# From drought to flood: AnNual variation in larval fish ASSEMBLAGES IN A HEAVILY REGULATED LOWLAND RIVER. 

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#### Abstract

One of the most severe anthropogenic impacts on river systems throughout the world has been drastic alterations to the natural flow regime. In Australia, many native freshwater fish have declined in range and abundance in response to anthropogenic changes to the flow regime. The MurrayDarling Basin recently experienced one of the worst hydrological droughts on record, this combined with extensive river regulation resulted in unfavourable conditions for spawning and larval survival for flow-induced spawners. The drought was recently ended by a sustained period of high rainfall, which resulted in widespread flooding and a flow that was more representative of natural flows than the managed regime. This study investigated the annual change in larval assemblages of native and alien species in the Lower River Murray during varying hydrological conditions. Larval fish were sampled during spring/summer during three distinct hydrological periods: 2005 under a withinchannel flow pulse and water level rising; 2006, 2007 and 2008 during a drought with very low regulated flows and stable water levels; and 2010 during a significant flow pulse and over bank floods. Data were analysed for annual, spatial and seasonal variations using multivariate techniques and correlations were identified between changes in larval assemblages and environmental variables (discharge, water level, conductivity and temperature). Three types of spawning characteristics were evident in the changes in the larval assemblage: 1) flow-induced spawners, 2) low- medium flow spawners and 3) seasonal spawners. The majority of small to medium-bodied native species spawned in low flow years, while for some species changes in abundance was more strongly correlated to seasonal variation. Larvae of Macquaria ambigua ambigua and Bidyanus bidyanus were not recorded during the low flow years, low abundances of larvae were recorded during the within-channel flow pulse year and significant increases in eggs and larval abundances were recorded during the high flow and over bank flood year. This study suggests that extended drought and low flow periods can have a significant negative effect on populations of large-bodied native species and that mitigation strategies, including water allocations aimed at maintaining or restoring necessary conditions for fish spawning and recruitment, should be planned prior to action being required.


## Introduction

Flow regimes are a major factor influencing fish spawning and recruitment in large rivers (Agostinho et al. 2004; Sparks 1995; Welcomme 1985; Winemiller 2005). The flood pulse concept is a riverine production model designed for large unaltered river systems with productive floodplains in the temperate, subtropical, or tropical regions (Junk et al. 1989). This model assumes that the majority of the primary production in rivers originates directly or indirectly from interactions with the floodplain and not from downstream transport of organic matter produced elsewhere in the basin (Junk et al. 1989). The flood pulse concept proposes that the strength of fish recruitment is linked to prey availability as a function of floodplain inundation. In temperate river systems high temperatures and high flows must coincide for successful utilisation of the floodplain by fishes for spawning and recruitment (Junk et al. 1989). This emphasises the importance of the lateral connectivity between the river channel and the floodplain for primary production, providing spawning cues, and food and habitat for fish (Junk et al. 1989). Following the principles of the flood pulse concept (Junk et al. 1989), the flood recruitment model was developed for Australian temperate rivers by Harris and Gehrke (1994). The flood recruitment model proposes two methods by which increased flows may enhance recruitment in river fish: flooding directly triggers spawning, or flooding indirectly enhances the survival of larvae and juveniles by providing suitable food and habitat on the inundated floodplain (Harris and Gehrke 1994). Despite widespread acceptance of the principles of the flood pulse concept and flood recruitment model, many fish in temperate rivers have developed adaptations to spawn and recruit during periods of low flow (e.g. Cheshire 2010; Humphries et al. 1999; King et al. 2003; Zeug and Winemiller 2008). The low flow recruitment hypothesis (Humphries et al. 1999), highlights that some species can successfully spawn and recruit during low withinchannel flows.

Anthropogenic changes, such as river regulation and water abstraction, affect the natural flow regimes of rivers by reducing the frequency and duration of major floods, the timing, magnitude and frequency of within-channel flows, and can often act to stablise water levels (Maheshwari et al. 1995; Richter et al. 1996). In south-eastern Australia, anthropogenic alterations have had a profound impact on the natural flow regimes of rivers throughout the Murray-Darling Basin (MDB), a large predominantly arid-zone lowland system. This is most pronounced in the lower River Murray, where the installation of levies, five tidal barrages and 11 low level (< 3 m ) weirs and a high level of upstream abstraction have resulted in serial impounding of the main river channel and created a heavily regulated system (Maheshwari et al. 1995; Walker 2006). During non-flood conditions the river has relatively stable water levels and has lost its lotic characteristics, with one of the most obvious effects being the loss of ecologically valuable low-medium within-channel flows (MallenCooper and Stuart 2003; Walker 2006). Between 2002 and 2009, these anthropogenic impacts were further compounded by one of the most severe hydrological droughts experienced in the MDB,
where above average ambient temperatures exacerbated the impacts of low rainfall (MDBC 2007; Murphy and Timbal 2008). This extended low flow period was broken in 2010 when above average rainfalls throughout most of the upper-catchment zones resulted in wide spread flooding throughout the MDB and the highest flow of water into South Australia since 1997.

Changes to the flow regime as a direct result of anthropogenic alterations, have been implicated in the decline of worldwide riverine fish communities (e.g. de Leeuw et al. 2007; Minkley 1991; Walker et al. 1995). Native fish throughout the MDB have declined in abundance and distribution following extensive modification of the system (Cadawallader 1978; Gehrke et al. 1995; Humphries et al. 2002). Knowledge of the role of flows and flooding in the life history cycles of many of the MDB fish has improved in recent years (e.g. Cheshire 2010; Humphries et al. 1999; King et al. 2003), but is still unable to describe the complex ecological mechanisms and environmental conditions required to enhance or maintain successful spawning and recruitment.

Successful spawning and recruitment of many species in the main channel has been demonstrated during low flow conditions (Cheshire 2010; Humphries et al. 2002; King 2004b). Specifically, the low flow recruitment hypothesis has been shown to be applicable in the Lower River Murray for the small to medium-bodied natives species (Cheshire 2010). The flood recruitment model, however, has yet be fully investigated in the Lower River Murray, where hydrological conditions are different to elsewhere in the MDB (Walker 2006). It is therefore important to understand the life history strategies of key species, and changes in populations during varying hydrological conditions, in an effort to improve knowledge for native fish conservation and management.

This study builds on previous studies conducted during low flow periods by Cheshire and co-workers (Bucater et al. 2009; Cheshire 2010; Cheshire and Ye 2008b) to assess how changes in hydrology influence larval abundance of native fish in the Lower River Murray. Larval fish were sampled in the Lower River Murray during the key spawning season in three distinct hydrological periods; 2005 during a within-channel flow; 2006, 2007 and 2008 during a drought with very low regulated flows; and 2010 during a significant flow pulse and over bank flood. The specific aim was to compare annual variability in larval assemblages between a within-channel flow pulse year, a series of low flow years and a high flow / overbank flood year. If annual differences occurred in larval fish assemblages, could these be correlated to changes in hydrology and other key environmental variables?

## Materials and methods

## Study sites

This study occurred in the main channel of the Lower River Murray in South Australia (Figure 1). The Lower River Murray has no significant tributaries and its hydrology is determined by flows from the mid- and upper- Murray and Darling Rivers. The main channel in this region is heavily regulated by six weirs (Figure 1), which have altered the natural hydrology, during low to medium flow periods this has resulted in a series of lentic weir pool habitats, where historically there was a highly variable lotic system (Walker 2006). The Lower River Murray encompasses four distinct geo-morphological zones including the floodplain and gorge regions, each with distinct ecological features.

Sampling was conducted in two reaches of the lower River Murray: in the tailwaters 5 km downstream of Weir 1 (Site $1,34^{\circ} 21.138^{\prime} \mathrm{S}, 139^{\circ} 37.061^{\prime} \mathrm{E}$ ), and Weir 6 (Site 6, 33 $59.725^{\prime} \mathrm{S}$, $140^{\circ} 53.152^{\prime}$ E) (Figure 1). The area surrounding site 1 is the gorge region, and the area surrounding site 2 is the floodplain region. Despite the surrounding floodplains being different, the main channel habitat is generally similar with wide, deep, slow flowing pool habitats. The downstream regulation of the two sites is substantially different. Site 2 occurs in the tailwater regions below Weir 6, in this reach the water level is managed and held at a stable level in years of low discharge by the downstream management of Weir 5 . Site 1 occurs downstream of Weir 1 , the first weir in the lower River Murray; approximately 275 km downstream of site 1 there are five tidal barrages separating the Lower Lakes from the Coorong region, there are no other regulatory structures present between these two regions (Figure 1).


Figure 1. The Lower River Murray and geomorphic regions in South Australia; inset shows extent and position of the Murray-Darling Basin in Australia. Sites are presented by the stars.

## Hydrology

For the purposes of this study, flow will refer to the mean daily water discharge in megalitres (MI.day ${ }^{-1}$ ) in the main river channel. Discharge (MI.day ${ }^{-1}$ ) in the lower River Murray in South Australia (SA) is extensively regulated. There are two figures relevant to water availability for SA; the MurrayDarling Basin Cap (for SA) and the Entitlement Flow under the Murray-Darling Basin Agreement which is Schedule 1 in the (Water Act 2007) (Cwlth). The Cap volume prescribes the amount of water that can be diverted or extracted from the River Murray for consumptive use (i.e. other than the environment). While Entitlement Flow for SA is the minimum flow SA will receive across the Victorian Border; Entitlement Flow comprises the Cap, with any additional being available for environmental use, system losses (evaporation and seepage) and system maintenance((Water Act 2007) (Cwlth). Entitlement Flow is a perpetual and exclusive right to a seasonal allocation of a minimum of $3,000 \mathrm{Ml}$ per day during winter to $7,000 \mathrm{Ml}$ per day during summer. An above Entitlement Flow occurred in 2005, when a period of within-channel flow pulses occurred. This increase in flow was the result of a combination of increased tributary inflows and the release of the Barmah-Millewa Forest environmental water allocation (BM-EWA) (King et al. 2008). Although, the BM-EWA was not specifically aimed at increasing flows in the Lower River Murray, that release resulted in a withinchannel flow pulse in the River Murray in SA during October to December of 2005. In conjunction with this flow pulse, the level of Weir 5 was raised by 50 cm , as a management intervention to enhance the inundation of low lying floodplains, although modelling suggested only an additional $2 \%$
of floodplain was inundated in this region as a direct result of the weir raising (RiM-FIM, Overton et al. 2006). 2006, 2007 and 2008 were hydrologically similar drought years of below Entitlement Flow and weir heights were maintained at the regulated pool level. A natural flood occurred in 2010, discharge was well over regulation flows, and the river 'broke' its banks inundating large areas of floodplain.

## Sampling regime

The sampling regime followed Cheshire and Ye (2008a; 2008b) to facilitate quantitative comparisons between sampling years. Larval fish were sampled during the spring/summers of 2005, 2006, 2007, 2008 and 2010. The sampling period was selected based on the peak larval abundance within the spawning seasons as determined in the upper River Murray catchment (Humphries et al. 2002; Meredith et al. 2002). Day and night samples were taken to gain a representative picture of the whole larval assemblage (Cheshire 2010). Six trips were conducted fortnightly from October to December in all years; additional monthly samples were conducted in January in 2005, 2006 and 2010. Each site was sampled during the day and at night, of the same day, and both sites were sampled within a three-day period.

## Collection and processing of fish larvae

(Cheshire 2010) determined that plankton tows were the best single method for collecting a representative sample of the fish species that occur in the main channel of the Lower River Murray and were therefore utilised for this study. Three day and three night plankton tows were conducted at each site. Plankton tows were conducted using a set of paired square-framed bongo nets with 500 $\mu \mathrm{m}$ mesh; each net was $0.5 \times 0.5 \mathrm{~m}$ and 3 m long. Nets were equipped with 30 cm pneumatic floats either side of the frame, which allowed the frame to sit 5 cm below the water surface. The net was towed in a circle, astern for 15 -minute intervals using a 20 m rope. The volume of water $\left(\mathrm{m}^{3}\right)$ filtered through each net was determined using a calibrated flow meter (General Oceanics ${ }^{\text {TM }}$, model 2030R), placed in the centre of the mouth openings. Volumes recorded among tows throughout the entire sampling period were similar between sites and within years, with the exception of 2006 and 2007 where lower volumes were recorded (Table 2).

Table 1. Mean ( $\pm$ standard error), minimum and maximum volume $\left(\mathrm{m}^{3}\right)$ recorded among tows for Site $\mathbf{1}$ and $\mathbf{2}$ for each year of sampling.

| Year | Site | Average $( \pm$ S.E) | Min | Max |
| :--- | :---: | ---: | ---: | ---: |
| $\mathbf{2 0 0 5}$ | 1 | $219.80( \pm 3.85)$ | 111.84 | 337.10 |
|  | 2 | $218.88( \pm 4.67)$ | 111.93 | 275.44 |
| $\mathbf{2 0 0 6}$ | 1 | $193.48( \pm 3.65)$ | 106.18 | 285.86 |
|  | 2 | $195.21( \pm 4.44)$ | 103.62 | 281.43 |
| $\mathbf{2 0 0 7}$ | 1 | $138.57( \pm 3.20)$ | 86.93 | 204.27 |
|  | 2 | $129.79( \pm 4.47)$ | 51.11 | 213.02 |
| $\mathbf{2 0 0 8}$ | 1 | $237.70( \pm 4.13)$ | 191.24 | 275.73 |
|  | 2 | $241.34( \pm 3.87)$ | 205.36 | 279.98 |
| $\mathbf{2 0 1 0}$ | 1 | $256.99( \pm 4.21)$ | 181.63 | 332.82 |
|  | 6 | $262.26( \pm 7.09)$ | 120.59 | 381.62 |

Samples were preserved in $95 \%$ ethanol in situ and returned to the laboratory for sorting using magnification lamps. All larvae were identified to species level where possible, with the aid of published descriptions (Lake 1967a; Neira et al. 1998; Puckridge and Walker 1990; Serafini and Humphries 2004), with the exception of carp gudgeon (Hypseleotris spp.) and hardyhead (Craterocephalus spp.). Each of these two genera were treated as a species complexes due to their close phylogenetic relationships and very similar morphologies making clear identifications difficult (Bertozzi et al. 2000; Serafini and Humphries 2004). It is most likely that the hardyheads collected in this study were the un-specked hardyhead (Craterocephalus stercusmuscarum fulvus) as the Murray hardyhead (Craterocephalus fluviatilis) has not been recently found in the main channel environment (Wedderburn et al. 2007). In 2010 eggs and newly hatched larvae were collected, it was confirmed that these were either Macquaria ambigua ambigua or Bidyanus bidyanus however, due to very similar morphologies they were subsequently grouped as 'Perch eggs' and 'Perch hatchlings'.

## Measurement of environmental variables

Data for flow (discharge in mega litres (MI) per day), water level (meters AHD, level relative to Australian Height Datum), water temperature ( ${ }^{\circ} \mathrm{C}$ ), and conductivity ( $\mu \mathrm{S} . \mathrm{cm}^{-1} @ 25^{\circ} \mathrm{C}$ ) were obtained for both sites, throughout the study, from the Department for Water Surface Water Archive (DFW 2011; http://e-nrims.dwlbc.sa.gov.au/swa/; Accessed 10/06/2011). The mean daily values from the week of sampling were used to generate a set of six replicates for each site and trip, to correspond to the six larval replicates.

## Data analysis

The volume of water sampled in each net was used to calculate the standardised abundance of fish per $\mathrm{m}^{3}$. To avoid pseudo-replication the left and right nets were treated as one replicate and therefore, the sum of the standardised abundance (number of fish per $\mathrm{m}^{3}$ ) was calculated from both left and right plankton tow nets for analysis to provide six replicates for each site during each trip. To account for the dispersion of fish under the extremely varied flow conditions this standardised abundance was multiplied by the discharge volume at the time of sampling to provide the relative
abundance of larvae, which was used for all analyses. Assemblage structure was defined by the relative abundance of each species and the species composition within each replicate for trips, sites and years.

Larval assemblage data were fourth root transformed, to prevent highly abundant species from unduly influencing the similarity measure (Clarke and Ainsworth 1993). All biological analyses were examined using Bray-Curtis similarity measures (Bray and Curtis 1957). All environmental variables were examined using a normalised Euclidean distance similarity measure. The patterns in larval assemblages between years, sites and trips were averaged within trips to provide one data point for each site within each trip and were examined using non-metric multidimensional scaling (NMS) ordination.

Data were analysed using permutational analysis of variance (PERMANOVA) for univariate and multivariate data (Anderson 2001). The six replicates for each sampling event were used for these analyses. Environmental parameters were examined using univariate designs, while assemblage structure was examined using a multivariate design. Both the univariate and multivariate analyses were performed using a three-way design, with year, site and trip as random factors, to determine if differences could be detected. Unrestricted permutations of data were performed for all analyses, with 999 permutations for the test, to detect differences at $\alpha=0.05$ (Anderson 2001). Where significant differences occurred pairwise analyses were performed

Mantel's test (Mantel 1967) was used to determine if there was a significant correlation between the larval assemblage composition and the environmental variables. The correlations between environmental variables and species abundances were further analysed using NMS ordination. Environmental variables and species were then added as vectors onto the NMS plots using a $0.1 \mathrm{R}^{2}$ cut-off. Correlations between the NMS axes, environmental variables and individual species were examined using Pearson ( $r$ ) and Kendall ( $\tau$ ) correlation coefficients, where the Pearson ( $r$ ) correlation explained the amount of variance attributable, and Kendall ( $\tau$ ) correlation provided the significance of the correlation (McCune and Mefford 1999).

Hydrology during each trip at each site in each year was categorised into three representative groups: 1) low-flow (discharge $<7,000 \mathrm{MI}$ per day), 2) low-medium within-channel flow (discharge 7,000-20,000 Ml per day) and 3) med-high within-channel flow (discharge 20,000-40,000 MI per day) and high flow (> 40,000 Ml per day). To identify which hydrological group was most correlated with individual species abundances Indicator Species Analysis (Dufrene and Legendre 1997) was performed on the untransformed larval assemblage data. Indicator species analysis combines information on the concentration of species abundances within a defined group and the faithfulness of occurrence of a species in a particular group. For example, a perfect indicator of a particular group would be exclusively present within the defined group (Dufrene and Legendre 1997). This test
provides indicator values for each species in each group on the basis in comparison to standards of the perfect indicator (McCune et al. 2002). Statistical significance of each defined indicator is tested by the Monte-Carlo randomisation technique, where data are computed against 4999 runs of the randomised data. A species that is not deemed to be a significant indicator of any particular group is either uncommon (found in low abundances) or widespread (occurs in more than one group in similar abundances) (Dufrene and Legendre 1997).

## Results

## Environmental variables

Discharge ( Ml per day) varied among years, between sites and through time but not in a uniform manner (Table 3). Discharge was generally greater in 2005 than the following three years, and was significantly greater in 2010 than all other years, (Figure 2a). Throughout 2005, discharge exceeded the summer entitlement allocation of $\sim 7,000 \mathrm{Ml}$ per day, reaching a maximum of $\sim 13,500 \mathrm{Ml}$ per day in November. Due to continuing drought conditions, discharge in 2006, 2007 and 2008 remained below Entitlement Flow (Figure 2a). The floods in 2010 resulted in a greater than six fold increase in daily discharge from that recorded in 2005 (Figure 2a).

There were significant differences in the patterns of water level among years, sites and trips, but this was also inconsistent (Table 3; Figure 2b). At Site 2 there was a step change in the water level from 2005 to 2006; no significant decrease occurred during 2007 and 2008 and a return to above pool height in 2010 (Figure 2b). Water level at Site 1, however, showed a consistent decline in each subsequent year, until 2010 (Figure 2b). The rise in discharge in 2010 resulted in a significant rise in the relative water level at both sites, resulting in the over bank water levels around late November (Figure 2b).

There were significant, but inconsistent differences in conductivity among years, sites and trips (Table 3; Figure 3a). Conductivity was consistently highest at Site 1, however, and increased from 2005 to 2007, decreased in 2008 and was significantly lower in 2010 during the period of increased discharge. At Site 2 conductivity was similar during 2005 and 2006, but was higher in 2007 and 2008 and returned to lower levels in 2010. Variations in mean daily water temperature reflected seasonal variation within the study period, and while there were differences these were not uniform among years, sites and trips (Table 3; Figure 3b). Within sites, the seasonal pattern was relatively consistent, with temperature increasing steadily from spring to summer.

Table 2. Three-way univariate PERMANOVA for differences among years, sites and trips for discharge, water level, temperature and conductivity. Bold text indicates significant value.

|  |  | Discharge |  | Relative water level |  | Temperature |  | Conductivity |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Source of variation | d.f | MS | $p$ | MS | $p$ | MS | $p$ | MS | $p$ |
| Year | 4 | 78.272 | 0.001 | 77.346 | 0.001 | 1.249 | 0.257 | 25.359 | 0.174 |
| Site | 1 | 0.595 | 0.473 | 7.406 | 0.048 | 3.101 | 0.108 | 168.440 | 0.004 |
| Trip | 6 | 2.069 | 0.579 | 1.370 | 0.755 | 23.903 | 0.001 | 0.629 | 0.764 |
| Year x Site | 4 | 0.614 | 0.007 | 0.536 | 0.753 | 0.578 | 0.891 | 14.610 | 0.001 |
| Year x Trip | 22 | 2.234 | 0.001 | 1.335 | 0.331 | 1.753 | 0.645 | 1.148 | 0.201 |
| Site x Trip | 6 | 0.188 | 0.183 | 2.115 | 0.121 | 1.532 | 0.630 | 0.882 | 0.415 |
| Year x Site x Trip | 22 | 0.117 | 0.001 | 1.101 | 0.001 | 2.017 | 0.001 | 0.814 | 0.001 |
| Residual | 330 | 0.002 |  | 0.004 |  | 0.416 |  | 0.052 |  |



Figure 2. Comparison of the a) mean daily discharge ( $\mathrm{MI} . \mathrm{d}^{-1}$ ) and b) mean daily change in water level (mAHD, AHD = Level relative to Australian Height Datum) from 'normal' pool height (Site 1: 0.75 m , Site 2: 16.3 m ) from 2005 to 2010, at Sites 1 (red line) and $\mathbf{2}$ (blue line). Sampling events are highlighted in grey. The seasonal entitlement allocation is presented in a) (black line).


Figure 3. Comparison of the a) mean daily electrical conductivity ( $\mu \mathrm{S} \mathrm{cm}{ }^{-1}$ at $25^{\circ} \mathrm{C}$ ) and b) mean daily water temperature $\left({ }^{\circ} \mathrm{C}\right.$ ) from 2005 to 2010, at Sites 1 (red line) and 2 (blue line). Sampling events are highlighted in grey.

## Annual and spatial variations in larval fish assemblages

## Catch summary

Eleven species (nine native and two exotic) were collected in the study. The small to medium-bodied native species, Retropinna semoni (Weber, 1895), Nematalosa erebi (Günther, 1868), Hypseleotris spp. and Philypnodon spp. were the most abundant in all years. Less abundant native species collected in all years included Craterocephalus spp., Maccullochella peelii (Mitchell, 1838), and Tandanus tandanus (Mitchell, 1838). Macquaria ambigua ambigua (Richardson, 1845) and Bidyanus bidyanus (Mitchell, 1838) were only collected in 2005 and 2010; eggs and newly hatched larvae from these species were only collected in 2010. The alien species, Cyprinus carpio (Linnaeus, 1758) and Perca fluviatilis (Linnaeus, 1758) were also collected in all years in low to moderate abundances. In all years, total catch was greater at Site 1.

## Assemblage structure

The larval fish assemblages varied among years, sites and trips, but not in a uniform manner as indicated by the year x site x trip interaction (d.f. $=22, \mathrm{MS}=1190.7, p=0.001$ ). NMS ordination highlighted a distinct separation of 2010 from all other years horizontally along axis 1 where 2006, 2007 and 2008 grouped together separate from the majority of 2010 observations, while some 2005 samples provided a mid point between these groupings (Figure 5). The assemblage characteristic of later season trips in 2005 was more similar to the 2010 assemblage due to the presence of $M$. $a$. ambigua, B. bidyanus and M. peelii larvae. The 2010 assemblage was most strongly characterised by M. a. ambigua, B. bidyanus and M. peelii larvae and the presence of perch eggs and hatchlings (Figure 4). The vertical distribution of samples along axis 2 suggests trip variation was a significant driver of seasonal assemblage structure (Figure 5). Spatial variation was not a distinguishing feature.


Axis 1

Figure 4. NMS ordination (stress 0.14) showing the annual separation of the larval assemblages, during 2010 from 2005, 2006, 2007 and 2008. Note sites and trips are not distinguished. Correlations for species (*) and environmental variables $(\rightarrow)$ are overlaid; vectors indicate the strength of the correlation with axes. RWL = relative water level.


Axis 1

Figure 5. NMS ordination (stress 0.14 ) showing the seasonal separation of the larval assemblages from throughout the five sampling years. Note years and sites are not distinguished. Correlations for species (*) and environmental variables ( $\rightarrow$ ) are overlaid; vectors indicate the strength of the correlation with axes. RWL = relative water level

## Linking environmental variables to larval fish assemblage

Hydrology and environmental variables were significantly correlated to changes in the larval assemblage (Mantel test: $r=0.46, p<0.0001$ ). Most of the variation in sample position along axis one was significantly positively correlated with discharge and water level, and negatively correlated to conductivity (although this was relatively weak), which helped to explain separation of years in the ordination (Figure 4; Table 4). Significant positive correlations with axis 1 were identified for M. peelii, M. a. ambigua, B. bidyanus, perch eggs and hatchlings and P. fluviatilis (Figure 4; Table 4) indicating that these species are positively correlated to periods of increased discharge and water levels, but negatively correlated to conductivity. Retropinna semoni was significantly negative correlated to axis 1, indicating a correlation with periods of lower discharge and higher conductivities (Figure 4; Table 4).

Axis 2 was significantly positively correlated to temperature (Figure 4; Table 4). R. semoni and P. fluviatilis had significant negative correlations with axis two, indicating higher abundances during periods of lower temperatures (Figure 4; Table 4). Nematalosa erebi, Hypseleotris spp. and Craterocephalus spp. had strong positive correlations with axis two, indicating that increases in abundance correlated with higher temperatures (Figure 4; Table 4).

Table 3. Pearson $(r)$ and Kendall $(\tau)$ correlation coefficients between each NMS axis and the environmental variables and species. Where Pearson ( $r$ ) correlation explained the amount of variance attributable, and Kendall ( $\tau$ ) correlation provides the significance of the correlation (Critical $\tau$ value for significance at $0.05=0.239$ ). Bold text indicates significant correlations.

|  | Axis 1 |  | Axis 2 |  |
| :---: | :---: | :---: | :---: | :---: |
| Variable | $r$ | $\tau$ | $r$ | $\tau$ |
| Discharge | 0.852 | 0.438 | 0.018 | 0.001 |
| Conductivity | -0.298 | -0.265 | 0.133 | 0.113 |
| Temperature | 0.156 | 0.138 | 0.557 | 0.489 |
| Water level | 0.843 | 0.472 | -0.052 | -0.094 |
| Retropinna semoni | -0.706 | -0.573 | -0.353 | -0.350 |
| Nematalosa erebi | -0.284 | -0.121 | 0.683 | 0.520 |
| Hypseleotris spp. | -0.259 | -0.087 | 0.592 | 0.425 |
| Philypnodon spp. | -0.278 | -0.222 | 0.321 | 0.164 |
| Craterocephalus spp. | -0.199 | -0.131 | 0.327 | 0.272 |
| Maccullochella peelii | 0.675 | 0.415 | -0.077 | -0.081 |
| Tandanus tandanus | 0.297 | 0.237 | 0.153 | 0.163 |
| Macquaria ambigua ambigua | 0.808 | 0.525 | 0.069 | 0.023 |
| Bidyanus bidyanus | 0.425 | 0.334 | -0.062 | -0.046 |
| Perch eggs | 0.853 | 0.528 | -0.230 | -0.202 |
| Perch hatchlings | 0.795 | 0.456 | -0.204 | -0.238 |
| Cyprinus carpio | 0.18 | -0.090 | -0.119 | -0.209 |
| Perca fluviatilis | 0.558 | 0.436 | -0.291 | -0.285 |

## Species relationships to hydrology

Given the significant relationship between hydrology (discharge) and the larval assemblages between years (Figure 4; Table 4) individual species patterns were further examined using indicator species analysis. Using the four hydrological groups (low flow; low-medium within-channel flow; medium-high within-channel flow; high flow), indicator species analysis identified some species had significantly correlations to one of the groups, while others showed no significant association (Table 5). Retropinna semoni and Philypnodon spp. were significantly correlated to the low flow group, occurring in highest percentage abundances ( 54 and $61 \%$, respectively) during periods of low flow (Table 5; Figure 7). Hypseleotris spp. was significantly associated with the low to medium withinchannel flow group occurring in highest percentage abundance (50\%) during periods of low to medium within-channel flow (Table 5; Figure 8). Maccullochella peelii (67\%) and the presence of perch eggs and new hatchlings (76\% each) were significantly correlated with the medium to high within-channel group, while M. a. ambigua larvae (86\%) were associated with high flow group (Table 5; Figure 9).

Table 4. Indicator species analysis using the relative abundance of species. Relative abundance (\%) of each species in each hydrological category (defined as 1) low-flow (discharge $<7,000 \mathrm{MI}$ per day), 2) low-medium within-channel flow (discharge 7,000-20,000 Ml per day) and 3) med-high within-channel flow (discharge 20,000-40,000 MI per day) and high flow (> 40,000 MI per day). Indicator group identifies the hydrological grouping each species most likely corresponds. Monte Carlo test of significance ( $p(\mathrm{MC})$ ) indicates the probability of each species as an indicator of the corresponding indicator group. Bold text indicates significant indicator group.

| Species | Relative abundance (n) | Relative abundance (\%) of species in hydrological groupings |  |  |  | Indicator group | $p$ (MC) |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | Low-flow | Lowmedium withinchannel | Mediumhigh withinchannel | High flow |  |  |
| Retropinna semoni | 240,687 | 54 | 42 | 2 | 2 | Low-flow | 0.036 |
| Nematalosa erebi | 9,0819 | 39 | 50 | 1 | 10 | Low-medium within-channel | 0.145 |
| Hypseleotris spp. | 139,327 | 38 | 50 | 6 | 5 | Low-medium withinchannel | 0.049 |
| Philypnodon spp. | 175,182 | 61 | 16 | 11 | 11 | Low flow | 0.003 |
| Craterocephalus spp. | 831 | 35 | 17 | 0 | 49 | Low flow | 0.733 |
| Maccullochella peelii | 2,034 | 0 | 3 | 67 | 29 | Medium -high withinchannel | 0.034 |
| Tandanus tandanus | 423 | 4 | 28 | 0 | 68 | High flow | 0.113 |
| Macquaria ambigua ambigua | 12,773 | 0 | 3 | 11 | 86 | High flow | 0.001 |
| Bidyanus bidyanus | 638 | 1 | 25 | 55 | 19 | Medium -high within-channel | 0.265 |
| Perch eggs | 198,864 | 0 | 0 | 76 | 24 | Medium -high withinchannel | 0.001 |
| Perch hatchlings | 6,777 | 0 | 0 | 76 | 24 | Medium -high withinchannel | 0.002 |
| Cyprinus carpio | 8,600 | 2 | 3 | 32 | 62 | High flow | 0.093 |
| Perca fluviatilis | 4,825 | 1 | 0 | 99 | 0 | Medium -high within-channel | 0.301 |



Figure 6. Changes in total relative abundance of identified low flow spawners (R. semoni and Philypnodon spp.) among years (2005, 2006, 2007, 2008 and 2010, presented sequentially from left to right at Site 1 and top to bottom at Site 2) Sites 1 and 2. Size of symbols is relative among years for individual species.


Figure 7. Changes in total relative abundance of identified low to medium within-channel flow spawner (Hypseleotris spp.) among years (2005, 2006, 2007, 2008 and 2010, presented sequentially from left to right at Site 1 and top to bottom at Site 2) Sites 1 and 2 . Size of symbols is relative among years for individual species.


Figure 8. Changes in total relative abundance of identified medium to high within-channel flow spawner (M. peelli) and high flow spawner (M. a. ambigua) among years (2005, 2006, 2007, 2008 and 2010, presented sequentially from left to right at Site 1 and top to bottom at Site 2) Sites 1 and 2. Size of symbols is relative among years for individual species.

## Discussion

## Composition of fish fauna in the main channel environment

Throughout the MDB, native fish populations have undergone significant declines in range and abundance (Gehrke et al. 1995) as a direct result of anthropogenic impacts, which is particularly evident in the Lower River Murray (Lloyd and Walker 1986). Eleven species were collected as larvae in this study, comprising nine native and two exotic species. The most abundant species were the small to medium-bodied native species (R. semoni, N. erebi, Hypseleotris spp. and Philypnodon spp.), which were collected in all years. Maccullochella peelii and T. tandanus, were also recorded in four of the five years being absent in the third consecutive low flow year (2008) but were collected in lower abundances throughout the study. Macquaria ambigua ambigua and B. bidyanus were only collected in the above Entitlement Flow years. The current study identified that spatial and within season variations were significant drivers of differences in larval fish assemblages within these years.

Spatial and seasonal variations in fish assemblages has been documented throughout the worlds river systems, with variations related to environmental conditions, food availability and habitat morphology (e.g. Habit et al. 2007; Holland 1986; Oberdorff et al. 1993; Ostrand and Wilde 2002; Schlosser 1982). Cheshire (2010) identified that species abundances varied considerably between the two sites surveyed in this study, perhaps indicating broader regional differences in habitat characteristics and hydraulic conditions along the river. Site was identified as a driver of assemblage differences in this study, however, these were not consistent and could not be correlated to specific variables. MDB fish exhibit seasonal variation in spawning; seasonal spawning guilds were suggested for MDB fish by King et al. (2003) using a review of larval occurrence from studies throughout the Murray region. Cheshire (2010) confirmed that the seasonal spawning patterns in the Lower River Murray were consistent with the spring/summer and summer seasonal spawning guilds defined by King et al. (2003).

The larval assemblage differed among years, with the flow pulse year (2005) and the high flow/overbank flood year (2010) characterised by different larval assemblages to the three low flow years. Three types of responses were evident in the larval assemblage to varying environmental conditions: larvae that were 1) positively correlated to increased discharge, 2) negatively correlated to the increased discharge and 3) correlated to temperature. The correlation between temperature and changes in larval fish assemblage most likely reflects within season differences in spawning of individual species (Cheshire 2010; King et al. 2003). There were differences in species associations with changing hydrological conditions. This study identified R.semoni and Philypnodon spp. as having highest abundances correlated to low flow periods, Hypseleotris spp. as having highest
abundances correlated to low to medium within-channel flow periods, M. peelii wth medium to high within-channel flow periods. Perch eggs and hatchlings had significant associations with medium to high within-channel flow periods and M. a. ambigua larvae were significantly associated with high flow periods. Given the earlier timing of eggs and new hatchlings compared to developed larvae, these results suggest that for $M$. a ambigua suitable spawning conditions occur during medium to high within-channel flow periods.

## Life history strategies and the influence of hydrology

The role of hydrology (flows and flooding) in the life cycles of freshwater fish have been studied throughout Australia (e.g. Harris and Gehrke 1994; Humphries et al. 1999; King et al. 2003; Lake 1967a) and the world (e.g. Dudley and Platania 2007; Junk et al. 1989; Winemiller and Rose 1992; Zeug and Winemiller 2008). Floodplain inundation is important for the life cycles of some fish (Welcomme 1985; Winemiller 2005), while others do not require regular floodplain inundation and are able to successfully spawn and recruit in main channel habitats (Haines and Tyus 1990; Humphries et al. 2002; King 2004b; King et al. 2003; Turner et al. 1994; Watkins et al. 1997). Observations from temperate Australian floodplain rivers have resulted in two models: the flood recruitment model (Harris and Gehrke 1994) and the low flow recruitment hypothesis (Humphries et al. 1999). The life history strategies for MDB fish (Humphries et al. 1999) were developed based around the opportunistic, equilibrium and periodic life history strategies (Winemiller 1989; Winemiller and Rose 1992).

The low flow recruitment hypothesis (Humphries et al. 1999) proposes that larvae utilise embayments, backwaters and shallow littoral zones under low flow conditions, because these areas are warm and have a higher availability of prey. King (2004a) identified that prey concentration in these habitats was not, however, greater than in the main river channel in a tributary of the mid Murray. Areas of low flow are often associated with higher zooplankton densities, thus in the main channel the combination of lower velocities and increased prey availability may provide suitable conditions for the growth and survival of larvae (Gehrke 1992; King 2005; King et al. 2003; Zeug and Winemiller 2008). Cheshire (2010) identified that small to medium-bodied native species exhibited an opportunistic life history strategy, significantly increasing in abundance during low flow years, which was supported in this study. This suggests that the annual patterns of abundance for the small to medium-bodied natives conform with, and support, the predictions of the low flow recruitment hypothesis (Humphries et al. 1999) (see Cheshire 2010 for a detailed discussion).

The flood recruitment model (Harris and Gehrke 1994) was developed for Australian temperate rivers, based on the principles of the flood pulse concept (Junk et al. 1989). The flood recruitment model proposes two methods by which increased flows may enhance recruitment in river fish;
flooding as a direct stimulus for spawning of some species, or flooding indirectly enhances the survival of larvae and juveniles by providing suitable food and habitat on the inundated floodplain (Harris and Gehrke 1994). The main assumption is that the main river channel does not support sufficient densities of prey during low flow conditions to provide adequate food for developing larvae and juveniles (Harris and Gehrke 1994; Humphries et al. 1999; Lake 1967a; b).

Macquaria ambigua ambigua and B. bidyanus are the only fish species in the MDB considered to require an increase in flow to initiate spawning (Humphries et al. 1999; King et al. 2009). Throughout the MDB significant M. a ambigua recruitment corresponds to years of increased within-channel or overbank discharge (King et al. 2009; Leigh and Zampatti 2011; Leigh et al. 2010; Ye et al. 2008). Recent (2004-2011) investigations in the Lower River Murray suggest that at flows less than 10,000 MI per day are insufficient to induce spawning or support recruitment of $M$. a ambigua (Leigh and Zampatti 2011; Leigh et al. 2010; Ye et al. 2008).

Maccullochella peelii and T. tandanus were collected in greater abundances and distribution during the within-channel flow pulse and high flow/overbank years. Maccullochella peelii and T. tandanus are circa-annual spawners and spawning is not believed to be initiated by changes in water levels or flow (Davis 1977a; b; Gilligan and Schiller 2004; Humphries 2005; Humphries et al. 2002; King et al. 2003; King et al. 2008; Koehn and Harrington 2006). Despite annual spawning events years of higher flows and over bank floods in the Lower River Murray have previously correlated with higher recruitment of M. peelii (see Ye and Zampatti 2007). Maccullochella peelii do not appear to alter spawning effort as a response to higher flows, but rather hydraulically diverse habitats may increase larval survival and therefore recruitment (Humphries 2005; King et al. 2009) . There are, therefore, two plausible explanations for the higher abundances recorded in 2010 in this study; more suitable spawning and larval habitats became available in the main channel under the increased flows, or higher abundances of larvae became entrained in the flow by the higher water velocities.

Heavily modified rivers can be harsh environments for all fish, but particularly for those species that are flow dependent or have narrow requirements for spawning, recruitment or dispersal of eggs and larvae (Humphries et al. 2002; Jobling 1995; Mackay 1973; Walker 2006; Welcomme 1985). While not all species rely on flows to stimulate migrations or spawning larval survival and subsequent recruitment of many species may benefit from enhanced river flows through environmental water allocations (Gehrke et al. 1995; Humphries et al. 1999; King et al. 2008). Large-bodied, longer-lived species are likely to be able to withstand unfavourable spawning and recruitment conditions for longer, but fish with long life spans, slow growth rates, low fecundity and late age to maturity are also potentially more at risk and slower to recover from population decreases (Baker et al. 2009; Denney et al. 2002). Under prolonged drought conditions, excessive periods of low flow and drying
of off-channel habitats may compound, restricting the reproduction and recruitment in some of the large-bodied species (Cheshire 2010; King et al. 2009; Leigh and Zampatti 2011; Ye et al. 2008).

## Conclusions

Restoring a more natural flow regime throughout the MDB is integral to maintain and potentially restore native fish populations. The challenges in heavily regulated river systems are vast, but a combination of environmental water allocation and river management has the potential to provide a flow regime more reminiscent of natural conditions, and return ecologically important within channel flow events. This study has highlighted that the abundance and distribution of larval M. peelii and $T$. tandanus was greater during higher flow conditions, and importantly larval M. a. ambigua and B. bidyanus were present only during the within channel flow pulse and high flow, overbank flood years. While a number of small to medium-bodied species will spawn and develop during low flow conditions in the heavily regulated weir pool environment, for M. a. ambigua and B. bidyanus continued low flow conditions likely pose a significant threat. This study has demonstrated that during years of low water availability the minimum Entitlement Flows into SA are not sufficient to induce spawning in flow dependent spawners.

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