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Regulated recruitment: native and alien fish responses to widespread floodplain inundation in the Macquarie Marshes, arid Australia

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ABSTRACT

Rivers and wetland ecosystems are degraded by diversions of water upstream. In response, governments have reallocated water to flood wetlands, mimicking natural inundation of habitats known to drive booms in native freshwater fish production. Individual flow events allow the ecological outcomes of restoration efforts to be evaluated, in order to improve ongoing adaptive management. This study investigated the population size and recruitment responses of seven native and three alien fish species to widespread floodplain inundation at 15 sites across the Macquarie Marshes, a regulated wetland in Australia's Murray–Darling Basin. Flooding during the late winter, when water temperatures were 4 to 12.6 °C below the spawning threshold for native fish species present in the system, promoted reproduction and recruitment by alien species, which were significantly more abundant than native species after flooding. Fish assemblage structure also differed significantly between main channel and floodplain habitats, with macrophytes, pH, emergent vegetation, flow velocity and small wood debris accounting for 59% of spatiotemporal variation in fish assemblage structure. Strong correlations were identified between the length of spawning window and post-flood abundance of young-of-year and recruit size classes in the most abundant alien and native fish species. Future environmental flows, particularly those that inundate floodplain habitats, need to be delivered in light of the confounding effects of flow–temperature coupling and the lower spawning temperature thresholds of alien species. Copyright © 2014 John Wiley & Sons, Ltd.

KEY WORDS discharge; environmental flow; wetland; floodplain; Murray–Darling Basin; Ramsar; disturbance; restoration

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INTRODUCTION

Natural flow regimes of dryland rivers are highly variable. Flooding punctuates extended dry periods, producing respective 'boom' and 'bust' phases (Puckridge *et al*., 1998; Kingsford *et al*., 1999; Bunn *et al*., 2006). In Australia, up to 90% of native fish species in dryland systems belong to a functional guild favouring well-vegetated habitats (Arthington and Balcombe, 2011). These species persist through dry periods by recruiting within the main channel (Balcombe *et al*., 2006; Kerezsy *et al*., 2011) but exploit floodplain habitats when they are available (Balcombe *et al*., 2007; Rolls and Wilson, 2010). Consequently, widespread floodplain inundation during the summer is associated with significant increases in native fish abundance and biomass (Balcombe and Arthington, 2009; Arthington and Balcombe, 2011), potentially disadvantaging alien species (Costelloe *et al*., 2010).

The regulation of rivers, with dams, other barriers and water diversions, has reduced the quantity and quality of habitats sustaining freshwater fish faunas (Grift *et al*., 2001; Aarts *et al*., 2004). In dryland rivers, the extent, duration, timing and frequency of low and high flows have been affected, leading to decline of native fish species richness and abundance (Bunn and Arthington, 2002). A key restoration measure has been to reinstate the natural flow regime by providing environmental flows (Poff *et al*., 1997; Naiman *et al*., 2002). This approach requires an understanding of relationships between fish biology, flows and floodplains, which remains poor in many systems (Buijse *et al*., 2002; Tockner and Stanford, 2002). As a result, determining how to best restore degraded dryland rivers using valuable environmental water allocations (EWAs) remains a key challenge for freshwater science (Gehrke *et al*., 1995; King *et al*., 2003).

The Macquarie Marshes is an internationally significant floodplain wetland located in the downstream reaches of the Macquarie River, Murray–Darling Basin, Australia (Figure 1). The system presents a useful case study because the natural flow regime has been affected since the late 1960s by large dams, plus hundreds of smaller structures that store

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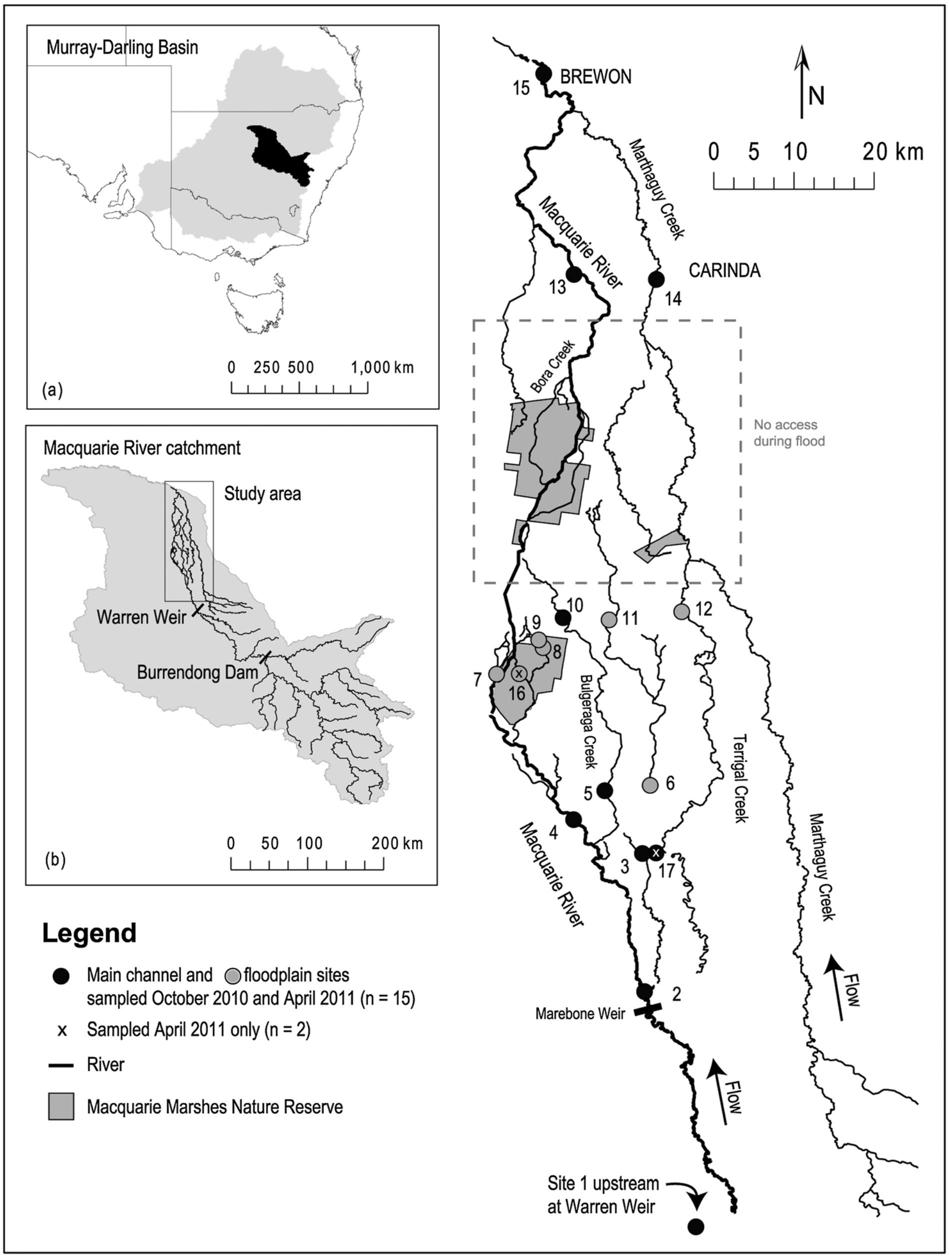

Figure 1. Location of the Macquarie Marshes within (a) the Murray–Darling Basin and (b) the lower Macquarie River. Fifteen sites were sampled (eight main channels and seven floodplains) in October 2010 and April 2011, with two additional sites (numbers 16 and 17) sampled in April 2011.

water and impede connectivity (Rayner *et al*., 2008; Steinfeld and Kingsford, 2011). Total diversions average 23% of annual surface water availability (CSIRO, 2008), and the proportion of long-term average annual flows reaching the Macquarie Marshes has declined to 57% (Ren and Kingsford, 2011). Additionally, cold water pollution may affect over 300 km of the main channel downstream from the largest impoundment, Burrendong Dam (Boys *et al*., 2009). Calls to redress ongoing ecological decline (Kingsford and Thomas, 1995; Kingsford and Auld, 2005) have led to a current environmental allocation of 319 Gl (Cth EWH, 2012).

Individual environmental flows provide opportunities to quantify the responses of fish populations, contribute to construction of response curves and inform adaptive management (Rogers *et al*., 2005; Anderson *et al*., 2006; Murchie *et al*., 2008; Kingsford *et al*., 2010). We previously investigated a relatively small flow, which mostly remained within channel habitats, in the Macquarie Marshes (Rayner *et al*., 2009). Dispersal and recruitment responses were exhibited by most fish species, but alien species dominated abundance and biomass. At the time, we speculated that inundation of the surrounding highly productive and extensive floodplains (Jenkins and Boulton, 2007; Thomas *et al.*, 2011) would support higher rates of fish recruitment, consistent with data from unregulated systems (e.g. Arthington and Balcombe, 2011). However, recent studies suggest that it is not just flood magnitude that controls recruitment by native fish species (e.g. King *et al.*, 2003; King *et al.*, 2010; Rolls and Wilson, 2010; Humphries *et al.*, 2012; Baumgartner *et al.*, 2013). Rather, the interaction between flow, water temperature and reproductive traits plays a key role in determining responses (Rolls *et al.*, 2013; Sternberg and Kennard, 2013).

The goal of this study was to investigate these dynamics in the Macquarie Marshes by quantifying native and alien fish responses to a large flood event that caused widespread floodplain inundation. We aimed to examine the influences of hydrology, habitat and water temperature on the population size and recruitment responses of individual fish species and therefore fish assemblage structure. We also aimed to consider what influence the presence of alien species might have on responses of native fish species to widespread floodplain inundation.

METHODS

Hydrology, habitat and water temperature

This study focused on a large natural flood event, supplemented by two EWAs, which inundated the Ramsar-listed Macquarie Marshes and its floodplain between July 2010 and June 2011 (Figure 2a). The volume of this flood was about six times greater than any flood during the preceding 7 water years. Of the ~955 Gl that entered the Macquarie Marshes, 270 Gl were unregulated tributary flows, regulated water orders and 'operational surplus', 490 Gl were flood mitigation releases from Burrendong Dam and 195 Gl (~20%) were environmental water (Figure 2b). The first EWA maintained inflows above 2000 ml $d-^{1}$ from late September 2010, when unregulated tributary flows ended, until early October 2010, when flood mitigation releases from Burrendong Dam began. These releases peaked discharge at 7300 ml d^{-1} at Marebone in December 2010. The second EWA extended flooding of the Macquarie Marshes from early February 2011 to March 2011, when discharge fell below 1000 ml d^{-1} and floodplains became disconnected.

Fifteen sites were selected in the lower Macquarie River, covering the latitudinal and longitudinal extent of the Macquarie Marshes floodplain system (Figure 1). Sites were classified as main channel or floodplain, based on their connectivity to the main channel and mesohabitat characteristics. Main channel sites ($n = 8$) carried flow in a deep channel incised into the floodplain, except during prolonged drought. Floodplain sites ($n = 7$) were shallow, well vegetated and ephemeral. A total of 28 abiotic variables were measured at each site, which distinguished the two habitats. These variables included geomorphology, substrate, vegetation and water quality (Pusey *et al.*, 2004). Macrophyte beds were estimated as a percentage of total surface area sampled on floodplains (10–750 m^2), but in river channels with undercut banks were estimated as the proportion of total bank length sampled. Three replicates of water quality variables (temperature, pH, dissolved oxygen and conductivity) were also measured at each site during each survey, at a depth of 0.5 m, using a multi-probe instrument (90-FLT, TPS Pty Ltd, Brisbane). Water temperatures during the study period followed a typical seasonal pattern, low during the winter and high in the summer: Water temperature did not exceed 15 °C until October 2010 and remained above this temperature until after April 2011 (Figure 2c). Mean water temperature recorded at the study sites (at differing times of day and under differing weather conditions) was 17.0 °C in October 2010 and 15.2 °C in April 2011, consistent with the logged temperature data recorded at Warren Weir (Figure 2b).

Fish surveys

Fish were sampled at each study site in October 2010 and April 2011, coinciding with the EWA components of the flood event (Figure 2). Two additional main channel sites, which were inaccessible in October 2010, were sampled opportunistically in April 2011. Combinations of boat electrofishing, backpack electrofishing and small traps were used, depending on water depth, to provide a representative sample of the fish assemblage present. In water <1.5 m deep, backpack electrofishing was used (up to 12 shots per site times 90 s of power-on time, Smith-Root Model 12; 500 V, setting I-9), whereas boat electrofishing was used in water deeper than 1.5 m (up to 12 shots per site times 120 s, Engineering Technical Services 5 kVA; 50–500 V, 120 Hz, 15–40% duty cycle, 6–8 A). Up to ten small traps ($40 \times 20 \times 20$ cm, 3-mm mesh; five on each bank) were set unbaited for 2 h at each site to sample small-bodied species. Fish were identified and measured to the nearest millimetre standard length, before being returned to the waterway.

Data analyses

Species catch data were range standardized for each separate gear type (boat electrofishing, backpack electrofishing and small traps) and then summed across gear types for each site, to provide a measure of relative species abundance at each site, on each sampling date. To allow comparisons between sites where different gear types were deployed, a further range standardization was applied using the total catch-per-unit-effort (CPUE) value for each site. This approach provides a relative measure of each

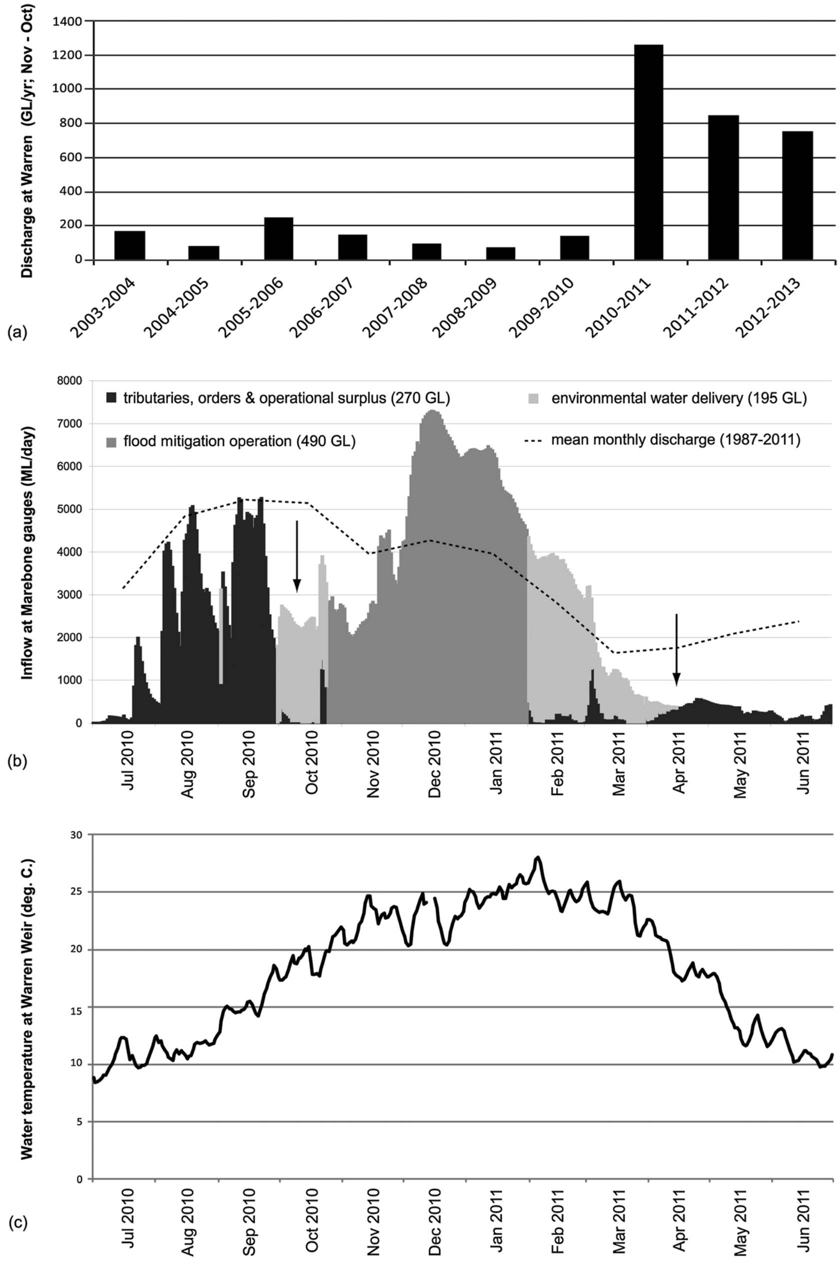

Figure 2. (a) Annual (July–June) river discharge at Warren, NSW for the period 2003–2013 (data: NSW State Water gauge 421004 – Macquarie River at Warren Weir). (b) Daily Macquarie Marshes inflows recorded at Marebone Weir gauges (data: NSW State Water gauges 421090 and 421088; site 2 in Figure 1) for the period July 2010 to June 2011, showing the management operations in place upstream and fish survey dates (data: Debbie Love, NSW Office of Environment and Heritage) plus post-regulation mean monthly discharge. Arrows indicate fish surveys. (c) Water temperature at Warren Weir (data: NSW Office of Water).

species' contribution to total CPUE, directly comparable across sites and sampling dates. Three-way, fixed-factor ANOVA was used to test for differences in CPUE between sampling dates, habitat types and fish conservation status (native vs alien species; SPSS 19.1; IBM Corp., 2010).

A resemblance matrix of $\log_{10}(x+1)$ transformed CPUE data was generated in PRIMER (Clarke and Gorley, 2006), using the Bray–Curtis dissimilarity measure (Bray and Curtis, 1957). Fixed two-factor permutational MANOVA (PERMANOVA) was used to test for differences in fish assemblage composition between sampling dates and habitat types, and similarity percentage (SIMPER) analysis was used to determine which fish species contributed most of the variation between groups based on the sampling date and habitat type. Pearson's correlation coefficient was used to examine relationships between species CPUE and fish assemblage structure and plotted when >0.5. Distance-based linear modelling (DistLM) and distance-based redundancy analysis (dbRDA) were used to assess the relative importance of geomorphology, substrate, vegetation and water-quality characteristics in structuring fish assemblages. The stepwise model selection routine was used, with the modified information criterion (AICc) that is most suitable for model selection when the number of variables exceeds the number of samples, based on 9999 permutations in PERMANOVA + for PRIMER (Anderson *et al.*, 2008). Abiotic data were unavailable for one floodplain (11) and one main channel site (12) because of malfunction of a water quality monitor so were excluded from DistLM analysis.

Length–frequency histograms were generated for October 2010 and April 2011 fish catch data. Individual fish from the five most abundant species were divided into three size classes [adults, young-of-year (YOY) and recruits] according to standard length (Rolls and Wilson, 2010). YOY minimum and maximum standard lengths were the following: goldfish, 75 and 100 mm; common carp 120 and 200 mm; Gambusia, 20 and 40 mm; spangled perch, 50 and 78 mm; and bony bream, 75 and 150 mm. Fish larger than the YOY maximum were classified as adults; fish smaller than the YOY minimum were classified as recruits. CPUE of these size classes was regressed against the spawning window of these species, defined as the number of days between 1 June 2010 (start of the flow event) and 12 April 2011 (date of second fish survey) that water temperatures at Warren Weir exceeded the threshold spawning value for each species (Table I; Figure 2). This was the nearest location with complete temperature data for the study period. Relationships between size-class abundance and spawning window were then analysed using linear regression.

RESULTS

Individual fish species

Seven native and three alien fish species were caught during the study. Each of these species has been caught in the Macquarie Marshes previously, although six native species predicted to have occurred under reference condition, including flat-headed gudgeon that was caught in 2007–2008, were not caught (Table I). The CPUE of the five species varied substantially between sampling dates, with three alien species dominating: common carp, Gambusia and goldfish (Figure 3). Common carp accounted for 55% of total CPUE in October 2010 and 41% of total CPUE in April 2011. Two native species, bony bream and spangled perch, were relatively abundant following floodplain inundation, reflecting their behaviour of actively dispersing during floods and reproducing on floodplains (Balcombe *et al.*, 2006; Rolls and Wilson, 2010). However, CPUE was low for the five remaining native species (golden perch, Murray cod, Murray River rainbowfish, Australian smelt and western carp gudgeon; Figure 3), although golden perch and Murray cod were observed moving upstream in mid-2010 following the first inflows from unregulated tributaries (Garry Hall, 'The Mole', personal observation). Mean CPUE was significantly higher for alien fish species than native fish species, significantly higher in April 2011 than October 2010 and significantly higher for alien fish species, relative to native fish species following flooding (Figure 4; Table II).

The species caught varied in regard to the water temperature required to initiate spawning (Table I). The

Table I. Fish species predicted to occur in the lowland zone of the Macquarie River valley and those actually caught in 2007–2011, with threshold spawning temperature of each species (Figure 4).

Common name *alien species	Scientific name	Reference condition[1]	2007–2008 26 sites[2]	2010–2011 17 sites[3]	Threshold spawning temperature (°C)[4]
Goldfish*	*Carassius auratus*		Y	Y	17
Common carp*	*Cyprinus carpio*		Y	Y	16
Gambusia*	*Gambusia holbrooki*		Y	Y	16
Olive perchlet	*Ambassis agassizii*	Y			22
Silver perch	*Bidyanus bidyanus*	Y			23.3
Unspecked hardyhead	*Craterocephalus stercusmuscarum*	Y			23.6
Western carp gudgeon	*Hyseleotris* spp.	Y	Y	Y	22.5
Spangled perch	*Leiopotherapon unicolor*	Y	Y	Y	20
Murray cod	*Maccullochella peelii peelii*	Y	Y	Y	20
Golden perch	*Macquaria ambigua*	Y	Y	Y	18.8
Murray River rainbowfish	*Melanotaenia fluviatilis*	Y	Y	Y	20
Purple-spotted gudgeon	*Mogurnda aspersa*	Y			20
Bony bream	*Nematolosa erebi*	Y	Y	Y	20
Flat-headed gudgeon	*Philypnodon grandiceps*		Y		15
Australian smelt	*Retropinna semoni*	Y	Y	Y	15
Freshwater catfish	*Tandanus tandanus*	Y			24

Data: 1. Davies *et al.* (2008); 2. Rayner *et al.* (2009); 3. this study; and 4. Boys *et al.* (2009) and Ebner *et al.* (2009). Five species, originally occurring in the system, no longer occur.

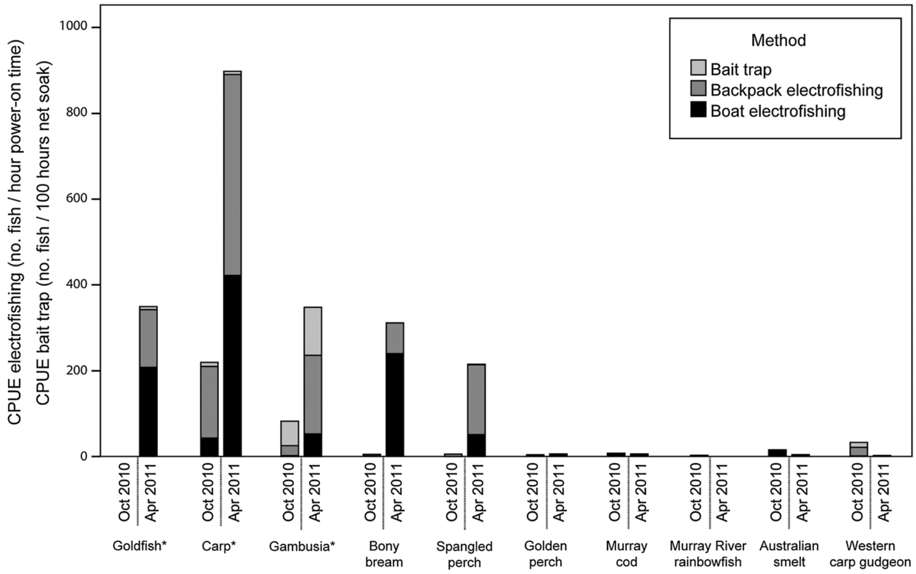

Figure 3. CPUE for ten fish species (*alien species) caught using three gear types (bait trap, backpack electrofishing and boat electrofishing) during October 2010 and April 2011.

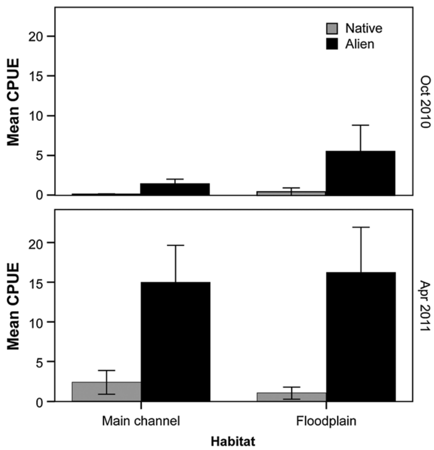

Figure 4. Mean catch per unit effort (CPUE) per site for native and alien fish species in floodplain and main channel sites in October 2010 and April 2011.

three alien species, known to spawn at water temperatures of 16–17 °C, recruited earlier in the flow event than native species, before temperatures were high enough to stimulate native fish spawning (Figure 2c; Table I). Adult common carp moved into floodplain habitats as water levels rose in August 2010 and spawned in shallow, recently inundated floodplain habitats, characterized by submerged terrestrial grasses, as water temperatures increased above 16 °C (8 September 2010 near site 12, Steve Clipperton, NSW Fisheries, personal communication; Figure 2b). Large cohorts of juvenile common carp were present in the Macquarie Marshes in October 2010, and by April 2011, common carp density was extremely high at some sites (particularly at site 10 in Figure 1). At this time, goldfish were one of the most widespread and abundant species in the Macquarie Marshes, with a large cohort averaging 88 mm standard length (SL) (ranging from 39 to 243 mm SL), present at 88% of sites (Figure 3).

Table II. ANOVA results for CPUE of fish across sampling dates, habitats and conservation status.

Source	Levels	F	Significance
Date	Oct 2010; April 2011	18.33	<0.01
Habitat	Floodplain; main channel	0.52	0.47
Status	Native; alien	29.93	<0.01
Date * habitat	—	0.55	0.46
Date * status	—	11.69	<0.01
Habitat * status	—	1.04	0.31
Date * habitat * status	—	0.04	0.85

Reproductive activity, as evidenced by changes in the size structure of individual fish species, underpinned changes in CPUE of individual species (Figure 5). Alien fish species, with lower spawning threshold temperatures than native species, spawned earlier in the flood and consequently had a longer spawning window available for reproduction and recruitment during the flood event itself than native species. Consequently, there were strong correlations between the length of spawning window and post-flood CPUE of YOY and recruit size classes of the five most abundant species, despite low post-flood abundances of adults (Figure 6). The mean threshold spawning water temperature for species that responded strongly to the flood event was 17.8 °C ± 2.1 S.D., 1.5 °C lower than the mean temperature of 19.3 °C ± 2.74 S.D for species that did not respond strongly, although this difference was not significant (t-test $p = 0.36$).

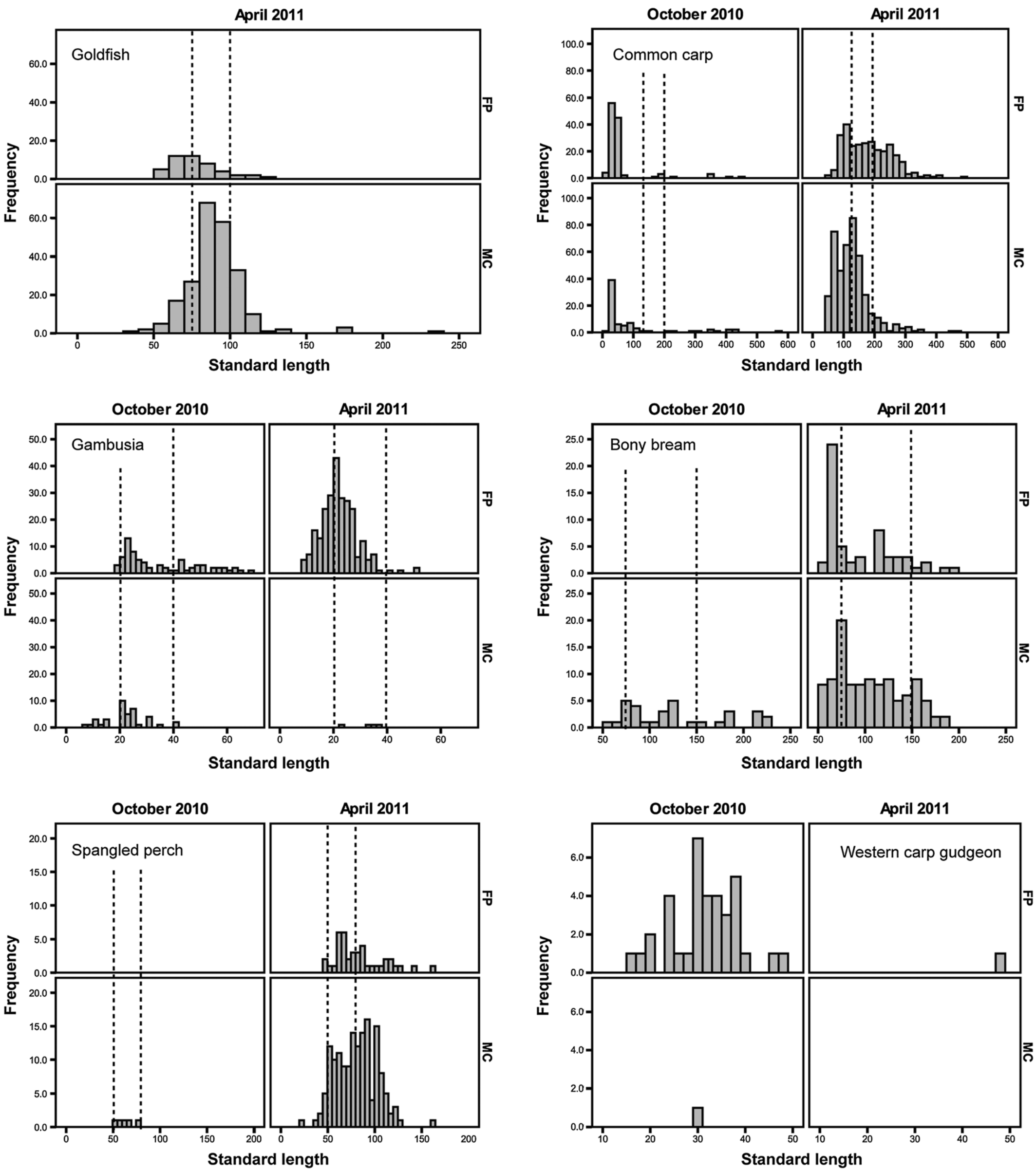

Figure 5. Length frequency histograms for the five most abundant fish species caught during the study in floodplain and main channel habitats, with size class divisions used in analysis, plus western carp gudgeons, in October 2010, but rare in April 2011.

Fish assemblage structure

Overall fish assemblage structure varied significantly between sampling dates and between floodplain and main channel habitats in relation to the responses of native and alien fish (Figure 7; Table III). Floodplain habitats were characterized by high abundance of Gambusia and common carp, whereas main channel habitats were characterized by common carp and goldfish, with smaller contributions to assemblage structure from bony bream, Gambusia and spangled perch (Figure 7; Table IV). Macrophyte cover, pH, emergent vegetation, flow velocity and small wood debris together explained 59% of total variability in fish assemblage structure (Table V). Floodplain habitats had a high percentage cover of macrophytes and emergent vegetation, whereas main channel habitats had a high percentage cover of small woody debris and increased water velocity, and pH increased from October 2010 (Figure 7).

DISCUSSION

Influences of hydrology, habitat and water temperature

Current evidence suggests that inundation of extensive areas of floodplain for several months, coinciding with high water temperatures, enhances recruitment success of native

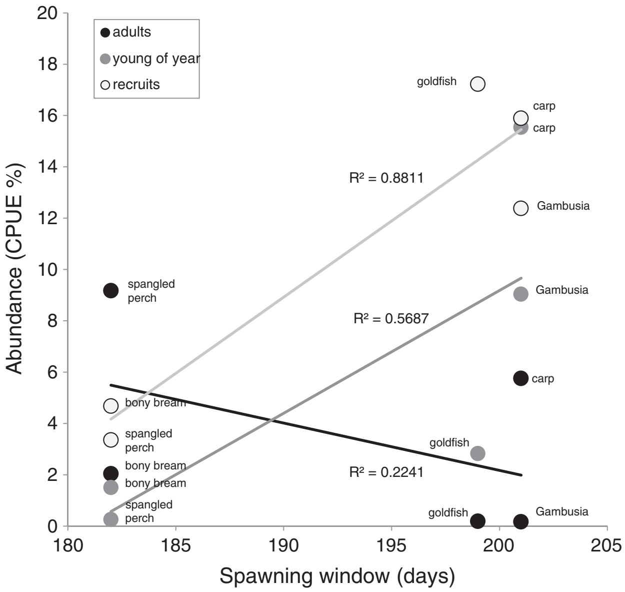

Figure 6. CPUE in April 2011 of adult, young-of-year and juvenile fish from the five most abundant species (two native and three alien species) in the Macquarie Marshes (as percentage of total CPUE of these species) following a large flood event, relative to the length of the spawning window (days of water temperature above threshold spawning temperature) for each species in the period 1 June 2010 to 12 April 2011.

fish species (Gorski *et al*., 2011). These dynamics underpin conceptual frameworks of fish use of inundated floodplains, which combine elements of the 'flood-pulse' (Junk *et al*., 1989) and 'low-flow' (Humphries *et al*., 1999) models of fish recruitment. Optimum conditions for floodplain use by fish occur when flows coincide with the spawning of individual species and seasonal rises in temperature (King *et al*., 2003),

Table III. PERMANOVA conducted on fish community composition between samples to generate a permutated F statistic (F) and permutated p-value (P) with calculated degrees of freedom (df) and sums of squares (SS) noted.

Source	df	SS	F	P	% variance
Date	1	6434	5.95	0.001	20.3
Habitat	1	5387	4.99	0.003	18.2
Date * habitat	1	2607	2.41	0.068	15.4
Residual	25	27 015			32.9
Total	28	44 217			

Factors are date (October 2010 or April 2011) and habitat (floodplain or main channel).

but river regulation can decouple this relationship (Sparks *et al*., 1990). We found that extensive floodplain inundation drove a 'boom' in fish productivity on the floodplain of a dryland river, despite a history of regulated flows. In this case, however, the floodplain habitats made available by the winter–spring flooding were initially exploited by alien species, rather than natives (Figure 4).

Fish responses are often linked to changes in habitat structure associated with flooding (Bice *et al*., 2014). In the Macquarie River, fish assemblage structure differed significantly between main channel and floodplain habitats throughout the study (Table III; Figure 7), with species' recruitment and habitat use largely corresponding to their functional classifications (Young *et al*., 2003; Ralph and Spencer, 2010; Baumgartner *et al*., 2013). All small-bodied native species were less abundant after flooding (Figure 4), contrasting their response to a much smaller flow in the summer of 2008 (Rayner *et al*., 2009), whereas larger bodied native species

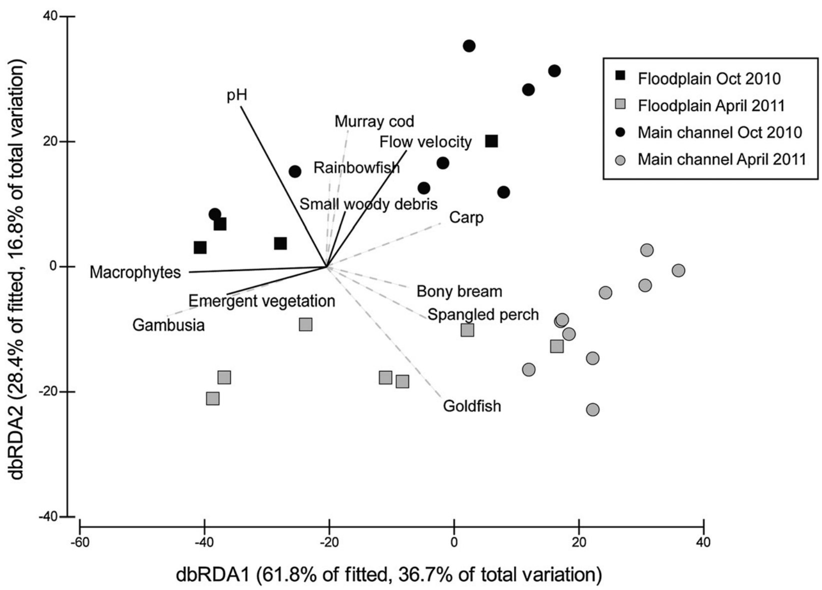

Figure 7. Distance-based redundancy analysis (dbRDA) axes of CPUE data showing clear differences in fish community structure between floodplain and main channel sites during October 2010 and April 2011. DistLM vectors explaining variation in fish community structure are shown as solid lines, with species vectors based on Pearson correlation coefficients >0.5 shown as dashed lines.

Table IV. Results of SIMPER analysis indicating species contributions to average similarity among sampling dates (October 2010 and April 2011) and habitat groups (floodplain and main channel).

Group	Average similarity	Species	Species contribution %	Cumulative contribution %
October 2010	47.48	Common carp	68.11	68.11
		Gambusia	17.75	85.85
		Murray cod	12.17	98.03
April 2011	66.22	Common carp	45.83	45.83
		Goldfish	24.32	70.15
		Gambusia	15.71	85.86
		Spangled perch	7.40	93.26
Main channel	59.74	Common carp	56.36	56.36
		Goldfish	21.78	78.14
		Bony bream	5.97	84.10
		Gambusia	5.46	89.56
		Spangled perch	5.18	94.74
Floodplain	60.13	Gambusia	45.28	45.28
		Common carp	39.69	84.97
		Goldfish	6.97	91.94

Table V. Environmental variables identified using DistLM as being significantly associated with variation in fish assemblage structure.

Variable	AICc	SS (trace)	Pseudo-F	*P*	Cumulative proportion of variance explained	res. df
Macrophyte cover	210	8963	6.86	0.0008	0.20	27
pH	206	7200	6.67	0.0001	0.36	26
Emergent vegetation cover	203	5228	5.73	0.0023	0.48	25
Water velocity	202	2642	3.14	0.0188	0.54	24
Small woody debris cover	202	2212	2.83	0.0436	0.59	23

moved into (bony bream and spangled perch) or out of (golden perch and Murray cod) the study area at the onset of flows. The same patterns were documented on the River Murray, corroborating the role of microhabitat associations and life history strategies in determining fish assemblage structure (Zampatti and Leigh, 2013; Bice *et al*., 2014).

Habitat associations alone, however, do not explain the dominance of fish assemblages by alien species in the Macquarie Marshes. Inundation occurred in the late winter, when water temperatures at Warren Weir were well below the spawning thresholds required by most native species but above those required by alien species (Table I; Figure 2). The resulting reproductive window was relatively long for alien species compared with native species, producing post-flooding dominance of the fish assemblage by alien species (Figures 4 and 6). Mean spawning temperature of the species present was 2.2 °C lower than that of the species predicted to have occurred under reference conditions (Table I). Further, the mean spawning temperature of the species that have colonized the system since reference condition (16 °C ± 0.82 S.D.) was significantly lower than that of the five native species that have not been caught since 2007 (22.6 °C ± 1.65 S.D.; *t*-test $p < 0.001$;Table I).

Differences in threshold spawning temperatures could reflect alterations to the seasonality of inundation over multiple decades and dam-induced changes to the thermal regime (Olden and Naiman, 2010). Burrendong Dam, upstream from the Macquarie Marshes, regulates most of the flows in the Macquarie River supplying the Macquarie Marshes. Releases of cold water from Burrendong Dam depress the annual thermal maxima by 8–12 °C and displace high temperatures by 1–3 months (Lugg, 1999; Preece and Wales, 2004). This cooling may extend to the Macquarie Marshes (Boys *et al*., 2009), contributing to low rates of native fish spawning and recruitment, and the dominance of alien species since flow regulation began in the late 1960s (Table I). However, further research is required (Boys *et al*., 2009), including assessment of water temperature differences between regulated flows from Burrendong Dam and unregulated flows from tributaries, and their respective effects on fish.

The influence of alien species on native fish responses

Irrespective of temperature effects, high densities of alien species may impact on effectiveness with which native species exploit inundation of both floodplain and main-channel habitats, through biotic regulation of niche occupancy (Rowe *et al*., 2008; MacDonald *et al*., 2012). The ratio of alien to native fish in October 2010 (4.3:1) was the highest recorded for the Macquarie Marshes (Jenkins *et al*., 2004; Jenkins and Wolfenden, 2006; Rayner *et al*., 2009). CPUE of common carp in April 2011 was 300% higher than the maximum CPUE reported for this species in the Murray–Darling Basin between 2000 and 2006 (Gilligan and Rayner, 2007). Common carp dominate assemblages in lowland rivers of the Murray–Darling Basin (Gehrke and Harris, 2001; Koehn, 2004), and the biomass of native species, including carp gudgeons and bony bream, can increase by over 1000% when carp are removed (Gehrke *et al*., 2011). Similarly, Gambusia are aggressive invaders whose presence has been shown to affect the occurrence, abundance and/or body condition of most common native wetland species in south-eastern Australia (Macdonald *et al*. 2012).

Today, conserving biological assets in large rivers depends on how flow-regulated segments of these rivers are managed (Freeman *et al*., 2001). However, provision of environmental flows based on limited knowledge carries risk (Gippel, 2001; Graham and Harris, 2005). The challenge is to deliver flows that enhance recruitment of native species, while suppressing responses of alien species (Marks *et al*., 2010; Beesley *et al*., 2011). In the Murray–Darling Basin, alien species adapted to regulated river conditions represent a threat to restoration centred on environmental flows. For restoration outcomes to be realized, future flow releases need to be synchronized with the ecological requirements of native fish; in the context of this study, flow delivery to the Macquarie Marshes should be avoided when water temperatures are below the spawning thresholds of native species, or Burrendong Dam could be fitted with a multi-level off take to reduce cold water pollution (Boys *et al*., 2009; Lugg and Copeland. 2014). However, improving post-flood abundances of native species could also be aided by limiting production of alien fish through range of coordinated local and ecosystem-scale control techniques (Macdonald *et al*., 2009; Price, 2010; Vilizzi *et al*., 2013).

CONCLUSION

Inundation of regulated floodplains opens ecological niches for fish. Adapted species exploit these niches, resulting in reproduction, recruitment and, ultimately, population increases post-flooding. Conversely, species with specialized or different requirements that are not met during a flow event may decline in abundance post-flooding. In the present study, floodplain habitat niches were occupied by Gambusia and carp early in the flood, facilitating the production of large cohorts of their juveniles. We speculate that this conferred numerical advantage to these species relative to native species upon arrival of the later flood peak, when warmer conditions may have been suitable for native species had alien species not been present. This hypothesis underlines the potential importance of flow-mediated niche suitability and potential interactions between native and alien fish, in determining outcomes of environmental flows in regulated rivers.

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