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ENVIRONMENTAL FLOW ENHANCES NATIVE FISH SPAWNING AND RECRUITMENT IN THE MURRAY RIVER, AUSTRALIA†

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ABSTRACT

Environmental flows aim to mimic components of a river's natural flow variability, including the magnitude, frequency, timing, duration, rate of change and the predictability of flow events. Aspects of the natural flow regime are thought to be linked to critical components of the life history strategies of many riverine fishes, including spawning and recruitment. In the Murray River, Australia, environmental flows are increasingly being used as a restoration tool; however, there is little information about the response of fish to these managed flow events. This study reports on the results from a 3-year study on the effects of water management on the spawning and recruitment of four native fish species in the mid-Murray River system. Two of these years were hydrologically similar, while the third year encompassed an extensive period of floodplain inundation, including the use of the largest environmental flow allocation to date in Australia. Drift nets were used to collect the drifting eggs and larvae of four iconic native species throughout their spawning season each year. Young-of-year were collected in the following autumn. Although golden perch and silver perch eggs were collected in all 3 years, both species increased their spawning activity during the major flood period compared to the previous two seasons. Murray cod and trout cod appeared not to increase their spawning activity in the flood year, but their recruitment may be increased when floodplain inundation occurs at times when their larvae and juveniles are present, most likely through the generation of abundant food resources. Whilst further study is required to confirm the role and mechanism of flooding in the spawning and recruitment of these species; this study provides important evidence of a link between the provision of an environmental flood and fish spawning and recruitment, and has significant implications for managing flows in regulated rivers. Copyright © 2008 John Wiley & Sons, Ltd.

KEY WORDS: fish larvae; river regulation; flooding; managed flood; Barmah-Millewa Forest

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INTRODUCTION

Rivers throughout the world support complex and highly diverse ecosystems. However, rivers also support human life and activities, and consequently many have been dammed and the water diverted for offstream purposes (Dynesius and Nilsson, 1994). There is little doubt that the alteration of flow regimes has led to substantial effects on the ecological sustainability and integrity of floodplain rivers throughout the world (Sparks, 1995; Ward *et al*., 1999; Bunn and Arthington, 2002). There is also an increasing awareness of the role of the natural flow regime in the ecology of floodplain rivers (Junk *et al*., 1989; Poff *et al*., 1997; Puckridge *et al*., 1998; Lytle and Poff, 2004). Consequently, an increasing number of scientists and managers have concluded that the recovery of a more natural flow regime could provide an effective restoration strategy, potentially allowing ecosystem recovery to occur through natural recruitment and growth processes (Stanford *et al*., 1996; Poff *et al*., 1997; Rood *et al*., 2003; Arthington *et al*., 2006). The relatively new field of 'environmental flows' has embraced the concept, with many restoration efforts aiming to mimic components of the rivers natural flow variability, including the magnitude, frequency, timing, duration, rate of change and the predictability of flow events (Arthington *et al*., 2006). However, as the field is relatively new, ecologists still have much to learn about the significance of individual flow events on

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†This study was conducted under the appropriate scientific animal collection and animal ethics permits.

specific biota, and therefore, long-term manipulative experiments are required (Bunn and Arthington, 2002; Poff *et al*., 2003; Arthington *et al*., 2006).

One of the most obvious, and often to the general community, most unacceptable effects of river regulation is the collapse of the riverine fish community. Indeed, aspects of the flow regime are linked to critical components of the life history strategies of riverine fishes, including pre-spawning condition and maturation, spawning cues and behaviour, larval and juvenile survival, movements and subsequent recruitment (Welcomme, 1985; Junk *et al*., 1989; Humphries *et al*., 1999; Poff *et al*., 2003; Lytle and Poff, 2004). As successful spawning and survival of the early life history stages of fish often dictates the strength of subsequent cohorts (Trippel and Chambers, 1997), understanding the relationship between the natural flow regime and its influence on the early life of fishes is vital to manage fish populations in flow altered rivers, but is generally poorly understood (e.g. Humphries *et al*., 1999; Marchetti and Moyle, 2001; King *et al*., 2003; Balcombe *et al*., 2006).

The effects of river regulation have been implicated in the decline in abundance and distribution of native fishes of the Murray–Darling Basin, Australia (Cadwallader, 1978; Walker and Thoms, 1993; Gehrke *et al*., 1995; MDBC, 2004). The Murray River is a highly regulated river system managed for multiple uses. The river has large upstream storages capturing the bulk of winter–spring flows to release for downstream consumptive use primarily in spring–summer, resulting in a seasonal reversal in flow regime and reduced flooding (Close, 1990). Recently, increasing attention has been given to improve the ecological condition of the river (Walker and Thoms, 1993; Thoms *et al*., 2000), and the provision of environmental flows has been recommended as part of a suite of restoration activities being undertaken in the river (MDBC, 2002a,b), (www.thelivingmurray.mdbc.gov.au). These environmental flows, whilst generally used to improve the ecological health of the system, may also target specific biota including enhancing native fish populations through increasing spawning and successful recruitment events. However, given the general lack of understanding about early life history requirements of Murray–Darling fish species (Humphries *et al*., 1999), predicting the response of these environmental flows is difficult.

This study reports on the results of a 3-year study on the effects of water management on the spawning and recruitment dynamics of four native fish species in the mid-Murray River system. While two of these years were hydrologically similar, with fully regulated in-channel flow conditions, the third year (2005/2006) encompassed an extensive period of floodplain inundation, including the use of the largest environmental flow allocation to date in Australia, to the Barmah-Millewa (B-M) Forest.

METHODS

Study area and hydrology

The B-M Forest is located on the Murray River floodplain upstream of the township of Echuca (Figure 1). The Murray River in this region is a lowland river with a maximum width of 100 m and has an annual average discharge of 11 250 gl (Close, 1990). The Forest, dominated by river red gum (*Eucalyptus camaldulensis*), is a 70 000 ha highly complex wetland, containing a range of aquatic habitats including rivers, permanent and ephemeral creeks, wetlands, swamps and the floodplain proper when it is inundated. The Forest is internationally recognized as an important wetland under the RAMSAR convention and has also received iconic status under the Murray–Darling Basin Commission's 'Living Murray Initiative' (www.thelivingmurray.mdbc.gov.au).

As a result of the flow regulation of the Murray River, the Forest now experiences a reduction in the frequency, duration and inundation area of winter–spring floods, altered timing of all floods and low flow periods, increased frequency of smaller summer floods and a reduced variability in flood flows (Bren *et al*., 1987;Thoms *et al*., 2000; Chong and Ladson, 2003). This massive alteration in flow regime is the major threat to the environmental values of the Forest (Ward, 2005) and the Murray River in this region (Walker and Thoms, 1993). In an attempt to mitigate some of the effects of the altered flow regime on Forest ecology, the Forest's water regime is highly managed through a series of offstream regulators and an annual environmental water allocation (EWA) of 150 GL per year. The EWA does not have to be used within any one year, and can be accumulated for a number of years and used in larger volumes.

The B-M EWA has been used three times since its inception in 1993. The EWA was first used in 1998 when 97 gl was provided to supplement a minor spring flood. Despite a range of flora and fauna generally responding to the event (no monitoring of fish occurred), in general, the event was believed to achieve only some of the desired

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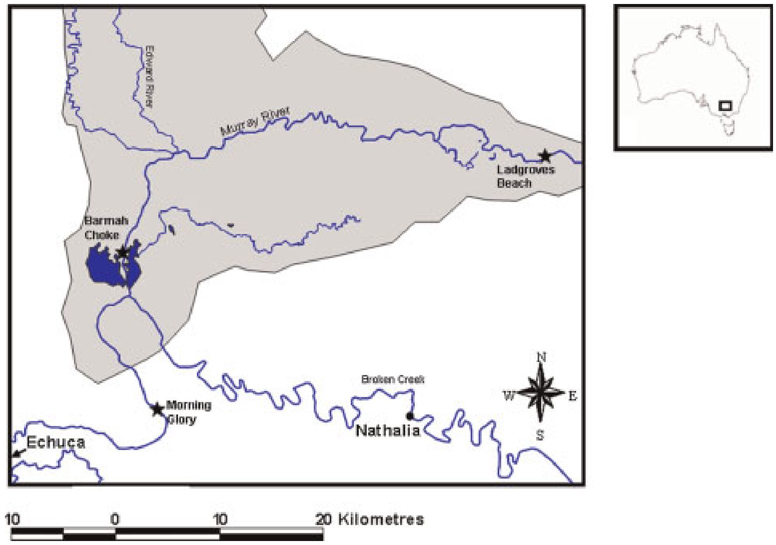

Figure 1. Map of the Barmah-Millewa Forest on the Murray River, Australia; showing the three river sampling sites: Landgroves Beach, Barmah Choke and Morning Glory (indicated by star). This figure is available in colour online at www.interscience.wiley.com/journal/rra

ecological objectives, as the period of inundation and depth was thought to be insufficient (Maunsell McIntyre Pty Ltd, 1999). The second use of the EWA occurred from spring 2000 to January 2001, and used a total of 341 GL to extend the duration of two large spring flood events (Maunsell McIntyre Pty Ltd, 2001). The event supplemented a one in 5-year flood event for the Forest, and resulted in a significant waterbird breeding event (Leslie and Ward, 2002) and vegetation responses. Again, little targeted monitoring of fish populations or spawning responses was undertaken at the time.

The B-M EWA was again used in October–December 2005, when 513 GL was used to extend the duration of floodplain inundation of a spring flood event (Figure 2). A team of multidisciplinary members from various government agencies actively managed the use and shape of the hydrograph of the EWA. The managed hydrograph resulted in fairly continuous flooding of the Forest from mid-August to mid-December, and included several naturally driven flood spikes from upstream tributary inflows, and mirrored the modelled natural decline in river discharge that would have occurred (modelled data courtesy Murray–Darling Basin Commission) (see also King et al.

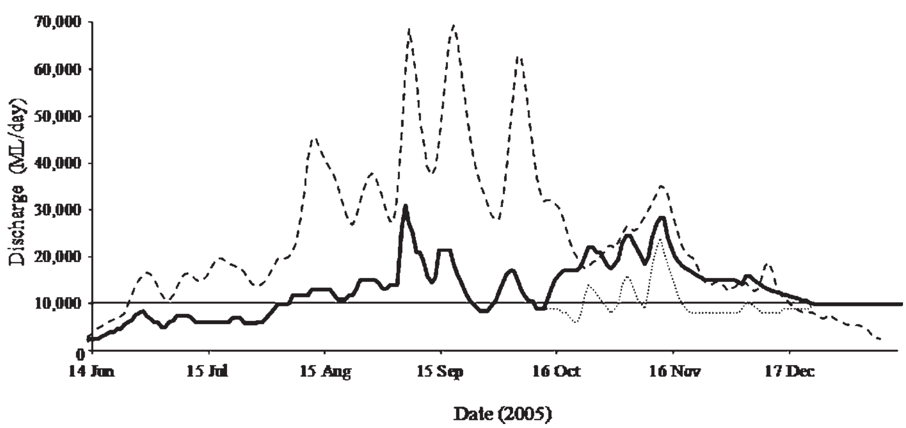

Figure 2. Actual mean daily discharge (solid line); simulated mean daily discharge without use of environmental water allocation (EWA) (dotted line); simulated natural flows (dashed line) during the 2005 use of the Barmah-Millewa EWA. All flows measured or simulated downstream of Yarrawonga on Murray River (upstream of Barmah-Millewa). Simulated natural flows refers to results of modelled flows based on tributary inputs and no upstream river regulation. Data supplied courtesy of Damien Green, Murray–Darling Basin Commission

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In press). Despite approximately 50% of the Forest being inundated, the height of the flood peaks was significantly lower than the 2000/2001 EWA use. Previous uses of the EWA were principally targeted at maintaining suitable breeding conditions for colonially nesting waterbirds and vegetation responses (Ward, 2005); however, the 2005 EWA was also aimed at enhancing spawning and recruitment events for native fish species. This was achieved by planning to incorporate peaks in the hydrograph during the floodplain inundation (although this was subsequently naturally achieved via upstream tributary inputs) and also maintaining floodplain inundation for 1–2 months. This approach to achieving benefits for native fish spawning was purely speculative in nature and was incorporated into the initial management of the EWA event as an experimental component that could be validated using the current study (see also King et al. In press).

Four target species investigated

This study focussed on four native fish species: golden perch (*Macquaria ambigua*), silver perch (*Bidyanus bidyanus*), Murray cod (*Maccullochella peelii peelii*) and trout cod (*Maccullochella macquariensis*); that are known to have important recreational, conservation and cultural significance. This study was part of a broader investigation into the effects of water management on spawning and recruitment of the entire fish community at B-M Forest.

The four target species are thought to exhibit two different recruitment strategies (see Humphries *et al*., 1999) in response to floods. Following the principles of the flood pulse concept (Junk *et al*., 1989); Harris and Gehrke (1994) proposed that flooding enhances recruitment in Murray–Darling fish via two mechanisms: either through the initiation of spawning or by indirectly enhancing larval and juvenile survival through the provision of abundant food and habitat. The first mechanism was attributed to species such as golden perch and silver perch, based on limited evidence of a link between floods and spawning from aquaculture studies (Lake, 1967), and various anecdotal accounts. Humphries *et al*. (1999) and King *et al*. (2003) questioned the widespread applicability of this relationship, as there is no field evidence to support that flooding is required to initiate spawning for these species; evidence that golden perch larvae actively avoid poor water conditions that would be encountered on floodplains (Gehrke, 1991) and evidence also suggesting that strong recruitment can occur for both species during non-flood years (Mallen-Cooper and Stuart, 2003). The second mechanism, was proposed for species such as Murray cod and trout cod, which do not require floods to spawn (Humphries, 2005; Koehn and Harrington, 2006), but may benefit from improved environmental conditions that could occur during floods to sustain their young. Although the data are very limited, there is some evidence from commercial catch records to suggest that strong recruitment can occur in Murray cod populations following years of high flows (Rowland, 1998; Ye *et al*., 2000).

Collection and processing of fish eggs and larvae

Fish eggs and larvae of the four target species were collected from three sites in the Murray River in the B-M Forest region (Ladgroves Beach, 35°51.677, 145°20.773; Barmah Choke, 35°54.947, 144°57.267 and Morning Glory, 36°04.765, 144°57.553) (Figure 1). Sampling was conducted overnight in mid-September, and fortnightly thereafter until the end of February during 2003/2004, 2004/2005 and 2005/2006 breeding seasons, resulting in a total of 11 sampling trips. Due to the occurrence of a late February natural flood pulse, two additional fortnightly sampling trips were also conducted in March 2005 (a total of 13 sampling trips for the 2004/2005 season). Sampling was conducted using passive drift nets, as the eggs and/or larvae of the four target species are known to exhibit a drifting dispersal phase (Humphries and King, 2004). All nets were set on dusk and retrieved as early as possible the following morning, generally before 11:00 h.

Drift nets were 1.5 m long, with a 0.5 m diameter mouth opening and were constructed of 500-μm mesh, which tapered to a removable collection jar. A General Oceanics Inc. (FL, USA) flow meter was fixed in the mouth of each drift net to determine the volume of water filtered, therefore, enabling raw catch data to be adjusted to a standard volume of filtered water (1000 m^3). At each site, two drift nets were attached to a 3 m long pole to sample the surface and bottom 50 cm of the water column. The pole was located in, generally, the same position (at least 3 m from the river bank) at each site on each of the sampling trips. The densities of drifting eggs and larvae are known not to be uniform across the channel (see e.g. Tonkin *et al*. 2007), and therefore, the densities recorded here do not represent a precise indication of the total density of eggs/larvae per river discharge at any one time, but rather, an

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estimate of relative density per standardized volume filtered that was appropriate given a number of logistical and safety constraints.

In the field, eggs were removed alive from the samples and returned to the laboratory to hatch, to enable correct identification. Remaining samples were preserved in 95% ethanol in the field and returned to the laboratory for processing, where fish were removed from the samples using a dissecting microscope. Identifications were made by experienced staff using available keys (Serafini and Humphries, 2004), and by collating a reference collection of all species and successive larval stages. The presence of eggs or larvae was used as an indication of spawning occurrence. Egg and larval catch data were adjusted to a standard volume of water filtered (number of eggs or larvae per 1000 m^3).

Collection of young-of-year

Standardized boat electrofishing surveys were conducted in May 2005 and 2006 at all three sites, after irrigation flows in the main river had dropped to very low, managed winter baseflows. Sampling was not able to be conducted during May 2004, due to a very small period of time available when river levels were low and therefore suitable for sampling. The 5.2 m electrofishing boats were equipped with on-board 7.5 Kva Smith–Root Model GPP 7.5 H/L electrofishing systems. The electrofisher was usually operated at 1000 V DC, 7.5 amps pulsed at 120 Hz and 35% duty cycle. Within each site, sampling was conducted for 1080 s (electrofishing time-on) at each of three randomly assigned inner bend, outer bend and straight reaches. Inner bend reaches occurred at large bends in the river in the mostly slower flowing, depositional half of the river, and were often associated with beach habitats. Outer bend reaches occurred at large bends, generally in the faster flowing, actively eroding zone of the river and were often associated with high steep banks and deeper water. Straight reaches were reaches where no bends occurred, with sampling restricted to one side of the river for each replicate. Each replicate reach was then divided into three zones, inner (closest to the bank), middle and outer (middle of the river), to allow a standardised effort sampling all available habitats within each reach. Sampling was conducted during the day and then repeated the following night at each of the replicate reaches, leaving at least 4 h between each sampling run. All fish captured were weighed and measured (standard length) and then released. Individuals were classified as young-of-year based on their length, as < 150 mm for Murray cod and trout cod, and < 100 mm for golden perch and silver perch; these lengths were based on otolith ageing of a small number of individuals of each species (unpublished data).

Data analysis

Comparison between sampling trips (or time) across seasons was possible, as sampling trips occurred at a very similar time in each of the three seasons. For the standardized egg and larval catch data, ‘sampling trips’ where there were zero counts of a particular response variable in all three sampling seasons were discarded. However, if there were counts in at least one season for that ‘sampling trip’, then all three seasons’ data for that ‘sampling trip’ was included in the analysis. This approach maintained a balanced sampled design, and assumed that the appearance of eggs or larvae (response variables) in one ‘sampling trip’ in any one season meant that they could occur at that time of the year. Data for top and bottom nets within a site were pooled for analysis. Generalized linear mixed-effect models were fitted to the count data assuming Poisson errors. Site was fitted as a random effect and season as a fixed effect. Due to high degree of overdispersion, most likely due to the excess of zero’s in the data, a quasi-likelihood was used in the analysis allowing the dispersion parameter to be estimated and used in the calculation of standard errors. For each response variable for the drift data, two models were fitted: Model 1—$Y \sim \text{season} + \text{random }(1|\text{site})$, Model 2—$Y \sim \text{random }(1|\text{site})$. Hence, the significance of the season effect was tested by comparing the reductions in the deviance between both models and comparing percentage points of a chi-squared distribution. No analysis was conducted for trout cod larvae as catches were too low. Significance levels and per cent deviance explained for Model 1 are presented for each response variable.

Young-of-year data were also analysed using generalized linear mixed-effect models assuming Poisson errors, to the count data pooled across day and night samples. Site was fitted as a random effect, and season and zone were fitted as fixed effects. Quasi-likelihood methods were again used to model over-dispersion in the count data as for the drift data. For each response variable three models were fitted: Model 1—$Y \sim \text{zone} + \text{year} + \text{random }(1|\text{site})$, Model 2—$Y \sim \text{year} + \text{random }(1|\text{site})$, Model 3—$Y \sim \text{random }(1|\text{site})$. Hence, the significance of the zone and

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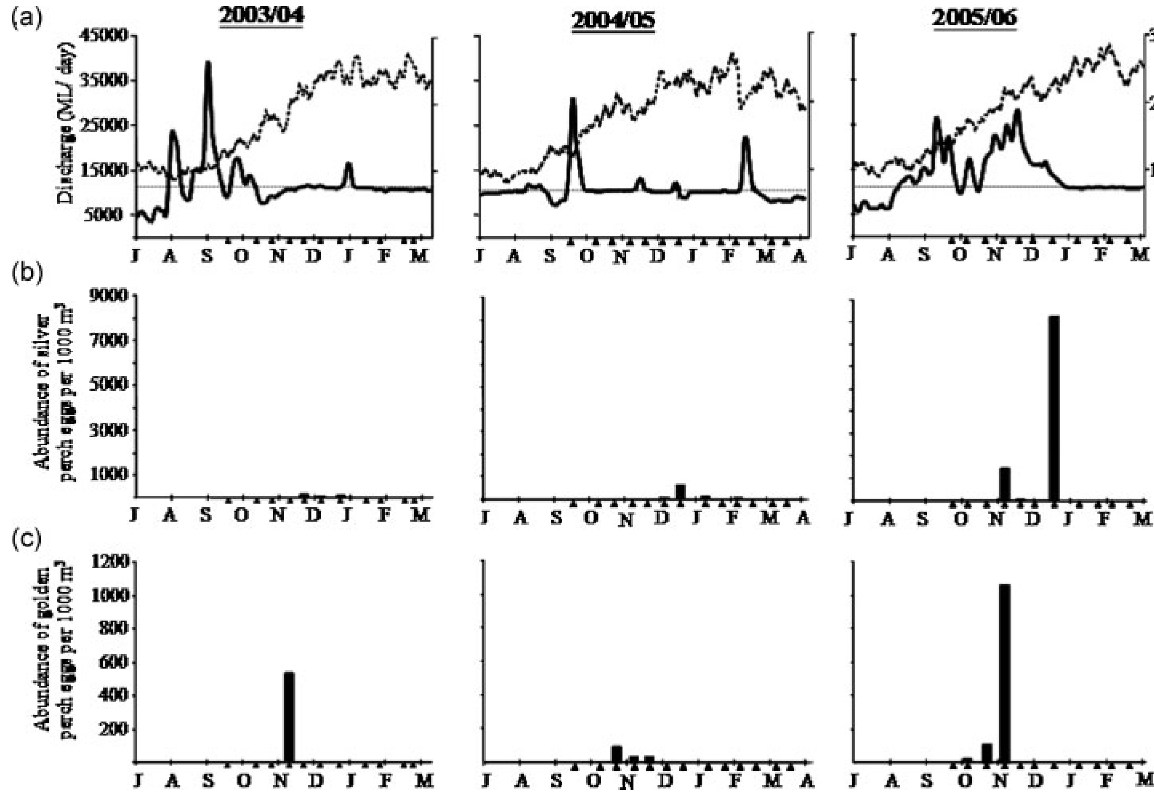

Figure 3. (a) Mean daily discharge (solid line), water temperature (dashed line) and adjusted total abundance of (b) silver perch and (c) golden perch eggs per 1000 m^{-3} collected in drift nets in the Murray River. Data pooled for three sites and net position. Discharge and temperature data from Tocumwal gauge on Murray River. Note: dotted line represents approximate floodplain inundation height at Barmah-Millewa Forest, solid triangles on x-axis indicates sampling event. Letters on x-axis represent calendar months in each year from July to March

season effects were tested by comparing the reductions in the deviance between Models 1 and 2, and 2 and 3, respectively.

RESULTS

Hydrographs

The hydrographs of the 3 years of this study were markedly different each year (Figure 3(a)). The 2003/2004 season was marked by three winter and early spring floods that inundated the Forest, and continued as fairly stable, bank-full conditions for the remainder of the season. A very minor flood event occurred in late December 2003, which inundated restricted areas of the Forest. The 2004/2005 season was characterized by one spring flood event, and again remained fairly stable, bank-full conditions for the rest of the season. A minor, natural flood event which inundated low lying areas of the Forest, occurred in late February 2005. This flood caused a minor blackwater event into the Murray River, but no fish kills or adverse environmental effects were observed (King, pers. obs.). The February flood was also associated with a marked decline in temperature. The 2005/2006 season hydrograph was obviously distinct from the two previous seasons, with floodplain inundation occurring for nearly five months from early August to late December. The flood had a number of peaks, which were principally driven by upstream inflows.

Occurrence of eggs and larvae

While golden perch (eggs and larvae), silver perch (eggs and larvae) and Murray cod (larvae only) were collected in all three years; trout cod larvae were only collected in 2005/2006 (Table I). The occurrence and total abundance

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Table I. Total raw abundance of eggs and larvae of golden perch (*Macquaria ambigua*), silver perch (*Bidyanus bidyanus*), Murray cod (*Maccullochella peeli peeli*), trout cod (*Maccullochella macquariensis*) and unidentified cod larvae collected during 2003/2004, 2004/2005 and 2005/2006 breeding seasons combined across the three collection sites

	Golden perch		Silver perch		Murray cod	Trout cod	Unid. cod
	Eggs	Larvae	Eggs	Larvae	Larvae	Larvae	Larvae
2003/2004							
Ladgroves beach	20	0	134	29	9	0	0
Barmah Choke	143	1	219	10	1	0	0
Morning glory	0	0	0	0	0	0	0
Total raw number	163	1	353	39	10	0	0
2004/2005							
Ladgroves beach	14	2	469	2	20	0	0
Barmah Choke	69	0	65	0	12	0	0
Morning glory	26	0	85	0	3	0	0
Total raw number	109	2	619	2	35	0	0
2005/2006							
Ladgroves beach	291	89	1682	176	45	1	3
Barmah Choke	656	14	1069	18	24	2	2
Morning glory	659	7	843	1	12	1	1
Total raw number	1606	110	3594	195	81	4	6
Total raw number	1878	113	4566	236	126	4	6

Total raw number across all years.

of the four species varied among the three sites sampled, with Morning Glory (downstream of the Forest) containing the least number of eggs and larvae of all species in all three years (Table I).

The models for both silver perch eggs and larvae suggest a significant effect of season ($p < 0.0001$), with 26.9 and 31.6% of the deviance explained by the model. The total raw abundance and adjusted abundance of silver perch eggs and larvae increased substantially in 2005/2006 compared to the previous two sampling seasons (Table I, Figure 3). The models for golden perch eggs suggested a significant effect of season ($p < 0.0001$), but explained only 12.4% of the deviance and should therefore be treated with some caution; while the model for golden perch larvae was also significant for season ($p < 0.0001$) and explained 49.0% of the deviance. The total raw abundance and adjusted abundance of golden perch eggs and larvae increased substantially in 2005/2006 compared to the previous two sampling seasons (Table I, Figure 3). The larvae of both golden perch and silver perch that were collected were younger than two days old (unpublished data), and therefore the presence of eggs or larvae of these two species can be used to indicate the spawning time of these species. The timing of silver perch spawning was fairly consistent each year, occurring between early November to mid-February, and were consistently collected in water temperatures above 20°C, ranging from 17.2 to 28.4°C (Figure 3(b)). By far, the greatest abundance of silver perch eggs were collected in the early November and late December 2005 sampling events. The first major spawning event in November occurred on a coinciding rise in water temperature and rise in water level during the extended flood conditions, while the second major spawning event in late December coincided with a rapid decline in water level, as flood waters were receding from the Forest (Figure 3(a) and (b)). The spawning time of golden perch was much shorter, and occurred earlier in all three years compared to silver perch (Figure 3(c)). Golden perch spawned from early October to mid December, with water temperatures ranging from 16.9 to 24.7°C. However, the spawning period did vary between the three years. A large golden perch spawning event occurred in early November 2003. However, as with silver perch, by far the greatest abundance of golden perch eggs were collected in 2005/2006 season, on the early November 2005 sampling event. This spawning event occurred on a coinciding rise in water level and rise in temperature during the flood conditions (Figure 3(c)).

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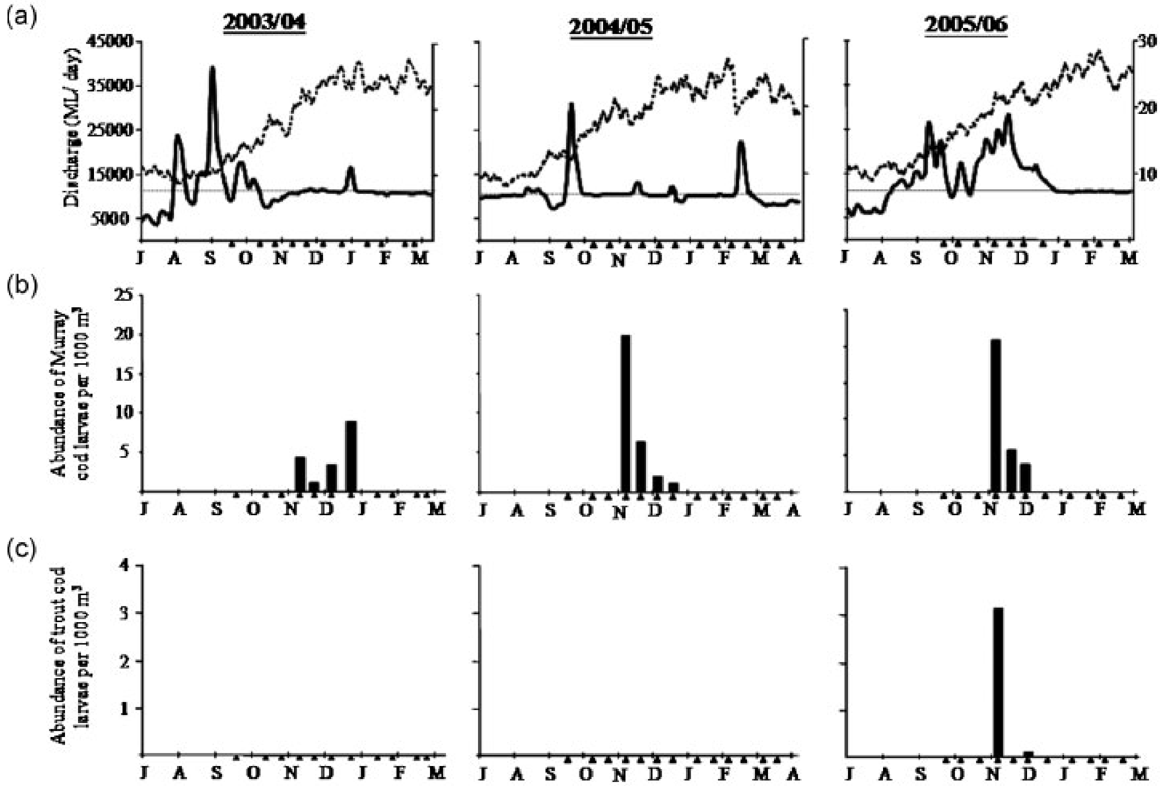

Figure 4. (a) Mean daily discharge (solid line), water temperature (dashed line) and adjusted total abundance of (b) Murray cod and (c) trout cod larvae per 1000 m^{-3} collected in drift nets in the Murray River in 2003/2004, 2004/2005 and 2005/2006. Data pooled for three sites and net position. Discharge and temperature data from Tocumwal gauge on Murray River. Note: dotted line represents approximate floodplain inundation height at Barmah-Millewa Forest, solid triangles on x-axis indicates sampling event. Letters on x-axis represent calendar months in each year from July to March

Murray cod larvae were consistently collected from early November to mid-December in all three years, in water temperatures ranging from 18.6 to 24.8°C (Figure 4(b)). The effect of season in the Murray cod larvae model only explained 2.9%, suggesting that season was not explaining a major component of the variance in the data. The larvae were collected in similar abundances among the three years and over a range of flow conditions (Figure 4(b)), with fewer individuals captured in 2003/2004 than in both of the following seasons (as adjusted or raw data). Trout cod larvae were only collected in low numbers only in 2005/2006 sampling season and therefore it is not appropriate to draw conclusions from this data (Figure 4(c)). The few individuals that were collected were present at the same time as the larvae of Murray cod (Figure 4(c)).

Abundance of young-of-year fish

In total, five golden perch, zero silver perch, 30 Murray cod and 71 trout cod young-of-year were collected during the two sampling years (Table II). The low abundance of golden perch and absence of silver perch young-of-year may be due to a suspected sampling inefficiency in the collection of smaller individuals of these two species, and it is hoped sampling in subsequent years may further elucidate the success, or otherwise, of the 2005/2006 cohort of fish compared to other years. The models for both young-of-year Murray cod and trout cod suggest no significant effect due to zone, but there was a highly significant effect due to season ($p < 0.0001$, explaining 33 and 72% of the model deviance, respectively), with greater numbers of both species captured in 2006 compared to 2005 (Figure 5(a) and (b)).

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Table II. Total catch per unit effort of young-of-year golden perch (*Macquaria ambigua*), silver perch (*Bidyanus bidyanus*), Murray cod (*Maccullochella peeli peeli*) and trout cod (*Maccullochella macquariensis*) collected during 2005 and 2006 sampling events at the three collection sites

	Golden perch	Silver perch	Murray cod	Trout cod
2005				
Ladgroves beach	0	0	5	2
Barmah Choke	1	0	0	1
Morning glory	2	0	0	1
Total CPUE	3	0	5	4
2006				
Ladgroves beach	0	0	15	57
Barmah Choke	2	0	5	9
Morning glory	0	0	5	1
Total CPUE	2	0	25	67
Total CPUE	5	0	30	71

Note: CPUE = catch per unit effort.

DISCUSSION

The role of flooding in spawning and recruitment of native fish

Much speculation has surrounded the role of flooding in the spawning and recruitment of native fish in the Murray–Darling Basin (Harris and Gehrke, 1994; Humphries *et al*., 1999; King *et al*., 2003). Harris and Gehrke (1994), following the tenets of the flood pulse concept (Junk *et al*. 1989), proposed two possible mechanisms about how floods could enhance recruitment of native fish. They suggested that fish could either spawn in response to floods or that flooding indirectly increases survival of young by providing suitable food and habitat resources on the inundated floodplain. However, evidence supporting the use of floodplains by Murray–Darling fish and the role of floods in spawning and recruitment has been limited and its broad applicability has been questioned (Humphries *et al*., 1999; King *et al*., 2003, Mallen-Cooper and Stuart, 2003). The present study found that the spawning and recruitment success of golden perch, silver perch, Murray cod and trout cod increased during a managed flood event, however, the exact cause of the response is largely unknown and the mechanism driving the response varied between the four species.

Both golden and silver perch are commonly referred to as flood recruitment specialists (Lake, 1967; Harris and Gehrke, 1994; Schiller and Harris, 2001), however, as discussed by various authors the evidence supporting this is limited and inconclusive (Humphries *et al*., 1999; King *et al*., 2003). Lake (1967), using results from constructed ponds on the floodplain, suggested that these two species were stimulated to spawn by increasing water levels and inundating dry ground when water temperatures exceeded 23°C. Although Lake (1967) is the first attributed to suggesting a flood recruitment model for these species, Mallen-Cooper and Stuart (2003) suggest that Lake's data also support the possibility that rises within the river channel at specific temperatures, might be enough to stimulate spawning. Mallen-Cooper and Stuart (2003) presented age verified year–class strength data of the two species from three years of sampling fish moving through the Torrumbarry weir fishway, on the Murray River downstream of Echuca. They concluded that golden perch recruitment was high in non-flood years and poor in flood years, and silver perch recruited in all flow years; supporting a non-flood recruitment model for the species. However, a significant problem with their conclusions is the unknown location of spawning and nursery site/s of the fish captured, making it difficult to confidently correlate year–class strength and the timing of spawning to flow conditions experienced by the fish. The present study demonstrates that at least low levels of spawning activity can occur for golden perch and silver perch during within channel flows (albeit regulated, fairly stable and irrigation flows) in spring and summer (2003/2004 and 2004/2005 seasons); but that a large increase in spawning intensity

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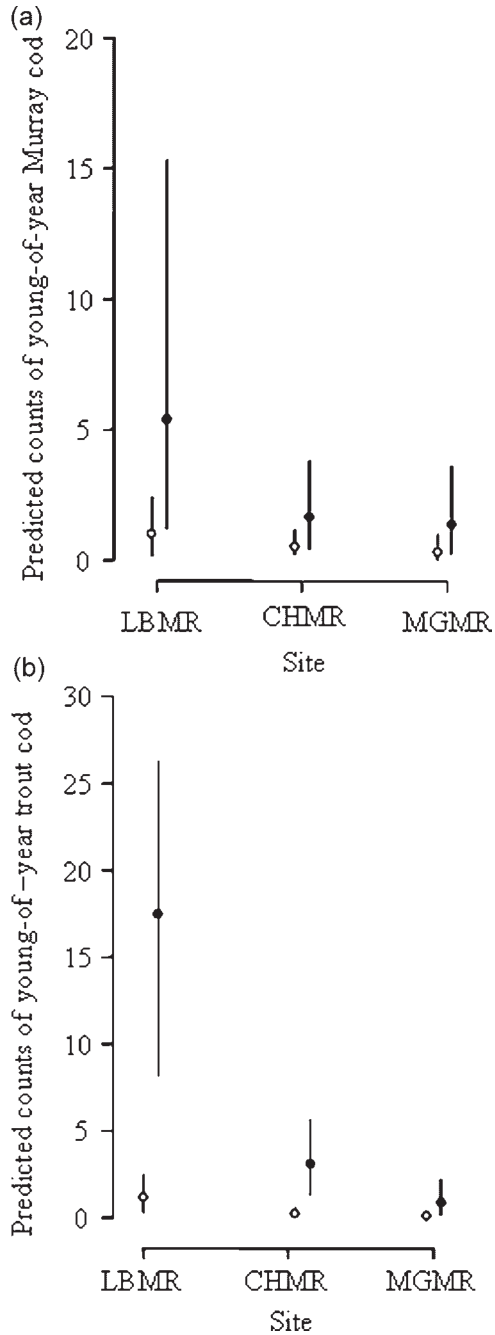

Figure 5. Predicted modelled mean counts (and 95% confidence intervals of young-of-year) (a) Murray cod and (b) trout cod collected using standardized boat electrofishing sampling in 2005 (empty circles) and 2006 (solid circles)

occurred during the 2005 flood conditions. The first major spawning event for both silver perch and golden perch appeared to occur during a coinciding rise in water temperature (of 2.5°C in the previous 7 days) and on a rise in water level in early November 2005, similar to that proposed by Lake (1967). Silver perch also demonstrated a second increase in spawning activity in late December 2005, as flows were slowly declining and the Forest was draining. However, as this was only one flood event in 1 year, it is difficult to confidently determine exactly what

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environmental cue or flow component of the flood that triggered the increased spawning activity. For example, was the spawning cue a sudden rise or fall in river discharge or the floodplain inundation itself, or a combination of both? This is an important consideration, because if spawning in these two species can be triggered by in-channel flow rises, management of environmental water may only need to be confined to restoring in-channel flow rises during the spawning period to target enhanced spawning opportunities for these two species. However, as there was limited response to some smaller flow peaks (both in-channel and small inundation events) that occurred during the first two seasons, this spawning mechanism alone seems unlikely. Further monitoring over a range of flow conditions is required before specific flow components such as these can be teased out and confidently used in water management. Additionally, although the increase in spawning recorded in this study of both of these species is likely to have resulted in an increase in subsequent recruitment, unfortunately we were unable to determine the strength of recruitment during these different flow years due to low capture rates of young-of-year fish of these species. Conclusions about the overall success of the spawning event and subsequent recruitment therefore cannot be made at this time, and should be the focus of future investigations.

While golden perch and silver perch spawning was enhanced during the 2005 flood conditions, Murray cod and trout cod spawning intensity (inferred from catches of drifting larvae) was relatively similar between the flood year and the two previous breeding seasons. This finding supports previous studies which have demonstrated that they can spawn irrespective of flow conditions in both regulated and unregulated rivers, and that spawning is not enhanced or triggered by flooding (Humphries *et al*., 2002; Gilligan and Schiller, 2003; King *et al*., 2003; Humphries, 2005; Koehn and Harrington, 2006). Again, in concert with these other studies, Murray cod and trout cod larvae were collected during November and December across all three years of this study, suggesting that the timing of spawning is more associated with day length or some other consistent interannual variable than flow (Humphries, 2005; Koehn and Harrington, 2006). However, while spawning intensity did not increase as a response to flooding, there was a substantial increase in catch per unit effort of young-of-the-year of both species after the 2005/2006 flood conditions compared to that in the 2004/2005 season. This suggests that the survival and subsequent recruitment of their young was greater during the flood conditions, however, this result needs to be confirmed by assessing the strength of recruitment in more years with variable flow conditions. Strong year classes of Murray cod following breeding seasons that have experienced high flows or floods have also been reported from analysing commercial catch records (Rowland, 1998; Ye *et al*., 2000), but these data have not been age validated and have to be treated with some caution.

The flood pulse concept (Junk *et al*., 1989) suggested that the inundated floodplain environment provides a suitable spawning habitat and/or high densities of food and habitat for increasing the survival of young fish. Indeed, rises in flow have been thought to provide essential cues for upstream movements in the four target species in this study (Reynolds, 1983), potentially also triggering lateral movements onto inundated floodplains to spawn or cueing in-channel spawning and allowing their drifting eggs and/or larvae to be washed into inundated nursery habitats on the floodplain (Lake, 1967). However, despite large floodplain areas of the B-M Forest wetland complex being accessible to all stages of fish, no golden perch and silver perch eggs or larvae, and low numbers of Murray cod and trout cod larvae were collected during intensive sampling of the Forest habitats over the three years of the study (King *et al*. 2007). Rather, the early life stages of these four species were either solely or mostly captured in the river, suggesting a within channel spawning preference for these species even under flood conditions; although it is not known whether this preference would still occur at higher flood magnitudes. Furthermore, this could suggest that the food resources required for the young to grow and survive in the main channel, were generated on the inundated floodplain environment and then transported to the main river channel (Junk *et al*. 1989). Whilst this indirect benefit of flooding for enhancing fish recruitment in the main channel environment requires further investigation, it does suggest that the early stages of some fish may not need access to the floodplain to harness the benefits of this ephemeral environment, highlighting the importance of undisrupted connection of the river to its surrounding floodplain (Junk *et al*., 1989).

This study has demonstrated that golden perch and silver perch are quite flexible in their spawning requirements and can spawn under flood and within channel flows; however, their spawning activity was greatly increased during the 2005 flood conditions. In contrast, Murray cod and trout cod spawning activity is not influenced at all by flow conditions, but their recruitment may be increased when floodplain inundation occurs at times when their larvae and juveniles are present.

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Can flooding using environmental flows be used to improve riverine fish populations?

With much of the world's riverine fish faunas under severe decline, managers are increasingly looking to improve or restore fish populations through a variety of restoration activities. Aspects of the flow regime are known to be linked to critical aspects of the life history of fishes (Welcomme, 1985; Junk *et al*., 1989; Humphries *et al*., 1999; Poff *et al*., 2003; Lytle and Poff, 2004), and therefore, providing more natural flow regimes in regulated rivers is seen as one potential restoration measures (Marchetti and Moyle, 2001; Arthington *et al*., 2006). However, examples of its use are limited and those that are available have had varying successes. For example, Travinchek *et al*. (1995) and Freeman *et al*. (2001) demonstrated some recovery in fish populations in hydropeaking reaches when stable minimum flows were returned. While a test flood in the Colorado River downstream of Glen Canyon Dam had little effect on the distribution, abundance or movement of native fish, and only short-term effects on the densities of some non-native species, suggesting that the flood was of insufficient magnitude to result in a response (Valdez *et al*., 2001). Conversely, the importance of the appropriate timing of rising flows or floods has been shown to be a strong spawning cue for some species (Nesler *et al*., 1988; King *et al*., 1998). King *et al*. (1998) studied the spawning response of an endangered cyprinid, the Clanwilliam yellowfish (*Barbus capensis*), in the Olifants River, South Africa, to experimental flow releases from a dam. They concluded that spawning success should increase following flow releases from the dam if they were delivered at the appropriate time and water temperatures were suitable. These examples all highlight the need to consider various key attributes of the natural flow regime in that river system to manage flows for improved fish populations.

King *et al*. (2003) suggested a range of environmental conditions would need to occur to allow successful spawning and recruitment of fish during flood conditions, including: (1) a coupling of high flows and temperatures, (2) a predictable flood pulse for that system and the fishes within in it, (3) the rates of rise and fall need to be slow, (4) the duration of the inundation period would need to be in the order of months and (5) that a large proportion of the floodplain is inundated. The 2005 flood at B-M Forest met all of these requirements; and therefore, perhaps the successful spawning and recruitment observed in these species and other floodplain dwelling species (King *et al*. 2007) may not have occurred if the B-M EWA was not used. Indeed, the use of the EWA not only increased the magnitude of the flood peaks, but also allowed the duration of the effective inundation period to be extended for an additional two months through October and December without disconnection of the floodplain (Figure 2). Importantly this use of environmental water coincided with natural tributary inflows creating the three flow peaks in October and November, and also closely mirrored the shape of the modelled natural hydrograph during these months (see King et al. In press) (Figure 2). The importance of providing as close to natural flow conditions in environmental flow allocations is increasingly being recognized (Arthington *et al*., 2006). Additionally, the flooding and the use of the environmental water occurred at a time when spawning had been recorded in this region for these species in previous years.

Whilst further study is required to elucidate and confirm the mechanism for the successful spawning and recruitment of some species observed during this study, this research has demonstrated that it is possible to optimize and manage flows to improve native fish spawning and recruitment opportunities. We believe that this is the first study to demonstrate a strong link between fish spawning and recruitment and the provision of an environmental flood at least in Australia, but perhaps in the world, and has important implications for managing flows in regulated rivers in the Murray–Darling Basin and wider. Careful monitoring and scientific input into the planning and management of the 2005 B-M EWA allowed us to input some considerations of fish spawning and recruitment into the management of the event (King *et al*., in press). The research provided valuable real-time and ongoing management input for optimising benefits of environmental water for restoration of fish communities. However, this event has to be viewed as only a single experiment, and as such, we still have much to learn about the role of various flows on fish and other biota. Therefore longer term manipulative experimental flows utilizing a variety of flow scenarios need to be encouraged and conducted (Bunn and Arthington, 2002; Poff *et al*., 2003; Arthington *et al*., 2006). This needs to occur in an adaptive management context whereby the flow manipulations happen when suitable monitoring is underway, and the lessons learnt from each event are then incorporated into future management of the system. As suggested by Poff *et al*. (2003), this experimental approach needs to be done in full collaboration with scientists, managers and other stakeholders, as was used in the implementation of this EWA.

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