of the structure of mainstem population contingents. Maintaining the unique hydrologic and habitat characteristic of tributaries is paramount, as is facilitating connectivity between tributary and mainstem contingents to ensure metapopulation integrity.

### Movement of adult golden perch

Fish movement and habitat use can also be investigated with non-destructive techniques, such as electronic tags (Lucas and Baras 2000), particularly where homogenous water chemistry can limit the efficacy of otolith chemistry approaches and where there is a need for fine spatial-scale data (Gillanders 2005). The utility of electronic tags, however, is subject to considerations of battery size and tag longevity, and in turn, transmitter size in relation to fish body size (e.g. Cooke *et al*. 2011). For this reason, studies pertaining to long-lived fish may be restricted to adult fish where the use of larger tags, with longer battery lives (i.e. years), is required.

In chapter 5 of this thesis, I used a combined radio-telemetry and passive integrated transponder (PIT) tag approach to investigate the habitat use and movement of adult golden perch in relation to flow, season and water temperature. Site fidelity was common, with 36% of fish remaining at the site of capture throughout the study period (~2 years), which included a spring-summer spawning season and a within-channel flow pulse. Over the same period, however, 29% of fish migrated long distances upstream (up to 270 km), coincident with steady, rising and falling flows. These movements were correlated with seasonal variation in water temperature and to a lesser extent, short-term (10-day) flow variability. These findings concur with previous studies of golden perch movement, which have also demonstrated the existence of mobile and sedentary individuals (Crook 2004; O'Connor *et al*. 2005), but contrast with the studies that have associated movement with increased discharge (O'Connor *et al*. 2005; Koster *et al*. 2017). Whilst environmental factors, such as flow, may indeed constitute an impetus for movement, we suggest that movement may also be driven by endogenous cues such as sexual maturity and age, which may act independently of flow. The role of these factors in promoting movement and interactions with flow, warrants further investigation.

A notable finding of our adult movement investigation was evidence of partial migration, whereby some fish in a population migrate and some do not (Chapman *et al*. 2012). Movement may beneficially expose fish to suitable habitats and environmental conditions for growth and reproduction, but it is also inherently risky, and may increase the incidence of individual mortality (Alerstam *et al*. 2003). Across a population's range, it is likely that a combination of retentive and dispersive behaviours minimises risks associated with habitat and environmental heterogeneity (Secor 1999). In large river basins, where climate variability, or indeed river regulation, lead to regionally diverse flow patterns, partial migration may increase the chance of at least some fish being in the right place, at the right time, to be exposed to hydrological conditions conducive to spawning and the survival of early life stages. In bird species, within-population variability in migratory movements and destinations (i.e. migratory diversity) promotes resilience to environmental change, with species exhibiting partial migration less likely to decline (Gilroy *et al*. 2016). This concept has also been demonstrated for freshwater, estuarine and diadromous fishes (e.g. Kerr *et al*. 2010; Moore *et al*. 2014; Gillanders *et al*. 2015), and for golden perch, may be a mechanism that contributes to the basin-wide persistence of this species.

### Plasticity and the portfolio effect

Life-history diversity, including partial migration, provides a mechanism by which populations can persist in dynamic or altered environments (Kerr *et al*. 2010; Araya *et al*. 2014). Behavioural bet-hedging, in conjunction with a diversity of spatially independent recruitment sources, means that whilst some contingents may experience high mortality or recruitment failure, concurrently others may experience lower mortality or environmental conditions more suitable for recruitment (Gahagan *et al*. 2015). Fish movement and connectivity between recruitment sources, however, is integral to promoting regional persistence (e.g. Scheurer *et al*. 2003).

Despite population decline, golden perch remain one of the most widespread and abundant large-bodied fishes in the MDB. The studies conducted in this thesis demonstrate that golden perch in the southern MDB have 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 strategy (chapters 2 and 3), spatially distinct recruitment sources (chapter 4), migratory diversity (chapter 5) and habitat flexibility (i.e. can persist in lotic and lentic waters). In contrast, in fishes where migratory diversity is absent or negligible, and where migration is an essential life history process (e.g. to access a spawning site), river regulation may lead to the demise of species (Godinho and Kynard 2009). For example, in the River Murray in the early 1900s, the construction of main-channel weirs impeded the annual upstream spawning migration of Macquarie perch (*Macquaria australasica*), isolating fish from essential spawning habitats (lotic reaches characterised by rock substrates). This lack of migratory diversity and life history flexibility led to rapid population decline (Mallen-Cooper and Brand 2007) and ultimately the loss of this species from the River Murray.

For golden perch, recruitment source diversity and intra-population behavioural plasticity potentially contribute to a meta-population somewhat resilient to environmental variability and anthropogenic impacts such as river regulation and harvesting. This construct is analogous to the *portfolio* effect initially described for Atlantic salmon (*Salmo salar*) in Bristol Bay, Alaska (Schindler *et al*. 2010), whereby life-history diversity has a stabilising effect on meta-populations due to differential responses of contingents to environmental variability. A key aspect of this buffering effect is the presence of spatially distinct, but connected, recruitment sources.

Notwithstanding the above, golden perch abundance in the MDB remains depressed compared to historical levels (Kaiola *et al*. 1994). Consequently, rehabilitation, particularly from a demographic perspective, will need to consider maintaining and rebuilding recruitment source diversity and connectivity, and reinstating the hydrological and hydraulic factors that promote spawning, recruitment and dispersal. Importantly, maintaining a mosaic of connected recruitment habitats and the spatial processes that link these, will likely promote greater population stability and resilience than relying on single recruitment sources (Kraus and Secor 2004; Kerr *et al*. 2010).

Ecological disturbance may also confer resilience to environmental change by selecting genetic traits that enable the persistence of individuals. For golden perch, contemporary genetic studies indicate that, despite anthropogenic fragmentation of many rivers in the MDB, high gene flow likely confers population resilience to environmental change due to the transfer of traits that have evolved elsewhere (Attard *et al*. 2017). Specifically, the wide-ranging movement of a portion of the population enables transfer of traits locally adapted to arid regions to those areas that may become more arid due to climate change. These genetic adaptations may bode well for the persistence of golden perch in the MDB. Indeed, the plasticity of golden perch population processes and high gene-flow, may confer greater resilience to climate change than many other fishes in the MDB (Balcombe *et al*. 2011).

### Integrating knowledge to inform management

To various extents, the reproduction, recruitment and movement of golden perch have been linked to flow (e.g. Humphries *et al*. 1999; Mallen-Cooper and Stuart 2003; King *et al*. 2016, Koster *et al*. 2017) and these key life history processes form objectives for environmental water allocation throughout the MDB (MDBA 2014). An ultimate goal of environmental water management and allied interventions (e.g. habitat restoration, stocking, fish passage, etc.), however, should be to rehabilitate native fish populations through population growth. To achieve this requires an understanding of population structure, the factors that influence population dynamics (i.e. recruitment, mortality, immigration and emigration), and the spatial scales over which these operate (Rieman and Dunham 2000). Considering this, conservation of golden perch populations would be well-served by a *resilience* approach that recognises the need to maintain the life history, population and habitat characteristics essential to promoting age structure diversity, and thus increasing the ability of a population to withstand and recover from disturbances (Waldman *et al*. 2016).

Such strategies will be most effective when informed by life history and population models that integrate knowledge obtained across a continuum of scales that are relevant to fish life histories and population function (Fausch *et al*. 2002; Durance *et al*. 2006). In flow-impacted rivers, conservation of pelagic-spawning fishes could be advanced by modelling approaches that forecast population persistence by integrating key population defining processes in a hydrological and hydraulic context. A range of population models have been employed to assimilate some of these processes, including for golden perch and Australian bass (*Percalates novemaculatea*) in Australia (Bond *et al*. 2015; Lin *et al*. 2017) and shovelnose sturgeon (*Scaphirhynchus platorynchus*) and shortnose sturgeon (*Acipenser brevirostrum*) in North America (Jager *et al*. 2013; Goto *et al*. 2015)

Modelling approaches that integrate connectivity and the influence of hydrology and hydraulics on population processes (e.g. spawning, drift of early life-stages, mortality and migration of juveniles and adults) would be particularly useful for pelagic-spawning riverine fishes with periodic life histories. Lin *et al*. (2017) utilised a spatio-temporal population model, informed by individual movement data, to explore the effect of migration barriers, modified migratory cues (hydrology) and fishing mortality on the population persistence of Australian bass. This promising approach could have utility for golden perch, particularly if it was extended to include: 1) the influence of hydrology/hydraulics on spawning and the dispersal of eggs and larvae, 2) the effects of hydrology/hydraulics and physical barriers on movements of juveniles and adults, 3) the effects of angling, including at bottlenecks/barriers, and 4) the influence of hydrology on year-class strength and population structure.

## Future Research

Contemporary flow restoration in regulated rivers primarily considers the impact of river regulation on flow volume and rate (i.e. discharge), and following the tenets of the Natural Flow Paradigm (NFP: Poff *et al*. 1997), aims to reinstate ecologically significant components of the flow regime. Such approaches, however, seldom consider the hydraulic and hydrodynamic impacts of river regulation (Mallen-Cooper and Zampatti 2018). An important next step in understanding the flow-related biology of golden perch is to elucidate the hydraulic factors (e.g. water velocity) that potentially promote spawning, and the spatial scale of such processes. If water velocity, or some other hydraulic descriptor can be identified, this will provide a transferrable hydrologic unit that may be applied to flow restoration in rivers with differing geomorphology and discharge.

Equally important are the critical water velocities required for the downstream drift of eggs and larvae, and the behaviour and fate of these life stages in relation to the hydraulics of large channels, including weir pools. Pelagic-spawning fishes with periodic life histories spawn large numbers of small eggs whose survival is maximised when large-scale environmental heterogeneity promotes patchy resources (Winemiller and Rose 1993). As such, the interrelationships of riverine hydrodynamics with primary and secondary productivity and the mechanisms of survival of early life stages, form fundamental questions. Indeed, concepts concerning the drift and retention of early life stages of fish in relation to resource patchiness, and the implications of this for survival and recruitment, form an important focus for contemporary research in riverine fish ecology (Hoagstrom and Turner 2015; Humphries *et al*. in press).

Further research on the movement of juvenile and adult golden perch is also warranted, particularly the influence of movement on meta-population structure. The telemetry study of adult golden perch movement (Chapter 5) was conducted during low flows, during which approximately 30% of fish migrated upstream in the River Murray. At the end of the Millennium Drought, however, flooding was associated with a substantial decrease in the abundance of older age-classes of golden perch in the lower River Murray (Chapter 4), potentially due to emigration. Some of the longest migratory movements for golden perch, including a >2000 km migration up the River Murray and Darling River, have been associated with floods (Reynolds 1983). In addition, in the upper reaches of the River Murray, immigration of adult golden perch post flooding may alter the age demography of receiving populations (Lyon *et al*. 2019). Ultimately, there is likely to be a redistribution of both adult and juvenile fish during flooding that will restructure meta-population demographics. The existence of these movements, their links with abiotic factors and influence on population structure could be explored retrospectively using otolith chemistry techniques.

## Concluding remarks

In this thesis, I have addressed concepts relating to the autecology, population structure and movement of golden perch and provided new insight regarding the spatial structuring of golden perch populations in the southern Murray-Darling Basin. These factors are considered key contemporary knowledge requirements for understanding the impacts of anthropogenic disturbance on riverine fish populations (Cooke et al. 2012; Crook *et al*. 2015; Cooke *et al*. 2016).

The results of my study have utility for the management of golden perch and pelagic-spawning fishes globally. Despite increasing recognition of the need to manage fishes, and indeed ecosystem function, at the river-scale (Schlosser 1991; Fausch *et al*. 2002), research and management of freshwater fishes is often undertaken in a spatially disaggregated manner (Durance *et al*. 2006). For example, in Australia’s Murray-Darling Basin, units of management often relate more to arbitrary sites or State boundaries (e.g. Commonwealth Environmental Water Office 2016; Murray-Darling Basin Authority 2018) than the scale of fish life histories or population structure. Ultimately, conservation and rehabilitation of riverine fishes, including golden perch, requires management at a spatial scale concordant with life history and population processes. It equally requires consideration of recruitment source, life history and migratory diversity, and connectivity.

In the MDB, golden perch movement has been associated with spawning (O'Connor *et al*. 2005; Koster *et al*. 2017), but it has seldom been considered in its own right as driver of population structure and dynamics (although see Lyon *et al.* 2019). Our data suggest that the demographics of golden perch populations in lower River Murray are substantially influenced by fish movement. Indeed, the passive and active movement of golden perch at all life stages (eggs, larvae, juveniles and adults), in both a downstream and upstream direction, and between tributaries and the main stem, highlights the importance of considering bi-directional longitudinal and lateral connectivity in rivers to support the conservation of riverine fishes (Calles and Greenberg 2009).

Rehabilitation and conservation of riverine fish populations will be advanced by approaches that integrate mainstem rivers, tributaries, and floodplains, and that recognise the fundamental importance of fluvial habitats in promoting pelagic-spawning fishes (Galat and Zweimuller 2001). Integral to such approaches is the rehabilitation of physical connectivity and consideration of the natural hydrological and hydraulic characteristics of rivers that support habitat maintenance and the critical life history processes that influence population dynamics.

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