

## The influence of weir pool raising in the South Australian lower River Murray on condition and growth of Australian smelt (*Retropinna semoni*)



C. M. Bice, B. P. Zampatti and Z. Tonkin

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## EXECUTIVE SUMMARY

The flow regime is the primary driver of ecological patterns and processes in riverine ecosystems, with water level variability and flooding, thought to be particularly critical in supporting the ecological function of floodplain rivers. River regulation and consumptive water use, however, alters the hydrological and hydraulic characteristics of rivers. In the lower River Murray, river regulation has reduced overall flow volumes and the frequency and duration of medium–high flows, whilst the construction of 10 low-level weirs (1920s) has transformed over 800 km of river into a series of contiguous weir pools. As such, the flow regime has been simplified and water levels are now relatively stable. Diminished water level variability and flooding frequency, have led to numerous impacts, including reduced productivity as a result of diminished river–floodplain connectivity and allochthonous carbon input.

Weir pool manipulation (i.e. raising or lowering river stage using existing weir infrastructure) is currently being undertaken by State and federal agencies as a tool for reinstating greater water level variability and achieving environmental benefits (e.g. improved condition of long-lived floodplain vegetation, localised freshening of groundwater) in the lower River Murray. In spring/summer 2015, water levels in the Lock 2–3 and Lock 5–6 weir pools were both raised to approximately +0.5 m above ‘normal pool level’ (NPL), before being returned to +0 m NPL, over a period of approximately 3 months. At maximum weir height, floodplain areas of ~120 and 770 ha were inundated in the Lock 2–3 and Lock 5–6 weir pools, respectively. To support weir manipulation, hypotheses were developed predicting the responses of a range of physico-chemical and biotic parameters to the raising events, including enhancement of secondary productivity as indicated by improved growth rates and condition of generalist small-bodied fishes.

The objective of the current study was to investigate the influence of raising water levels in the Lock 2–3 and Lock 5–6 weir pools in 2015 on aspects of the early life history (i.e. spawning, condition, growth) of Australian smelt (*Retropinna semoni*). We sampled Australian smelt from the Lock 2–3 and Lock 5–6 weir pools, as well as reference weir pool (Lock 3–4), and utilised otolith microstructure analysis, to determine:

1. Density of early life stages (<30 mm in length);
2. Estimated ages and spawning dates;
3. Morphometric condition;
4. Seasonal growth rates; and
5. Daily growth rates.

Australian smelt (*Retropinna semoni*) is a common small-bodied fish species, widely distributed in the lower River Murray and a potential indicator species of secondary productivity. The species is short-lived, but exhibits a protracted spawning season and is predated by higher trophic level species. Importantly, substantial research has been conducted on the early life history of the species, including validation of otolith increment formation, establishment of relationships between length, age and weight, and the influence of temperature, food availability and environmental conditions on growth. We hypothesised that larval/juvenile Australian smelt from the raised weir pools would be derived from broader spawning seasons and exhibit greater morphometric condition, and growth rates, than larvae/juveniles from the reference weir pool, due to increased habitat availability and improved primary productivity, following liberation of allochthonous resources. We also hypothesised that seasonal progression would influence these parameters.

We sampled larval/juvenile Australian smelt from the Lock 2–3, Lock 3–4 and Lock 5–6 weir pools in October 2015 (two weeks following peak inundation) and December 2015 (immediately following recession back to NPL), using night-time plankton-net tows. Larvae/juvenile Australian smelt sampled from the Lock 2–3 and Lock 5–6 weir pools were derived from broader spawning seasons (105 and 113 days, respectively), which commenced earlier (August) than the Lock 3–4 weir pool (79 days). This may represent a typical regional difference in the timing of spawning of Australian smelt or alternatively, improved survival of larvae spawned early in the spawning season (i.e. August) in raised weir pools, relative to Lock 3–4. Improved survival would presumably be driven by improved resource availability in raised weir pools, but this was untested.

As hypothesised, morphometric condition increased significantly between sampling events in all weir pools and was significantly greater in the raised Lock 5–6 weir pool than the unraised Lock 3–4 weir pool in October 2015, potentially reflecting higher resource availability (e.g. zooplankton and terrestrial insects) in this weir pool in the immediately preceding period. Nonetheless, counter to hypotheses, condition was greatest in the unraised Lock 3–4 weir pool in December 2015. Length-at-age relationships suggested mean seasonal growth rates did not differ significantly between weir pools. Furthermore, analyses of daily growth histories using marginal increment widths and linear mixed-effects modelling, suggested the fixed-effects of sampling trip and fish age had the greatest influence on growth rates; fish sampled during December 2015 grew faster than like aged fish sampled in October 2015, whilst fish from both sampling trips grew fastest in the days immediately preceding capture, among all weir pools. Contrary to our hypothesis, differences among weir pools were non-significant.

Analysis of spawn dates and morphometric condition, but not growth rates, of early life stage Australian smelt indicated minor positive responses to weir pool raising. A parallel investigation observed enhanced primary productivity in association with weir pool raising, in the upper reaches of the Lock 5–6 and Lock 2–3 weir pools, but limited response in primary productivity in the lower reaches of these weir pools, suggesting rapid assimilation of organic matter and potentially a limited spatial scale to productivity responses. Enhanced primary productivity was also noted throughout these weir pools upon drawdown to +0 m NPL in December, but the relative influences of weir pool manipulation and seasonal progression could not be determined. Minor responses in condition and a lack of difference in growth rates of Australian smelt among weir pools suggests either: 1) increases in primary productivity were not of a sufficient magnitude to elicit major responses in secondary productivity; 2) organic matter that was rapidly assimilated within the weir pools did not enter a trophic pathway that directly benefited Australian smelt; and/or 3) downstream transport of organic matter from raised weir pools influenced condition and growth in December in the reference weir pool (Lock 3–4). Whilst the third mechanism cannot be discounted, we consider it unlikely given the spatial patterns in primary productivity during peak raising. These results are important given water level variability, increased inundation and positive responses of primary productivity are commonly implied to infer diversity and productivity of food webs, and thus, likely enhancement of secondary productivity. In some cases, this may not be true and patterns of carbon transfer are likely to be highly complex. This highlights the need to better understand trophic pathways and links between primary and secondary productivity in the lower River Murray. Replication of the current study during a year of no weir pool manipulation would assist in differentiating the influences of weir pool manipulation and typical seasonal progression on condition and growth.

## 1. INTRODUCTION

### 1.1. Background

The flow regime is the primary driver of ecological patterns and processes in riverine ecosystems (Poff *et al.* 1997). In floodplain rivers, connectivity between the main channel and floodplain, mediated by water level variability and flooding, is thought to be critical in supporting ecological function (Junk *et al.* 1989). The flood-pulse concept (FPC, Junk *et al.* 1989) proposes that the production of animal biomass (e.g. fish) in rivers is predominantly driven, directly or indirectly, by allochthonous carbon and nutrients derived from terrestrial floodplain environments. This concept was largely developed for large tropical river–floodplain systems with annually predictable flood pulses, and its applicability in arid and semi-arid rivers of Australia has been questioned (Bunn *et al.* 2003, Hadwen *et al.* 2010). Revision of the FPC, namely the extended flood pulse concept (EFPC) (Tockner *et al.* 2000), better caters for highly variable systems, like the Murray-Darling Basin (MDB), and proposes the importance of rises in water level constrained ‘within-channel’, in providing pulses of allochthonous carbon and similar productivity responses to floodplain inundation. Alternatively, the Riverine Productivity Model (RPM) (Thorp and DeLong 2002), proposes that higher trophic level productivity in rivers is largely driven by autochthonous carbon production (i.e. phytoplankton), rather than allochthonous carbon, as much terrestrial carbon is recalcitrant. Recent research, however, suggests different aspects of these alternative concepts may describe fish productivity in the MDB (Tonkin *et al.* 2011), with the importance of different sources of carbon varying with hydrology. Indeed, the importance of allochthonous carbon in supporting riverine foodwebs and productivity in the MDB, during high flow events, has been recently highlighted (Cook *et al.* 2015).

River regulation alters riverine flow regimes through changes in the frequency, duration, timing and magnitude of flow events, to the detriment of riverine biota (Bunn and Arthington 2002). The lower River Murray (downstream of the Darling River junction) was historically a lotic system, which experienced highly variable discharge (Puckridge *et al.* 1998); however, river regulation and increased consumptive water use has reduced overall flow volumes and subsequently reduced the frequency and duration of medium–high flows (Maheshwari *et al.* 1995). Furthermore, the construction of 10 low-level weirs in the 1920s and 1930s, transformed over 800 km of river into a series of contiguous, weir pools which are predominantly lentic in character (Walker and Thoms 1993). As such, the flow regime has been simplified and water levels are now relatively

stable (Maheshwari *et al.* 1995, Blanch *et al.* 2000). Diminished water level variability and flooding frequency, and duration, have led to numerous impacts, notably salinization and declining condition of long-lived floodplain vegetation (e.g. river redgum, *Eucalyptus camaldulensis*), declines in biota adapted to lotic environments (e.g. Murray crayfish, *Euastacus armatus*) and reduced productivity as a result of diminished river–floodplain connectivity and allochthonous carbon inputs (Walker 1985, Walker and Thoms 1993).

Weir pool manipulation (i.e. raising or lowering river stage using existing weir infrastructure) are currently being undertaken by state and federal agencies as a tool for reinstating greater variability in water level in the lower River Murray (downstream of the Darling River junction). In South Australia, there has been considerable interest in the utility of raising weir pools with the objective of inundating littoral zones and low-level floodplain, and thus achieving environmental benefits associated with water level variability and floodplain inundation, in the absence of elevated discharge.

From late-August to mid-December 2015, water level manipulations were undertaken in the Lock 2–3 and Lock 5–6 weir pools, with both raised to approximately +0.5 m above ‘normal pool level’ (NPL), before being returned to +0 m NPL. This followed raising events in the Lock 1–2 and Lock 2–3 weir pools in 2014, and similar events in Lock 5–6 weir pool in 2000 and 2005. To support/justify weir manipulation, hypotheses were developed predicting the responses of a range of physico-chemical and biotic parameters, including changes to soil moisture and salinity, in-channel hydraulics, growth and condition of floodplain vegetation, and enhanced secondary productivity (DEWNR 2015).

Small-bodied fishes, and particularly their early life stages (e.g. larvae and juveniles), are useful models for testing hypotheses regarding secondary productivity. Small-bodied fishes are often short-lived, but are fast-growing and abundant, and represent important links between low (e.g. zooplankton) and high trophic levels (e.g. piscivorous fishes and birds). Importantly, prey availability influences growth and condition, which in turn have a large bearing on survival through early life stages and subsequent fish recruitment, cohort strength and abundance (Houde 1997). As such, investigations of growth and condition of fish early life stages may provide insight on system productivity and the influence of hydrology and management interventions, including weir pool raising.

Otolith microstructure analysis is a commonly used tool to investigate the early life history of fishes (Campana and Neilson 1985). Otoliths are calcareous structures that typically form periodical

increments (i.e. daily and annual) and often exhibit relationships between otolith growth and somatic growth (Campana and Neilson 1985). As such, the analysis of otolith microstructure can provide information on individual fish ages, spawn/hatch dates and growth rates.

Australian smelt (*Retropinna semoni*) is a pelagic, small-bodied fish species that is abundant and widespread throughout the lower River Murray (Lintermans 2007). The species is short-lived, but exhibits a protracted spawning season in the lower River Murray from August to December (Leigh 2002). It is also predated by higher trophic organisms including fishes and birds (Baumgartner 2007). Importantly, substantial research has been conducted on the early life history of Australian smelt in the mid-Murray region including: validation of otolith daily increment formation and influence of temperature and feeding regimes on otolith growth (Tonkin *et al.* 2008a, 2008b); determination of relationships between length, weight, otolith size and age (Tonkin *et al.* 2008c); and the influence of aspects of the flow regime on morphometric condition and growth rates (Tonkin *et al.* 2011). Given the biological characteristics of Australian smelt and body of knowledge on early life history, it is an ideal candidate to investigate the influence of weir pool raising on secondary productivity.

## 1.2. Objectives

The primary objective of the current study was to investigate the influence of raising water levels in the Lock 2–3 and Lock 5–6 weir pools in 2015 on aspects of the early life history (e.g. spawning, condition, growth) of Australian smelt. We sampled Australian smelt from the Lock 2–3 and Lock 5–6 weir pools, as well as reference weir pool (Lock 3–4), and utilised otolith microstructure analysis, to determine:

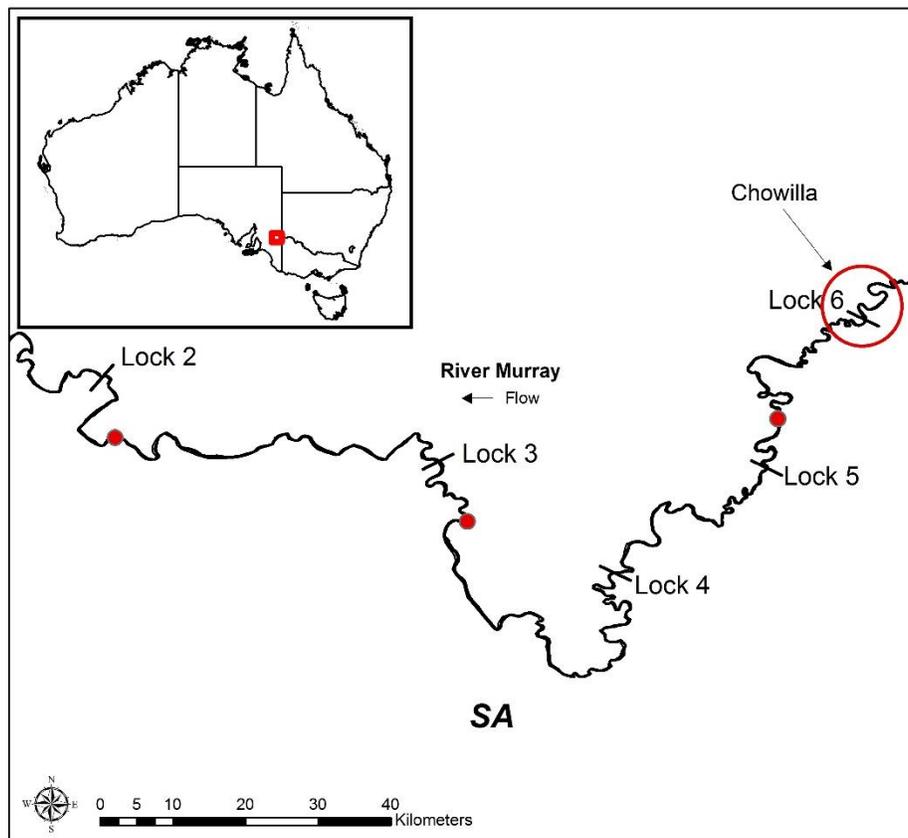
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3. Morphometric condition;
4. Seasonal growth rates; and
5. Daily growth rates.

We hypothesised that larvae/juvenile Australian smelt from the raised weir pools would be derived from broader spawning seasons and exhibit greater morphometric condition and growth rates than larvae/juveniles from the reference weir pool, due to increased habitat availability and improved primary productivity, following liberation of allochthonous resources. We also hypothesised that seasonal progression would influence these parameters.

## 2. METHODS

### 2.1. Study site and weir pool raising

This study was conducted in the lower River Murray, South Australia, in the reach bounded by Lock 2 downstream and Lock 6 upstream (Figure 1). From the South Australia-New South Wales State border, the river meanders downstream for approximately 200 km over expansive (10–20 km wide) floodplains containing numerous riparian wetlands, anabranches and billabongs (hereafter the floodplain geomorphic region: Locks 6 to 3, inclusive), before flowing through a limestone gorge (hereafter the gorge geomorphic region: Locks 3 to 1, inclusive) where the floodplain is more constrained (2–3 km wide) and associated wetland diversity decreases (Walker 2006).

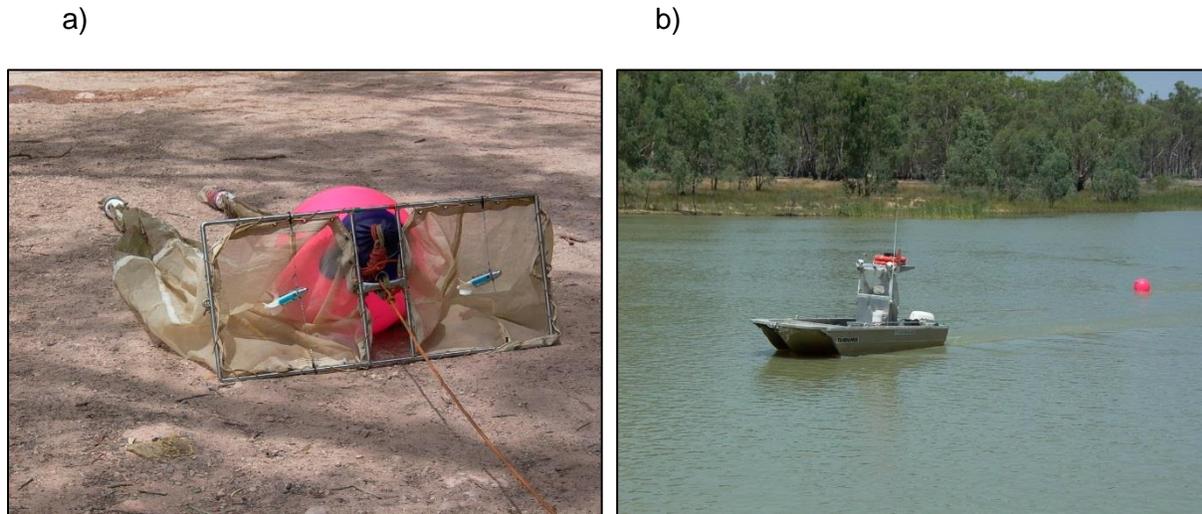


**Figure 1.** Map of the study area in the lower River Murray, South Australia, depicting the Locks 2, 3, 4, 5 and 6, and sites (red dots) where larval tows and electrofishing were undertaken in the lower reaches of the Lock 2–3, Lock 3–4 and Lock 5–6 weir pools. The location of the Chowilla system is also indicated.

In 2015, weir pool raising occurred in the Lock 2–3 and Lock 5–6 weir pools. The Lock 2–3 and Lock 5–6 weir pools are ~69 km and ~58 km in length, respectively, and the Lock 5–6 weir pool has the greatest area of floodplain (16,449 ha vs. 4867 ha, below 1956 flood-line) and wetland habitat (2404 ha vs 957 ha) (DEWNR 2015), owing to its location in the floodplain geomorphic region. The objectives of the weir pool manipulation were to raise water levels in both weir pools to +0.5 m NPL during September–November, with average rates of rise and fall of ~2 cm.day<sup>-1</sup> (DEWNR 2015). It is important to note that the Chowilla Regulator was operated over the same period to promote a ‘within-channel’ rise and minor floodplain inundation; from early September to early December, water levels were raised behind the regulator to a peak of 1 m above normal level, inundating an area of floodplain and wetland habitat of 337 ha (J Whittle pers. comm.). The Chowilla system (Figure 1) discharges into the Lock 5–6 weir pool and the operation of the regulator may have affected productivity and the early life history of fish in this weir pool. Furthermore, water level raising events occurred upstream in the Lock 7–8, Lock 8–9 and Lock 9–10 weir pools over the same period, which may have influenced productivity downstream, although we propose this would be unlikely.

## 2.2. Fish sampling and processing

Larval and juvenile fish were collected from sites in the lower reach of the Lock 5–6, Lock 3–4 and Lock 2–3 weir pools (Figure 1) over two sampling events in October (12<sup>th</sup>–14<sup>th</sup>) and December (7<sup>th</sup>–9<sup>th</sup>) 2015, using night time vessel-assisted plankton tows. Previous studies in the lower River Murray have indicated diel variability in the density of Australian smelt larvae/juveniles, with typically greater density at night (Cheshire 2010), and this method has been used extensively (Cheshire et al. 2012). Plankton tows were conducted using a set of paired square-framed (0.5 x 0.5 m) bongo nets 3 m in length with mesh size of 500 µm (Figure 2a). A large float, centralised on the net frame, allowed the nets to be towed approximately 0.05 m below the water surface. Nets were tethered to the vessel by a rope approximately 20 m in length and towed in an upstream direction, in a zigzag pattern between opposing banks, for a period of 15 minutes (Figure 2b). Four replicate night-time tows were conducted at each site during each sampling event. The volume of water filtered through each net was estimated using a General Oceanics™ flow meter, fixed in each of the net mouth openings. Port and starboard samples were mixed and preserved in 95% ethanol *in situ* and returned to the laboratory for sorting using magnification lamps. Further sampling was undertaken to collect additional larval/juvenile Australian smelt for morphometric and otolith analysis when required using a Smith-Root® 7.5 KVA vessel-mounted electrofishing unit.



**Figure 2.** a) Paired square-framed bongo-nets used to sample larval/juvenile Australian smelt and b) image of net tow being undertaken.

All larval/juvenile fish <30 mm, were identified to species (Lake 1967, Puckridge and Walker 1990, Neira *et al.* 1998, Serafini and Humphries 2004) and enumerated. Samples of up to 100 Australian smelt were measured for standard length ( $L_s$ , nearest 0.1 mm) and weight (nearest 0.001 g) after a minimum of 10 days to allow shrinkage associated with preservation to have stabilised (Fey and Hare 2005).

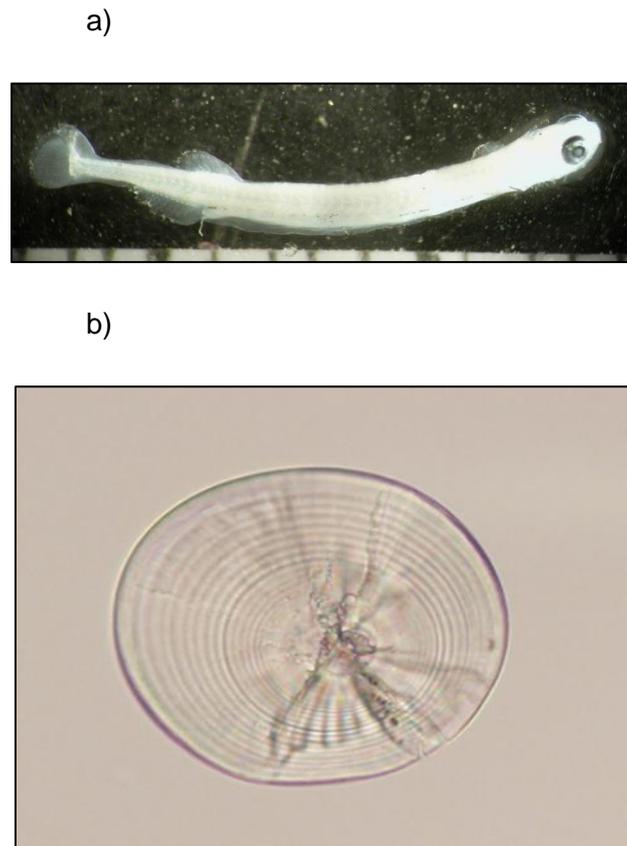
The density of larval/juvenile Australian smelt was standardised to fish per 1000 m<sup>3</sup> of water sampled. Differences in density between weir pools and sampling events were investigated using two-factor univariate PERMANOVA (permutational ANOVA and MANOVA), in the software package PRIMER v. 6.1.12 and PERMANOVA+ (Anderson *et al.* 2008). Analyses were performed on Euclidean distance similarity matrices of fourth-root transformed density data. To allow for multiple comparisons between weir pools and sampling events, a false discovery rate (FDR) procedure presented by Benjamini and Yekutieli (2001), hereafter the 'B–Y method' correction, was adopted ( $\alpha = \sum_{i=1}^n (1/i)$ ; e.g. for  $n_{comparisons} = 6$ , B-Y method  $\alpha = 0.05 / (1/1 + 1/2 + 1/3 + \dots + 1/6) = 0.02$ ) (Benjamini and Yekutieli 2001, Narum 2006).

### 2.3. Otolith preparation, increment counts and measurements

Sagittal otoliths were removed from a subsample of Australian smelt previously measured for length and weight ( $n = 30$  per each weir pool x sampling event), using a stereo microscope, and prepared following the method of Tonkin *et al.* (2008b). In brief, otoliths were mounted on thermoplastic cement (proximal side down) and ground to the level of the primordium across the

proximal plane using 3  $\mu\text{m}$  lapping film. In the case of very small otoliths, grinding was not required.

Ages of larval/juvenile Australian smelt were estimated via daily increment counts (Figure 3). The number of increments between the first major increment outside of the primordium and the otolith edge were counted three times by a single reader, and mean increment count calculated. Time of formation of the first increment (i.e. at hatching or time of first feeding) has not been validated for Australian smelt and thus, increment count is expressed as 'estimated age'. Nonetheless, Tonkin *et al.* (2008b) suggest error margins are likely  $\leq 3$  days given exogenous feeding typically begins at 1–2 days of age. Spawning dates and frequency distributions were determined for each weir pool by subtracting estimated age from capture dates.



**Figure 3.** a) Larval Australian smelt and b) sagittal otolith from a larval Australian smelt. Note clear daily increments.

Photographs of marginal increments on the dorsal section of Australian smelt otoliths ( $n = 22\text{--}30$  per weir pool  $\times$  sampling event) were taken using a compound microscope (400–1000x magnification) under transmitted light. Individual widths ( $\mu\text{m}$ ) of the marginal increments in a single-plane focus (usually outer 10–40 increments) were measured along the widest radius on the dorsal section of the otolith. All measurements were made using the image analysis software *Stream* (Olympus).

#### 2.4. Morphometric condition and mean seasonal growth rates

The length-weight relationships for Australian smelt in each weir pool and sampling event were described using the polynomial models of Tonkin *et al.* (2008c). Morphometric condition was estimated by calculating the relative condition factor ( $K_{rel}$ ) of individual Australian smelt from each weir pool during each sampling event ( $n = 100$  per weir pool  $\times$  sampling event) (see Froese 2006). Weight was first expressed as a function of fish length by the Equation 1:

**Equation 1.  $W = aL^b$** 

Where  $W$  is weight (g),  $L$  is standard length (mm), and  $a$  and  $b$  are constants. Length-weight relationships were then be used to assess condition for each individual using  $K_{rel}$  where:

**Equation 2.  $K_{rel} = W/aL^b$** 

Differences in morphometric condition ( $K_{rel}$ ) of individuals sampled among weir pools and sampling events were assessed using two-factor univariate PERMANOVA. To allow for multiple comparisons between weir pools and sampling events, the 'B–Y method' significance correction was applied (see above).

Mean seasonal growth was described by applying length-at-age relationships to data from each of the weir pools (sampling events pooled) using the Gompertz growth model:

**Equation 3.  $L_x = \beta_0 e^{-e(-\beta_1(x-\beta_2))}$** 

Where  $L_x$  is the length at age  $x$ ,  $\beta_0$  is the asymptotic length,  $\beta_1$  is the instantaneous growth rate and  $\beta_2$  is the inflection point of the curve where growth rate begins to decline. Mean seasonal growth rate was calculated as the function of  $L_s$  (mm) and age at capture (mm). Differences in mean seasonal growth rate among weir pools were assessed using univariate PERMANOVA.

**2.5. Daily growth**

Seasonal growth is a measure of the average daily growth of an individual across the span of its life and thus, lacks finer-scale information on variability in daily growth. Consequently, measurements of daily increment widths were used to investigate the influence of weir pool raising on daily growth of larval and juvenile Australian smelt. Each increment was assigned to a 'growth day' (i.e. date converted to Julian day) as determined by back-calculation of estimated age from capture date, for each individual. Mixed-effects linear modelling (LMM) was used to predict otolith derived measures of daily growth (repeated growth measures for individual fish) for fish collected during each sampling trip, within each of the weir pools. Predictors included weir pool, Julian day, sampling trip and age, thus testing the hypothesis that growth rates will differ between weir pools, but also as a function of time of year, and as a function of fish age. A saturated model was first fitted to the data, which included the fixed effects of age, weir pool and Julian day, and the random effects of fish ID (random intercept for each individual) and fish age (random slope). Specifically:

Growth ~ Age + WP + Julian day + Sampling trip + (1|ID) + (1|Age)

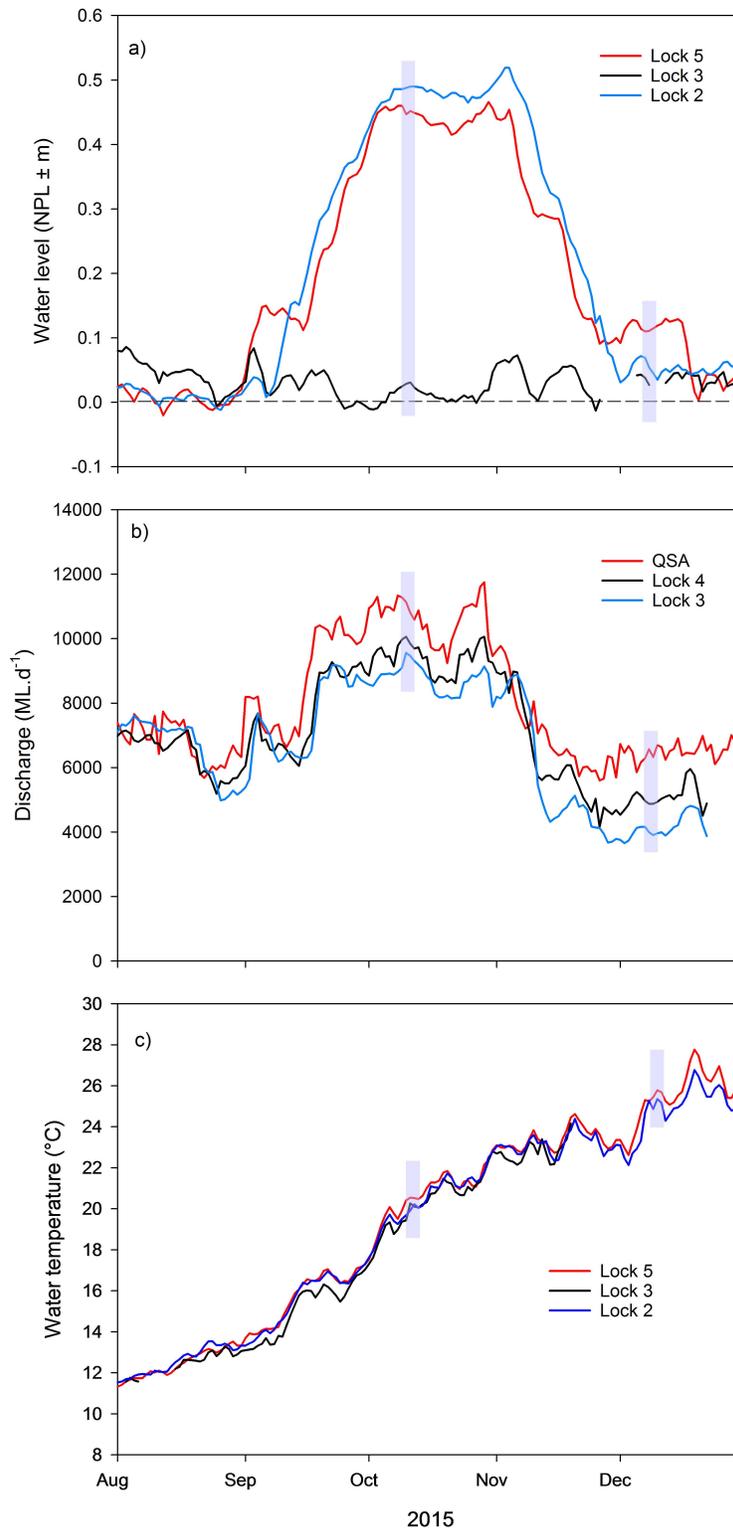
The residuals of this model showed no outliers, suggesting this general model structure was appropriate. Initial modelling focused upon determining the appropriate random-effects structure for subsequent modelling using combinations of fish ID (random intercept), fish age (random slope) and fish age given ID (random intercept and slope), resulting in a total of five different model structures. This random-effects structure allowed each individual fish to have its own random age ~ growth relationship (correlated slopes and intercepts). These different model structures were examined to investigate whether growth rates differed between the fixed effects of weir pool, Julian day, sampling trip and fish age. The relative support for each of the random effects and fixed effects models were assessed using Akaike's Information Criteria (AIC), corrected for small sampled sizes ( $AIC_c$ ) (Burnham and Anderson, 1998).  $AIC_c$  values were rescaled as the difference between each model and the model with the lowest  $AIC_c$ . All linear mixed effects models were fitted using the lmer function within the package lme4 (Bates et al. 2011) using the R statistical programming environment (R Development Core Team 2013).

### 3. RESULTS

#### 3.1. Water level, discharge, temperature

Raising of water levels in the Lock 2–3 and Lock 5–6 weir pools began in late August 2015 and occurred over a period of approximately 6 weeks (Figure 4a). Water level in the Lock 5–6 pool reached  $\sim+0.4$  m in early October and was maintained between  $+0.40$  and  $+0.46$  m until 6 November before receding to  $\sim+0.1$  m by 25 November. Water level was maintained at  $\sim+0.1$  m for a period of three weeks before receding to  $\sim+0$  m by 19 December. Water level in the Lock 2–3 pool also reached  $\sim+0.4$  m in early October and was maintained between  $+0.44$  and  $+0.52$  m until 9 November before receding to  $+0.03$  m by 1 December. Whilst not specifically raised, water level in the Lock 3–4 weir pool was  $+0.015$  m and  $+0.038$  m during monitoring in October and December 2015, respectively. All water levels are relative to the NPL of each weir pool (weir pool 2, 6.1 m AHD; weir pool 3, 9.8 m AHD; weir pool 5, 16.3 m AHD). Raising in the Lock 2–3 and Lock 5–6 weir pools inundated  $\sim 120$  and  $\sim 770$  ha of low-lying floodplain and wetland, respectively. Operation of the Chowilla Regulator also inundated  $\sim 337$  ha of floodplain and wetland habitat; with discharge from the Chowilla system ultimately entering the Lock 5–6 weir pool.

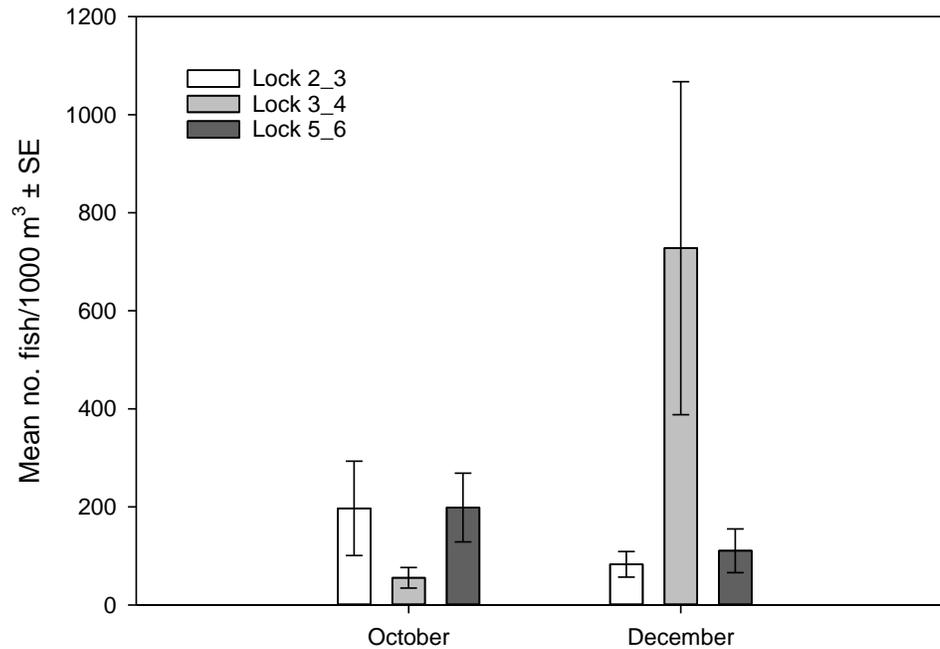
Discharge was generally low, but variable over the study period (Figure 4b), ranging  $5000$ – $8000$   $\text{ML}\cdot\text{d}^{-1}$  during August, before increasing in September with the onset of raising, and ranging  $8000$ – $11,000$   $\text{ML}\cdot\text{d}^{-1}$  at peak water levels. Discharge then receded through November and ranged  $4000$ – $8000$   $\text{ML}\cdot\text{d}^{-1}$  in December 2015. Water temperature followed typical seasonal patterns in all weir pools, with gradually increasing temperature from a low of  $\sim 12^\circ\text{C}$  in early August to  $\sim 23^\circ\text{C}$  by early December (Figure 4c). Water temperature was generally similar among weir pools, but on several occasions (i.e. September and early November) water temperature in the Lock 3–4 weir pool was slightly lower ( $0.5$ – $1.0^\circ\text{C}$ ) than the other two weir pools.



**Figure 4.** a) Daily pool level ('normal pool level' NPL ± m) upstream of Lock 5, Lock 3 and Lock 2, b) daily discharge (ML.d<sup>-1</sup>) over the SA-NSW border (QSA), Lock 4 and Lock 3, and c) daily mean water temperature upstream of Lock 5, Lock 3 and Lock 2 from August 2015 to December 2015. The timing of sampling events are indicated by shaded boxes. Water level and discharge data were sourced from the Department of Environment, Water and Natural Resources (DEWNR 2015).

### 3.2. Density of larval/juvenile Australian smelt

A total of 3884 larvae/juvenile fish, representing 10 species, were sampled using night-time plankton net tows in October and December 2015 (Appendix 1), with Australian smelt comprising ~42% of the total catch. There was substantial variability in the mean standardised density (hereafter 'density') of Australian smelt larvae/juveniles between weir pools and sampling events in October and December 2015 (Figure 5). PERMANOVA indicated a significant interaction between the factors of 'weir pool' and 'sampling event', suggesting variability in these parameters between weir pools was not consistent across sampling events (Table 1). Pairwise comparisons indicated density in both the Lock 2–3 and Lock 5–6 weir pools was significantly greater than in the Lock 3–4 weir pool, in October 2015. Alternatively in December 2015, density was substantially greater in the Lock 3–4 weir pool, than both the Lock 2–3 and Lock 5–6 weir pools (Figure 5), but this difference was not statistically significant (Table 1). This difference was likely statistically non-significant due to a low capture of Australian smelt ( $n = 4$ ) in one replicate in the Lock 3–4 weir pool and resultant high standard error (Appendix 1). Nonetheless, density in Lock 3–4 was at least five-times greater than that recorded in the other weir pools.



**Figure 5.** Mean standardised density (mean number of larvae per 1000 m<sup>3</sup> . net tow<sup>-1</sup>) ± standard error (SE) of Australian smelt larvae/juveniles sampled during night-time plankton tows ( $n = 4$ ) in the Lock 2–3, Lock 3–4 and Lock 5–6 weir pools of the lower River Murray in October and December 2015.

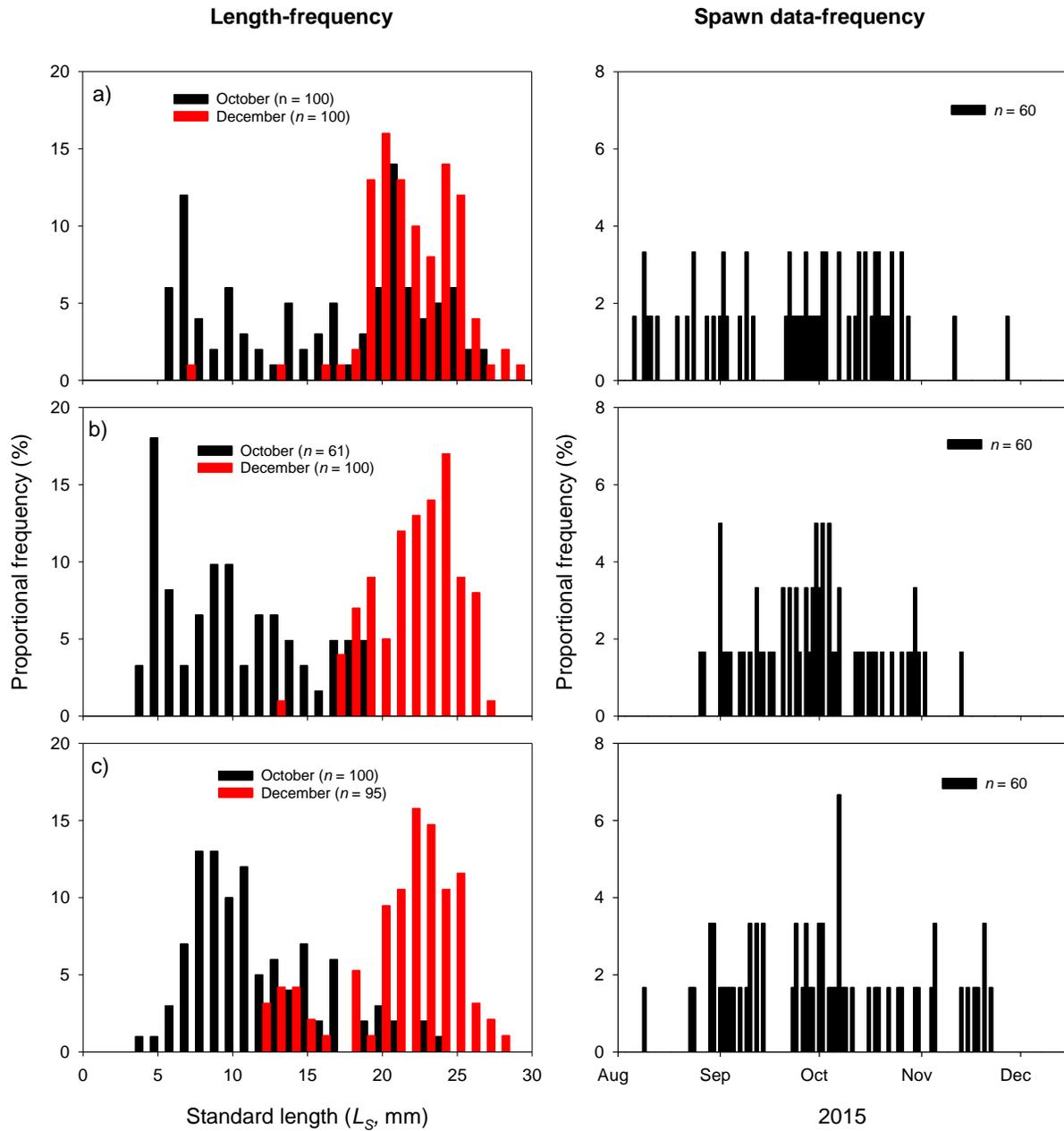
**Table 1.** Summary of two-way univariate PERMANOVA comparing the density of Australian smelt between weir pools and sampling events. When significant differences occurred, pairwise comparisons were used to determine the groups that drove this difference.  $\alpha = 0.05$  for all analyses. Significant  $p$ -values indicated in bold.

Factor	<i>df</i>	Pseudo-F	<i>P</i>	Pairwise comparison
Weir pool	2, 23	0.38	0.560	-
Event	1, 23	0.26	0.783	-
Weir pool x event	2, 23	4.62	<b>0.021</b>	October: 3–4 < 2–3 = 5–6 December: 5–6 = 2–3 = 3–4

### 3.3. Length and spawn dates

Australian smelt larvae/juveniles sampled from the Lock 2–3, Lock 3–4 and Lock 5–6 weir pools ranged in length from 3.9 to 28.6 mm ( $L_S$ ) and length frequency distributions indicated progression in length between sampling events in each weir pool (Figure 6). Length-frequency distributions

were significantly different between all weir pools in October 2015 (Table 2). Australian smelt collected in the Lock 5–6 weir pool exhibited a broader length distribution (5.4–26.8 mm  $L_S$ ), with a greater proportion of individuals >20 mm  $L_S$  than the other weir pools. In turn, individuals from the Lock 2–3 weir pool exhibited a broader length-distribution (4.1–23.6 mm  $L_S$ ), with a greater proportion of individuals >20 mm  $L_S$  than the Lock 3–4 weir pool (3.9–19.3 mm  $L_S$ ). Length-frequency distributions were not significantly different between weir pools in December 2015 (Table 2), ranging 11.5–27.7, 12.5–26.5 and 6.6–28.6 mm  $L_S$  (Figure 6) in the Lock 2–3, Lock 3–4 and Lock 5–6 weir pools, respectively.



**Figure 6.** Length-frequency (left-hand column) and spawn date-frequency (right column) distributions of larvae/juvenile Australian smelt sampled in the a) Lock 5–6, b) Lock 3–4 and c) Lock 2–3 weir pools of the lower River Murray in October and December 2015. Length-frequencies are presented by sampling event, whilst sampling events are pooled for spawn date-frequencies

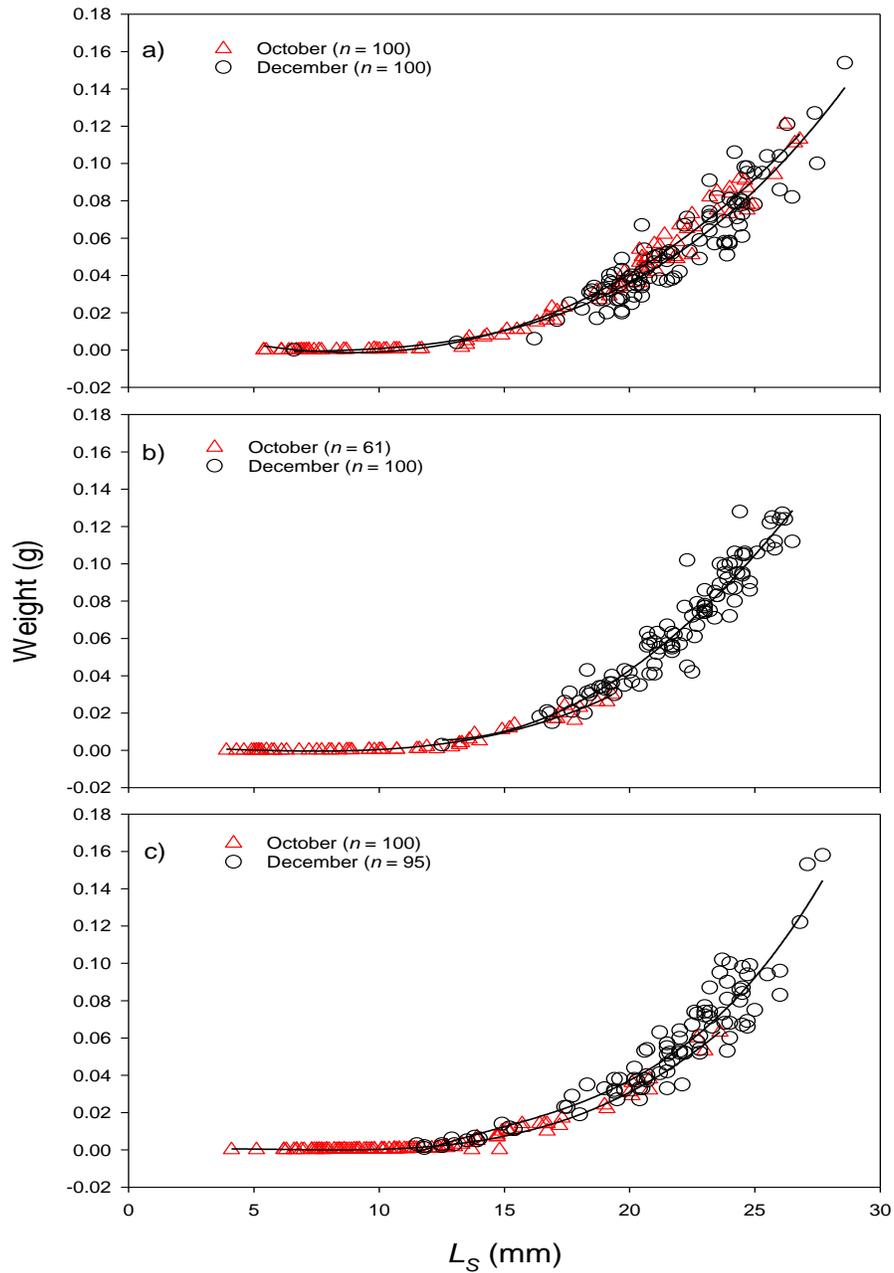
**Table 2.** Results of Kolmogorov-Smirnov ‘goodness-of-fit’ comparisons ( $D$  statistic and  $p$ -value,  $\alpha = 0.05$ ) of length-frequency distributions of Australian smelt between the Lock 5–6, Lock 3–4 and Lock 2–3 weir pools of the lower River Murray in October and December 2015.

Comparison	October			December		
	<i>df</i>	<i>D</i>	<i>p</i> -value	<i>df</i>	<i>D</i>	<i>p</i> -value
Lock 5–6 v Lock 3–4	100, 61	0.450	<b>&lt;0.001</b>	100, 100	0.150	0.193
Lock 5–6 v Lock 2–3	100, 100	0.400	<b>&lt;0.001</b>	100, 95	0.140	0.274
Lock 3–4 v Lock 2–3	61, 100	0.259	<b>0.010</b>	100, 95	0.137	0.295

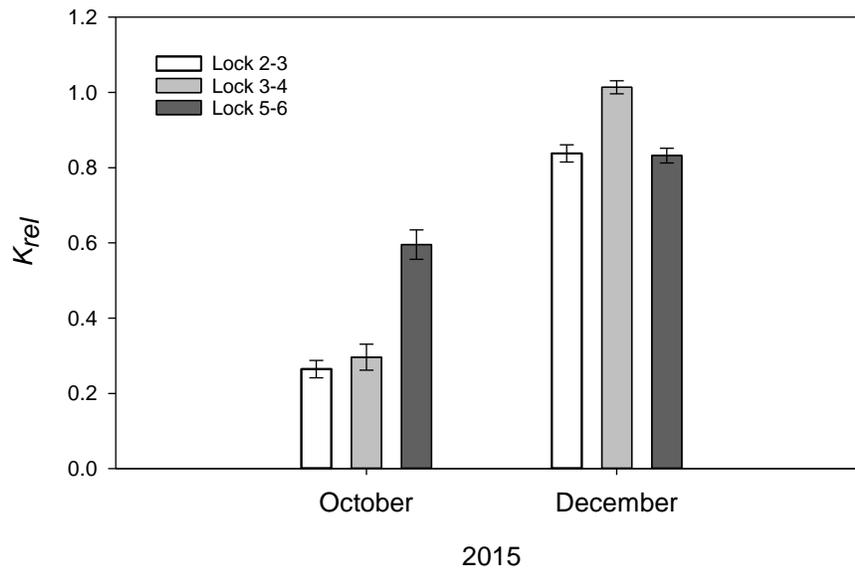
Estimated ages of larval/juvenile Australian smelt ranged from 10 to 76 days. Australian smelt collected in the Lock 2–3 and 5–6 weir pools, were derived from broad spawning seasons of 105 (9/08/2015–22/11/2015) and 113 days (6/08/2015–27/11/2015), respectively, in contrast to a narrower spawning season of 79 days (26/08/2015–13/11/2015) in the Lock 3–4 weir pool (Figure 6). Spawning began earlier in August, in both of the raised weir pools, particularly Lock 5–6 where 20% of fish sampled were derived from spawning in August, compared to ~3% from Lock 3–4. A greater proportion of fish were also spawned in November in the Lock 2–3 weir pool (~17%), relative to the other weir pools (both ~3%). Peak spawning, however, was consistent across weir pools and occurred from late September to mid-October, with >40% of larvae/juveniles from each weir pool derived from spawning in this period.

### 3.4. Morphometrics and seasonal growth

A cubic polynomial of  $L_S$  was used to model length–weight relationships for Australian smelt (*sensu* Tonkin *et al.* 2008c) in each weir pool during each sampling event (Figure 7). Differences in body condition of Australian smelt larvae/juveniles were assessed by comparing the relative condition index ( $K_{rel}$ ) between weir pools and sampling events (*sensu* Macdonald *et al.* 2012) (Figure 8) using PERMANOVA (Table 3). A significant interaction existed between weir pool and sampling event, suggesting  $K_{rel}$  was significantly different among weir pools, but differences were not consistent across sampling events. Pairwise comparisons revealed that in October 2015,  $K_{rel}$  was significantly greater in Lock 5–6 than the other weir pools, whilst in December 2015,  $K_{rel}$  was significantly greater in Lock 3–4 than the other weir pools.



**Figure 7.** The relationship between weight and standard length ( $L_S$ ) of Australian smelt sampled in October and December 2015 predicted by linear regression models for a) the Lock 5–6 weir pool (Oct: weight =  $0.02 - 0.0045 \times \text{Length} + 0.0002 \times \text{Length}^2 + 0.0001 \times \text{Length}^3$ , Dec: weight =  $-0.0025 - 0.0009 \times \text{Length} - 0.0002 \times \text{Length}^2 + 0.00001 \times \text{Length}^3$ ), b) the Lock 3–4 weir pool (Oct: weight =  $0.002 - 0.0001 \times \text{Length} - 0.00009 \times \text{Length}^2 + 0.000009 \times \text{Length}^3$ , Dec: weight =  $0.110 - 0.018 \times \text{Length} + 0.0008 \times \text{Length}^2 - 0.000003 \times \text{Length}^3$ ), and c) the Lock 2–3 weir pool (Oct: weight =  $-0.0014 + 0.0012 \times \text{Length} + 0.0002 \times \text{Length}^2 + 0.00001 \times \text{Length}^3$ , Dec: weight =  $-0.150 + 0.026 \times \text{Length} - 0.0015 \times \text{Length}^2 + 0.00004 \times \text{Length}^3$ ).

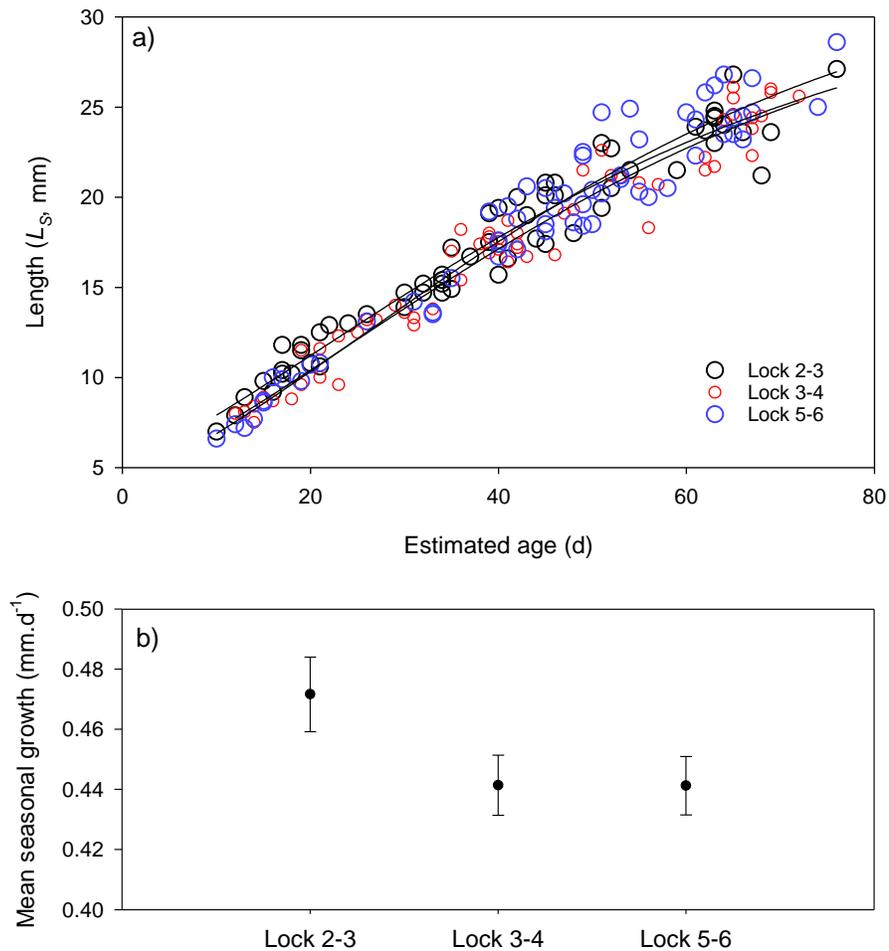


**Figure 8.** Mean relative condition index ( $K_{rel}$ ) ± SE of larval/juvenile Australian smelt

**Table 3.** PERMANOVA pairwise comparisons of the relative condition index ( $K_{rel}$ ) of larval/juvenile Australian smelt between weir pools in October and December 2015. Significance differences are presented in bold ( $\alpha = 0.02$ ).

Location	Pairwise comparison		<i>t</i>	<i>p</i> value
October	Lock 2–3	Lock 3–4	0.79	0.435
	Lock 2–3	Lock 5–6	7.28	<b>&lt;0.001</b>
	Lock 5–6	Lock 3–4	5.27	<b>&lt;0.001</b>
December	Lock 2–3	Lock 3–4	6.18	<b>&lt;0.001</b>
	Lock 2–3	Lock 5–6	0.19	0.840
	Lock 5–6	Lock 3–4	6.95	<b>&lt;0.001</b>

Relationships between length and age for Australian smelt collected from each weir pool (sampling events pooled) were similar (Figure 9a). Correspondingly, whilst mean seasonal growth rate in the Lock 2–3 weir pool was slightly higher than both Lock 3–4 and Lock 5–6 (Figure 9b), this difference was determined to be non-significant (PERMANOVA,  $Pseudo-F_{2, 179} = 2.61$ ,  $p = 0.08$ ).



**Figure 9.** a) Relationship between standard length ( $L_s$ , mm) and estimated age (d) for larval/juvenile Australian smelt, based on the Gompertz model, for the Lock 2–3, Lock 3–4 and Lock 5–6 weir pools; and b) mean seasonal growth rate ( $\text{mm.d}^{-1}$ )  $\pm$  SE of larval/juvenile Australian smelt from each of the weir pools.

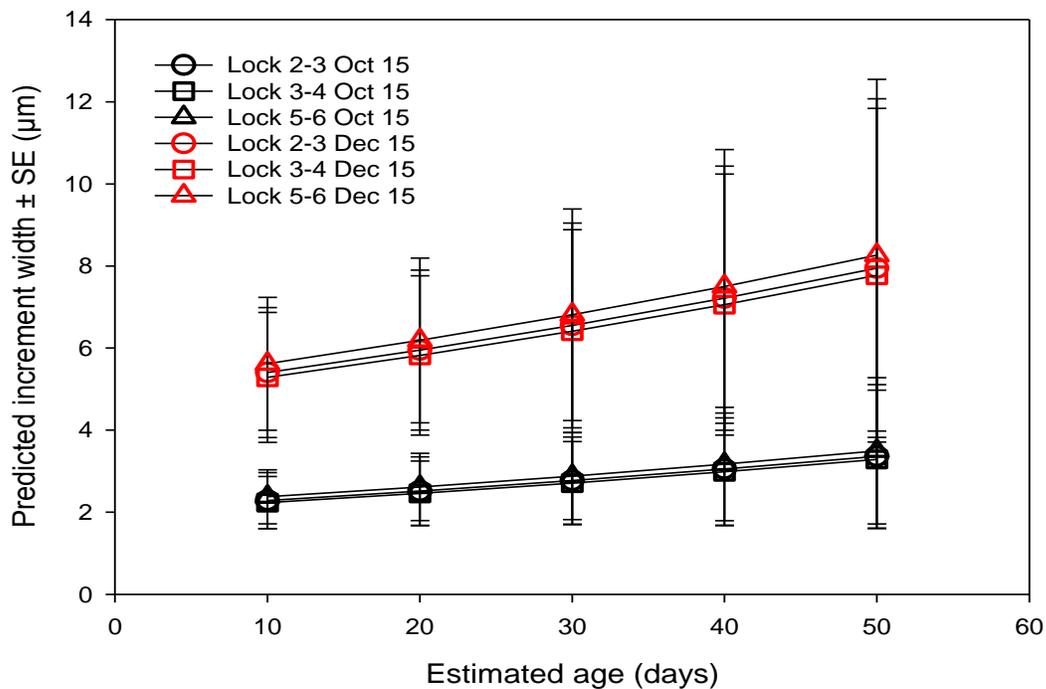
### 3.5. Daily growth

Analysis of five random effects models suggested a model that included the random-effects of individual fish ID (random intercepts) and age within fish ID (random intercept and slope) had the most support based on differences in  $\text{AIC}_c$ . Further analysis of the fixed-effects models suggested a model that included the fixed-effects of weir pool, age and sampling trip had the most support. This model indicated the fixed effects of sampling trip and fish age had significant positive effects on daily growth, with daily otolith growth rate increasing between October and December 2015, and with fish age (across the range of ages sampled), across all weir pools (Table 4 and Figure

10). Daily growth rates were similar among weir pools, with no significant differences (Table 4 and Figure 10).

**Table 4.** Output table of linear mixed effects model including the fixed effects of weir pool and Julian day. *t*-values >2 are deemed significant and presented in bold.

Fixed effect	Estimate	SE	<i>t</i> -value
(Intercept)	0.729	0.072	16.129
Age	0.010	0.002	<b>4.367</b>
Weir pool 3–4	-0.022	0.087	-0.253
Weir pool 5–6	0.039	0.085	0.457
Sampling trip 2	0.861	0.070	<b>12.320</b>



**Figure 10.** Daily increment growth  $\pm$  standard error ( $\mu\text{m}$ ) of Australian smelt aged 10–50 days predicted from the mixed-effects model for the October and December 2015 sampling events in the Lock 5–6, Lock 3–4 and Lock 2–3 weir pools.

## 4. DISCUSSION

The current study investigated aspects of the early life history (spawning, condition, growth) of Australian smelt to assess the influence of raising water levels in the Lock 2–3 and Lock 5–6 weir pools, in spring/summer 2015, on secondary productivity. We hypothesised that larval/juvenile Australian smelt from the raised weir pools would be derived from broader spawning seasons and exhibit greater morphometric condition, and growth rates, than larvae/juveniles from the reference weir pool, due to increased habitat availability and improved primary productivity, following liberation of allochthonous resources. We also hypothesised that seasonal progression would influence these parameters. The results of the study were varied, with minor differences in spawning seasons and condition among weir pools in agreement with our hypotheses, but counter to our hypotheses, these responses were not reflected in significantly improved growth rates in raised weir pools. Indeed, seasonal progression appeared to have a greater influence on condition and growth than weir pool raising.

Larval/juvenile Australian smelt were more abundant and exhibited broader length and age ranges in the two raised weir pools in October 2015, relative to Lock 3–4, corresponding with a broader range and earlier spawning dates in these weir pools, particularly Lock 5–6. This pattern is the result of either: 1) broader and earlier commencement of spawning in the raised weir pools; or 2) greater survival of larvae spawned early in the season (e.g. August) in raised weir pools. Spawning in many species native to the lower River Murray is related to circa-annual rhythms of temperature and/or photoperiod (Humphries *et al.* 1999), consequently, spawning may be initiated earlier in some regions if temperature thresholds are met. Spawning in Australian smelt in the lower River Murray has previously been recorded from August to December (Leigh 2002), with spawning thought to be initiated at water temperatures from 11–15 °C (Milton and Arthington 1985, Humphries *et al.* 2002). Water temperature in the lower reaches of each weir pool, as measured by mid-channel water quality stations, was similar and >12 °C by mid-August 2015. The Lock 5–6 weir pool has a greater area of shallow permanent wetland habitat than the Lock 2–3 weir pool. These microhabitats are likely to warm faster than main channel habitats through early spring, potentially resulting in increased availability of suitable spawning areas. As such, the spatial variation in spawning seasons of Australian smelt sampled may be a regular occurrence and unrelated to weir pool raising.

Alternatively, a broader range and earlier spawn dates of fish sampled from the raised weir pools, may be the result of greater survival of larvae spawned early in the season (e.g. August), relative

to Lock 3–4. Whilst we generated putative spawning seasons for fish from the three weir pools, these represent the seasons from which the fish sampled were derived rather than representing absolute spawning seasons within each weir pool. For instance, spawning may have occurred in the Lock 3–4 weir pool in August, but poor survival in this weir pool, relative to the raised weir pools, may have resulted in an absence of these individuals from sampling in October and December 2015. This mechanism is in agreement with the findings of Humphries *et al.* (2013) who suggest that survival and recruitment of Australian smelt to juvenile stages is typically greatest for individuals spawned later in the spawning season, relative to earlier, in several rivers across the Murray-Darling Basin. Humphries *et al.* (2013) proposed that temperature, as well as prey density as a function of the interaction between temperature and discharge, plays a large role in the timing and magnitude of recruitment to the juvenile life stage. If this mechanism is the driver of patterns observed in spawn dates of Australian smelt collected in the current study, it suggests a potential benefit to larval survival in association with weir pool raising, which would presumably be driven by increased prey availability (e.g. zooplankton).

Morphometric condition of Australian smelt increased as expected between sampling events in all weir pools, but differences occurred between weir pools that were not consistent across the sampling events. Small-bodied fishes typically have high metabolic rates and energy requirements (Wooten 1998), and consequently, morphometric condition is likely to reflect short-term somatic growth over periods of days. Under conditions of low-flow in the River Murray, like those experienced in our study, zooplankton abundance and thus, resource availability for larval/juvenile Australian smelt, typically increases in association with water temperature (Humphries *et al.* 1999, King 2005) and may account for differences in condition between October and December 2015 in the current study. In October 2015, Australian smelt from the Lock 5–6 weir pool exhibited morphometric condition double that of the Lock 2–3 and Lock 3–4 weir pools, which may indicate relatively elevated resource availability in this weir pool in the immediately preceding period, and a potential positive response to water level raising. This sampling event occurred approximately four weeks following the commencement of water level raising in the Lock 5–6 weir pool, and in association with operation of the Chowilla Regulator. High relative condition of Australian smelt may be a result of enhanced zooplankton and terrestrial insect (preyed upon by juvenile and adult Australian smelt (King 2005)) abundance, with inundation promoting emergence of zooplankton from sediment egg banks and liberation of insects from terrestrial vegetation. The disparity in condition between the two raised weir pools may be explained by the

comparatively minimal floodplain inundation that occurred in the Lock 2–3 weir pool, relative to Lock 5–6, and potentially minimal changes in resource availability

The pattern of variability in morphometric condition among weir pools, differed in December 2015. Counter to our hypothesis that weir pool raising would promote increased condition in Australian smelt, the condition of Australian smelt larvae/juveniles in December 2015 was greater in the un-raised Lock 3–4 weir pool than the two raised weir pools. The density of larval/juvenile Australian smelt was also greatest in the Lock 3–4 weir pool. High density of early life stages can lead to density-dependence in fish populations and increased intra-specific competition for finite resources, ultimately leading to diminished condition (Post *et al.* 1999), but this was not the case here. Greater condition in Lock 5–6 in October 2015 suggests resource availability may have been improved immediately following the initiation of raising, but low condition, relative to Lock 3–4 in December 2015, may indicate the resource availability benefits of water level raising may be short-lived. Additionally, high relative condition in Lock 3–4 may reflect compensatory somatic growth in this weir pool immediately preceding sampling in December, following relatively poor resource availability and condition in October (Tonkin *et al.* 2008a). Another possible explanation, is that productivity benefits derived in the Lock 5–6 weir pool, were transferred downstream and enhanced condition of Australian smelt in the Lock 3–4 weir pool in December 2015, masking potential difference among weir pools. Whilst this may represent a potential confounding factor in our experimental design, we consider this unlikely given observed patterns of primary productivity (Wallace and Cumming unpublished).

Morphometric indices are useful for assessing instantaneous condition and potentially, recent resource availability, but analyses of otolith derived growth measures may provide greater insight on growth throughout life. In this study, the results of otolith-related growth analyses were consistent with the seasonal progression observed in morphometric condition, but differences in morphometric condition among weir pools were not reflected in differences in growth rates. Indeed, length-at-age relationships were similar among weir pools and suggested that mean seasonal growth rates over the life of the fish sampled (*i.e.* 10–76 days in the current study) were slightly greater in the Lock 2–3 weir pool, albeit without statistical significance. As this metric integrates growth over the life of a fish, it dilutes any differences in instantaneous growth that may occur throughout life, and thus, may be a coarse tool for assessing differences in growth among weir pools unless differences are large. The assessment of short-term growth patterns (*i.e.* daily otolith growth), provides a better means of assessing variability in growth throughout life and between weir pools. Our analyses demonstrated that daily growth of the Australian smelt sampled

was mostly influenced by seasonal progression. Fish sampled during December 2015 grew faster than like aged fish sampled in October 2015, whilst fish from both sampling trips grew fastest in the days immediately preceding capture. Contrary to our hypothesis that weir pool raising would promote increased daily growth rates of Australian smelt, differences among weir pools were non-significant.

Otolith growth in Australian smelt has previously been associated with food density and temperature in a laboratory setting, with high temperature-high food density treatments exhibiting greatest growth rates (Tonkin *et al.* 2008a). The significant influence of seasonal progression, and implicitly increasing temperature, on daily growth rates may be a reflection of increased metabolic rates and/or food availability, as a function of season throughout the lower River Murray, irrespective of weir pool. Nonetheless, the lack of significant difference in daily growth rates between weir pools was surprising given the difference in inundation area (Lock 5–6 ~6-fold that of Lock 2–3) and primary productivity between weir pools.

Patterns of primary productivity were variable and complex in the Locks 5–6 and 2–3 weir pools in spring/summer 2015. Gross primary productivity (GPP) downstream of Lock 6 (also downstream Chowilla Creek junction) and Lock 3 increased by approximately 100% and 30%, respectively, coincident with peak raising in spring 2015 (Wallace and Cummings unpublished) and October sampling in the current study. A substantial increase in GPP was also concurrently measured in Punkah Creek and Chowilla Creek upstream of the Chowilla Regulator. Similar responses were not observed in the unraised Lock 6–7 weir pool, suggesting these responses were a result of water level manipulation. Nonetheless, increased GPP was not measured in the lower reaches of these weir pools immediately upstream of Lock 5 and Lock 2, respectively, despite the greatest variability in water levels as a result of weir manipulations, occurring in these reaches. Wallace and Cummings (unpublished) suggest the muted responses in GPP detected in the lower reaches of the Lock 5–6 and Lock 2–3 weir pools may indicate rapid assimilation of organic material and limited downstream transportation during peak raising. Increased primary productivity, relative to 'before raising', was also observed throughout the Lock 2–3 and Lock 5–6 weir pools during early summer and drawdown to +0 m NPL post-raising, but the association of enhanced productivity with water level manipulation was inconclusive as enhanced productivity was also observed during this period in the Lock 6–7 weir pool. The enhanced productivity observed in the Lock 6–7 weir pool may be a seasonal pattern or may be a result of the influence of raising events that occurred upstream in the Lock 7–8 and Lock 8–9 weir pools and downstream transport of organic matter.

Whilst changes in primary productivity were complex, there are several consistencies with observed condition and growth of Australian smelt. In particular, greater increases in primary productivity in the Lock 5–6 than the Lock 2–3 weir pool, during peak raising, concurred with greater morphometric condition of Australian smelt in this weir pool. Broadly increased primary productivity in all weir pools investigated by Wallace and Cummings (unpublished, i.e. Lock 2–3, Lock 5–6 and Lock 6–7) in early summer is also consistent with increased morphometric condition and growth rates of Australian smelt among all weir pools investigated in our study in December, compared to October 2015. Nonetheless, teasing apart the influence of seasonal effects and upstream weir pool manipulations on responses in primary productivity and Australian smelt condition and growth in unraised weir pools (i.e. Lock 6–7 and Lock 3–4) is difficult. The proposition by Wallace and Cummings (unpublished) that organic matter was rapidly assimilated in the Lock 5–6 and 2–3 weir pools during peak raising does suggest that downstream transport of organic matter derived in the Lock 5–6 weir pool, to the Lock 3–4 weir pool, and subsequent masking of differences between weir pools in our study is unlikely. Nonetheless, the relative contribution of weir pool manipulation and seasonal effects could only be confirmed with replication of the current study and that of Wallace and Cummings (unpublished) in a year with no weir pool manipulations.

The results of the current study and the parallel investigation of Wallace and Cummings (unpublished) raise several questions regarding the link between primary and secondary productivity as influenced by weir pool manipulations, and more generally. Limited response of fish growth rates, despite putative increases in primary productivity, suggests either: 1) increases in primary productivity were not of a sufficient magnitude to elicit measurable responses in growth rates; 2) organic matter that was rapidly assimilated within the weir pools did not enter a trophic pathway that directly benefited Australian smelt; and/or 3) productivity benefits were transported downstream to the unraised Lock 3–4 and masked differences between weir pools. Whilst the third mechanism cannot be discounted, we consider it unlikely given the spatial patterns in primary productivity during peak raising. Recent research indicates that biofilms may play a large role in the assimilation of allochthonous carbon in the River Murray (Cook *et al.* 2015). Consequently, assimilation of carbon by biofilms may preclude benefits to production of small-bodied pelagic fishes such as Australian smelt, which are unlikely to feed directly on biofilms or prey upon species that do (e.g. *Paratya australiensis*). Indeed, an increase in the abundance of *P. australiensis* in the lower reach of the Lock 2–3 weir pool coincided with weir pool raising in 2015, which was not observed in the unraised Lock 3–4 weir pool, suggesting a potential positive response of this

species to increased habitat and resource availability (Cummings *et al.* unpublished). In concurrence with morphometric condition and growth rate results from the current study, elevated abundance of *P. australiensis* was not observed following recession to NPL, suggesting positive responses were short-lived. The findings of the current study are important given increased primary productivity is commonly implied to infer diversity and productivity of food webs, and thus, likely enhancement of secondary productivity. In some cases, this may be incorrect and patterns of carbon transfer are likely to be highly complex. This highlights the need to better understand trophic pathways and links between primary and secondary productivity in the lower River Murray.

## 5. CONCLUSION

We hypothesised, that following the raising of water levels within the Lock 2–3 and Lock 5–6 weir pools in spring 2015, larvae/juvenile Australian smelt from the raised weir pools would be derived from broader spawning seasons and exhibit greater morphometric condition and growth rates than larvae/juveniles from a reference weir pool, due to increased habitat availability and improved primary productivity, following liberation of allochthonous resources. In support of our hypotheses, larvae/juvenile Australian smelt from raised weir pools were derived from broader spawning seasons that commenced earlier than in Lock 3–4, which may indicate greater relative larval survival, whilst in October 2015, the morphometric condition of larvae/juvenile Australian smelt was greater in Lock 5–6 than the other two weir pools, suggesting a potential immediate response to improved resource availability with weir pool raising. Nonetheless, contrary to our hypotheses, these responses were not reflected in growth rate analyses, and there was no indication of improved morphometric condition in December 2015, in relation to weir pool raising. Overall, the major determinant of condition and growth of larvae/juvenile Australian smelt appeared to be seasonal progression, with condition and growth rates increasing in all weir pools from October to December.

Wallace and Cummings (unpublished) demonstrated increases in primary productivity in the uppermost reaches of weir pools, but not in the lower reaches, coincident with peak raising in spring 2015, whilst Cummings *et al.* (unpublished) suggested potential short-lived positive responses in the abundance of *Paratya australiensis* in the Lock 2–3 weir pool. These studies suggest the potential for spatially and temporally confined productivity responses to weir pool raising, which are in agreement with the condition and growth analysis in our study. Increased primary productivity is often suggested to elicit more diverse and productive foodwebs, but benefits for individual species (e.g. Australian smelt) may only be realised if trophic upsurge is of sufficient magnitude to elicit a response and carbon follows the trophic pathway with which they are associated. Ultimately, trophic dynamics and the links between primary and secondary productivity remain knowledge gaps in lowland floodplain rivers, including the lower River Murray. Developing an improved understanding of these patterns and processes, which are putatively critical to riverine ecosystem function, will help inform efforts at river restoration, including the utility of weir pool manipulations.

Enhancement of secondary productivity in association with weir pool raising could be more rigorously evaluated by incorporating multiple years of sampling/analysis and monitoring of further biotic parameters. Sampling in our project was limited to one year when weir pool raising occurred

in multiple weir pools. Greater inference may be derived from replication of the study across the same weir pools in years with no weir pool manipulation. This could confirm if differences in the spawning seasons from which juvenile recruits were derived and morphometric condition (and lack of difference in growth rates) among weir pools were indeed related to weir pool raising or are typical spatial differences between weir pools. Furthermore, concurrent monitoring of food resource availability (e.g. zooplankton community structure and density) would assist interpretation of condition and growth indices.

Whilst evidence of promotion of secondary productivity in association with +0.5 m raising of water levels in the lower River Murray remains inconclusive, the minor positive responses detected in the current study are promising. Raising events of greater magnitude (e.g. +1.0 m NPL) or during periods of differing discharge may illicit greater secondary productivity responses.

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## APPENDICES

**Appendix 1.** Species and number of larvae/juveniles (<30 mm length) sampled from each replicate night-time plankton tow in the Lock 2–3, Lock 3–4 and Lock 5–6 weir pools of the lower River Murray in October and December 2015. The volume of water (m<sup>3</sup>) filtered during each replicate tow is also presented.

Species		October 2015												December 2015															
Common name	Scientific name	Lock 2-3				Lock 3-4				Lock 5-6				Lock 2-3				Lock 3-4				Lock 5-6							
	Replicate	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
	Water volume filtered (m <sup>3</sup> )	302	274	271	297	292	265	280	277	358	355	344	339	254	527	402	461	333	256	270	324	269	294	437	317				
Unspecked hardyhead	<i>Craterocephalus fulvus</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Common carp	<i>Cyprinus carpio</i>	0	0	1	1	5	3	1	3	0	2	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eastern gambusia	<i>Gambusia holbrooki</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Carp gudgeon complex	<i>Hypseleotris</i> spp	2	0	0	0	1	0	0	0	10	17	16	21	25	24	25	17	5	5	4	2	5	1	2	0				
Murray cod	<i>Maccullochella peelii</i>	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Murray rainbowfish	<i>Melanotaenia fluviatilis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0
Bony herring	<i>Nematalosa erebi</i>	0	0	0	0	0	0	0	0	13	0	0	1	531	649	389	93	67	42	52	46	0	0	4	7				
Flat-headed gudgeon	<i>Philypnodon</i> spp	0	1	0	0	0	0	1	0	2	0	1	0	17	22	11	4	29	6	19	4	7	2	8	5				
<b>Australian smelt</b>	<b><i>Retropinna semoni</i></b>	122	42	60	36	11	26	21	3	35	44	47	129	5	19	29	41	4	125	224	450	12	12	68	60				
Freshwater catfish	<i>Tandanus tandanus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	0	3				
Unknown spp	-	1	0	0	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	4	0	1	0	5	0				