

Small environmental flows, drought and the role of refugia for freshwater fish in the Macquarie Marshes, arid Australia

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ABSTRACT

Fish in arid-zone rivers are dependent on waterholes for refuge during drought. In heavily regulated systems, water extraction for human use has the potential to exacerbate drought conditions and increase the reliance of fish on refugia. This study investigated this hypothesis by surveying fish communities at 25 sites in the Ramsar listed Macquarie Marshes, before and after a 23-GL environmental flow event. Although such flows are central to restoration efforts in the Murray-Darling Basin, limited water availability often forces water managers to make difficult triage decisions regarding which ecological assets to service. This study aimed to provide an update on the current health and status of native fish populations in the Macquarie Marshes and discuss how small flows may best be delivered to meet their ecological needs, particularly during droughts. Eight native species were collected, but they were outnumbered by three alien species by more than 3 : 1. Post-flooding recruitment was observed in most species and mean species richness of sampling sites increased significantly, as fish moved out of drought refugia to utilize a more diverse array of microhabitats. This study presents a conceptual model of fish use of refugia and recommends that key low-flow refugia be targeted for remediation efforts. Copyright © 2009 John Wiley & Sons, Ltd.

KEY WORDS disturbance; floodplain; dryland; flood; boom; bust; discharge; variability

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INTRODUCTION

Intense droughts cause major disturbances for freshwater fish (Matthews and Marsh-Matthews, 2003). When widespread drying occurs, floodplain habitats fragment and water quality deteriorates. Fish are either stranded in shallow habitats or forced to retreat into deeper main-channel refugia, such as waterholes (Magoulick and Kobza, 2003). Here, biotic interactions, including competition for limited food resources and predation from waterbirds, are concentrated. Species become locally extinct as their ecological tolerances are exceeded, with final population persistence determined by the habitat characteristics of an individual refuge, the rate of evaporative water loss, the resilience of the taxa present and disturbance intensity (Closs and Lake, 1996; Arthington *et al.*, 2005; Hamilton *et al.*, 2005). If a drought is particularly severe or protracted, loss of entire fish communities may occur at large spatial scales (e.g., river reaches).

Despite these negative effects on fish, droughts are integral to the ecological function of arid-zone rivers (Humphries and Baldwin, 2003; Lake, 2003). Dry phases cause ecological 'busts' and stimulate biological and physicochemical processes which are the basis for future 'booms' (Bunn *et al.*, 2006). As a result, the maintenance of natural patterns of wetting and drying is central to

the conservation of dryland fish populations (Arthington *et al.*, 2005). However, flow regimes in arid-zone rivers have been heavily regulated worldwide—many rivers and wetlands now experience more frequent low flows and less frequent large floods (Kingsford, 2000; Jenkins *et al.*, 2005). As a consequence of extended dry periods, 'booms' have diminished in the aquatic food webs that support fish communities (Ellis *et al.*, 1999; Valett *et al.*, 2005; Capon and Brock, 2006; Jenkins and Boulton, 2007). In the Macquarie Marshes, in Australia's Murray-Darling Basin, flow regulation has contributed to large-scale losses of ecological health and declines in key biotic communities (Kingsford, 1995; Jenkins, 2006; Nairn, 2008; Sabella, 2009). There is some historical evidence that native fish stocks have also declined in the Macquarie Marshes (NSW DPI unpublished data), but rigorous fish surveys have been limited in frequency, spatial extent, duration and intensity (Swales and Curran, 1995; Jenkins *et al.*, 2007).

Increasing recognition of flow regulation impacts has stimulated considerable investment in the purchase and delivery of environmental flows (Naiman *et al.*, 2002; Arthington and Pusey, 2003). These efforts aim to restore priority river and wetland sites by delivering water in ways which mimic natural floods, but most environmental flows are relatively small. Water managers are often forced to make difficult triage decisions regarding which ecological assets to service, especially during droughts (Cole, 1999). In the Macquarie River catchment, 160 GL.yr⁻¹ (plus about 18 GL of recently purchased water)

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is presently allocated for environmental use, although this water can only be delivered in its entirety if the major upstream water storage, Burrendong Dam, is filled to capacity (1188 GL). From 1980 to 2008, dry conditions throughout the Central West region of NSW meant the mean annual volume of environmental water releases was just $38.5 \text{ GL.yr}^{-1} \pm 9.1 \text{ S.E.}$ (NSW DECC unpublished data, gauged at Warren), far below the 200 GL thought to be required for successful waterbird recruitment (Kingsford and Thomas, 1995).

There is a real demand for rigorous scientific information which can be used to guide environmental flow delivery. For scientists, this is a challenge: flow requirements for native fish are poorly understood; large-scale factors (including seasonality, catchment health and antecedent conditions) confound responses to individual flow events; and empirical response data are unavailable (Zedler, 2000; Arthington *et al.*, 2006). This study hypothesized that one key effect of flow regulation on freshwater fish in arid-zone rivers has been an amplification of drought effects, including an increased reliance on refuge habitats relative to reference conditions. This study investigated this hypothesis by comparing fish populations in waterholes within the Macquarie Marshes before and after a 23 GL environmental flow event. This study aimed to (1) document the present health and status of fish communities in the area; (2) quantify responses in community composition, population size structure, species' distributions and microhabitat use; and (3) inform the potential targeted delivery of environmental water to support fish at specific refuge sites during drought.

METHODS

Study area and antecedent conditions

The Macquarie Marshes is a large floodplain wetland system at the lower end of the Macquarie River (Figure 1). About 10% of the >200 000 ha Macquarie Marshes floodplain is within the Nature Reserve (19 433 ha) which is internationally recognized by its inclusion in the Ramsar Convention as a wetland of international importance (Kingsford *et al.*, 2007). Several creeks dissect the floodplain and form a complex network of aquatic and floodplain habitats for freshwater fish. As with most temperate, dryland rivers, natural flows in the lower Macquarie River are naturally highly variable. However, over the past decade the Macquarie Marshes have experienced extremely low rainfall and flows, which have been exacerbated by flow regulation and extractive use (Figure 2; Ren *et al.*, 2009). In February 2008, a small environmental flow (20 952 ML, ~14% of maximum annual environmental flow) was delivered to the northern Macquarie Marshes Nature Reserve, via Bulgeraga Creek, to support a breeding colony of intermediate egrets (*Egretta intermedia*).

Fish surveys

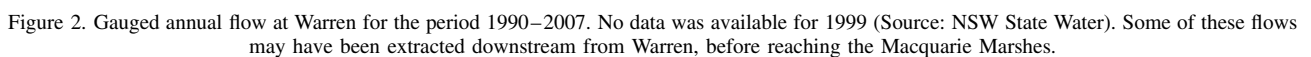
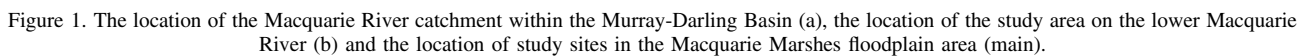
Fish surveys were conducted at key refugia throughout the lower Macquarie River system, including main channel and floodplain sites. A total of 25 sites was sampled over the course of the study (Figure 1), with 17 sites sampled before the environmental flow (October 2007). These sites represented all major wetted habitats in the study area at that time. Twenty-four sites were sampled after the environmental flow (March 2008), including 15 of the sites which had been sampled before the flow event and 9 additional sites which had previously been dry. Two sites sampled before the flow event could not be resampled because they were inaccessible.

At each site, combinations of electrofishing, traps and fyke nets were used according to local habitat conditions. This is standard practice in arid-zone floodplain systems (Balcombe *et al.*, 2006; Jenkins *et al.*, 2007), where standardized methodologies are difficult to deploy (Davies *et al.*, 2008). At shallow sites, up to 12 backpack electrofishing shots were completed (each shot = 90 s of power-on time, Smith-Root Model 12; 500 V, I-9). At deeper sites, up to 12 boat electrofishing shots were completed (each shot = 120 s, Smith-Root 2.5kVA; 50–500 V, 120 pulses per second 15–40% duty cycle, 6–8 A). Ten small traps (40 cm × 20 cm × 20 cm, 3 mm mesh; five on each bank) were set unbaited for two hours at all sites to sample small-bodied cryptic species in littoral habitats. Two large (5 mm mesh, 10 m wide entrance, 1.2 m hoops) and two small (5 mm mesh, 5 m wide entrance, 50 cm hoops) fyke nets were also set at sites with sufficient flow to allow movement of fish between mesohabitat units (e.g., between pools). Fish caught during sampling were identified and measured to the nearest millimeter (standard length), before return.

Microhabitat variables (substrate, vegetation and water quality) were recorded after each shot of fishing effort using a standard habitat assessment method (Pusey *et al.*, 2004; Kennard, 2005; Rayner *et al.*, 2008). Habitat elements that varied across the river bed (e.g., macrophytes beds) were estimated as the percentage of total surface area sampled (10–750 m²), whereas those confined to river margins (e.g. undercut banks) were estimated as the linear portion/percentage of total bank length sampled. Three replicates of water quality variables (temperature, pH, dissolved oxygen and conductivity) were measured at each site during each sampling date, at a depth of 0.5 m, using a multi-probe instrument (90-FLT, TPS Pty Ltd, Brisbane).

Data analysis

Traditional analysis of catch-per-unit-effort data was not appropriate due to differences in gear types employed across study sites. Instead, fish species were classified into four groups based on their abundance and distribution across sampling sites before and after the environmental flow event (Figure 3). The method developed by Angermeier and Smogor (1995) was then applied, but calculated using the percentage of sites at which a species



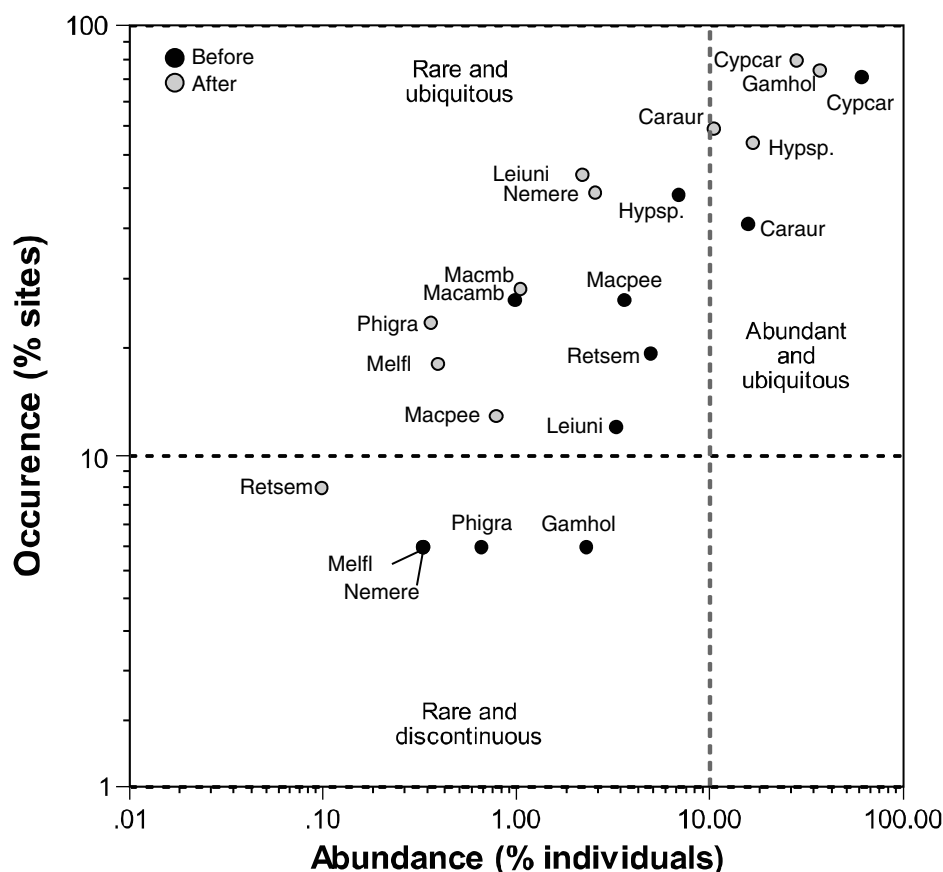


Figure 3. Fish species' relative abundance (percentage of total abundance) versus frequency of occurrence (percentage of sites occupied) before (October 2007) and after (March 2008) the environmental flow event. Each point represents one species sampled using a variety of gear types, including electrofishing and netting. Data are plotted on log scale. Rare species are defined as forming less than 10% of total abundance and discontinuous species are defined as occurring in less than 10% of sites. Taxon codes are the first three letters of the genus and species (Table I).

occurred during each sampling date (not the percentage of mesohabitats occupied) and the percentage of the total number of individuals caught during each sampling date by species (rather than mean abundance). Temporal changes in population structure were then examined using length–frequency histograms for each species. Difference in mean species richness across all sites before and after the flow event was tested using a two-tailed *t*-test.

Two-dimensional semi-strong hybrid multi-dimensional scaling (SSH MDS) was used to assess habitat use by each species before and after the environmental flow event (PATN version 3.03—Belbin 1991; Bray Curtis association measure, cut-off value = 0.9, 10 random starts, random seed number = 1235, 100 iterations). Habitat use was defined as the mean value of each habitat variable recorded where any individual of a species was captured. To identify which variables were most associated with spatial and temporal variation in habitat use, principal component correlation [(PCC); using PATN v.3.11 Belbin, 1991] was applied to habitat variables and tested using the Monte-Carlo Attributes in Ordination (MCAO) permutation test (seed value = 1235, 1000 iterations). PCC vectors were plotted on ordination figures if the percentage of MCAO permutation r^2 values exceeding the real r^2 (the r^2 value from the real groups) were less than or equal to 5%. PCC vectors with 'significant'

results were described as 'strongly' correlated with the distribution of samples in ordination space. Analysis of similarity [(ANOSIM); Clark and Green, 1988] was used to test for differences between *a-priori* sampling groups (i.e., before and after flow). The flexible unweighted pair-group method, using arithmetic averages (UPGMA) was also carried out on this (using PATN) habitat-use matrix, to classify species into habitat guilds.

To further examine habitat use by fish species, each fish species was assigned to one of three functional groups, based on examination of length–frequency histograms and age. The first group contained small-bodied species with poorly defined cohorts: *Gambusia*, Western carp-gudgeons (*Hypseleotris* spp.), flat-headed gudgeon (*Philypnodon grandiceps*), Australian smelt (*Retropinna semoni*), spangled perch (*Leiopotherapon unicolor*) and rainbow fish (*Melanotaenia fluviatilis*). The two other groups were juveniles (<150 mm SL) and adults (>150 mm SL) of large-bodied species: European carp (*Cyprinus carpio*), goldfish (*Carassius auratus*), bony bream (*Nematalosa erebi*), golden perch (*Macquaria ambigua*) and Murray cod (*Maccullochella peelii peelii*). The percentage of individuals in each group was plotted for three habitat depth classes (>0.25 m, 0.3–0.7 m and >0.7 m), separately for alien and native species.

Table I. Comparison between the fish species predicted to occur in the lowland zone of the Macquarie River valley and those actually caught during the present study and the Sustainable Rivers Audit (SRA; Davies *et al.*, 2008).

Common name	Scientific name	Taxonomic authority	Reference condition	Present study (26 sites)	SRA (7 sites)
Goldfish*	<i>Carassius auratus</i>	Linnaeus, 1758		Y	Y
European carp*	<i>Cyprinus carpio</i>	Linnaeus, 1758		Y	Y
<i>Gambusia</i> *	<i>Gambusia holbrooki</i>	(Girard, 1859)		Y	Y
Olive perchlet	<i>Ambassis agassizii</i>	Steindachner, 1867	Y		
Silver perch	<i>Bidyanus bidyanus</i>	(Mitchell, 1838)	Y		
Un-specked hardyhead	<i>Craterocephalus stercusmuscarum</i>	Ivanstoft <i>et al.</i> , 1987	Y		Y
Western carp gudgeon	<i>Hypseleotris</i> spp.	(Ogilby, 1989)	Y	Y	Y
Spangled perch	<i>Leiopotherapon unicolor</i>	(Gunther, 1859)	Y	Y	Y
Murray cod	<i>Maccullochella peeli peeli</i>	(Mitchell, 1839)	Y	Y	
Golden perch	<i>Macquaria ambigua</i>	(Richardson, 1945)	Y	Y	Y
Murray River rainbow fish	<i>Melanotaenia fluviatilis</i>	(Castelnau, 1878)	Y	Y	Y
Purple-spotted gudgeon	<i>Mogurnda aspersa</i>	(Castelnau, 1878)	Y		
Bony bream	<i>Nematalosa erebi</i>	(Gunther, 1868)	Y	Y	Y
Flat-headed gudgeon	<i>Philypnodon grandiceps</i>	(Kreft, 1864)		Y	
Australian smelt	<i>Retropinna semoni</i>	(Weber, 1895)	Y	Y	
Freshwater catfish	<i>Tandanus tandanus</i>	Mitchell, 1838	Y		

Note: The SRA project does not sample wetland habitats (Davies *et al.*, 2008).

* alien species.

RESULTS

A total of 11 fish species (8 families) was caught during the study (Table I). All species were caught before and after the environmental flow event, although their relative abundances, distributions, size distributions and use of aquatic habitats changed substantially between sampling dates. The total catch at the 15 replicated sites was 302 individuals prior to the flow event and 2227 following the flow event, with 2 and 822 individuals caught at the additional sites, respectively. The three alien species (European carp, goldfish and *Gambusia*) dominated fish biota, outnumbering native fish by 3.8:1 before and 3.1:1 after the flow. *Hypseleotris* gudgeons were the most abundant native species, comprising 7% of the total catch before and 17% of the total catch after the flow. The seven other native species contributed little more than 5% each of the total number of individuals caught.

Changes in the longitudinal distribution of individual species were evident for all species (Figure 4). Before the flow event, most native species were highly restricted in their spatial range, with 7 of the 8 species found at 3 or less of the 17 sites surveyed. Murray rainbow fish, bony bream and flat-headed gudgeon were recorded at only one refuge site. Following the flow event, most species expanded their range within the study area, notably *Gambusia*, spangled perch, Murray River rainbow fish, bony bream and flat-headed gudgeon. These increases in the extent of species' distributions were reflected in a significant increase in mean species richness, from 2.4 ± 0.5 to 4.4 ± 0.4 ($t = -3.194$, d.f. = 39, $p = 0.003$).

Water quality and habitat structure were also strongly influenced by flow. Mean water temperature was significantly higher before the flow event than after the flow event, whereas mean conductivity and mean dissolved oxygen concentration were significantly lower ($P < 0.5$;

Figure 5). Mean habitat width and depth remained consistent before and after the flow event, but mean water velocity was significantly higher after the environmental flow. Instream habitat diversity increased after the flow, particularly with respect to vegetation variables such as percent cover of macrophytes, percent cover of submerged and emergent plants and the abundance of overhanging vegetation. Structural elements, such as large and small woody debris, were similar during both sampling rounds (Figure 6). These changes in habitat structure were associated with changes in fish habitat use (Figure 7; ANOSIM between *a-priori* round groups: Real F = 1.309, Best F = 1.121, % random > real = 0). Before the environmental flow, fish were restricted to drying pools and waterholes with mud substrates and abundant leaf litter. As a result, all species were members of a single habitat-use guild (Figure 8). Following the environmental flow event, the fish fauna utilized a wide variety of microhabitat types, including areas with higher flow velocities, cobble, coarse gravel, fine gravel and sand substrates and overhanging and emergent vegetation. At this time, five habitat-use guilds were identified, ranging from a guild comprised solely of bony bream (deep, open water habitats), to a guild of Murray River rainbow fish and Australian smelt (cobble substrates; Figure 8).

Habitat use differed between alien and native species along a gradient of water depth, although there was also an interaction with sampling date (Figure 9). Before the environmental flow, introduced species were proportionally more abundant in shallow (<0.25 m) and mid-depth (0.3–0.7 m) habitats than in deep habitats (>0.7 m). In contrast, native species were proportionally more abundant in mid-depth and deep habitats. This pattern was consistent across three functional groups of fish: small-bodied species, juvenile large-bodied species and adult

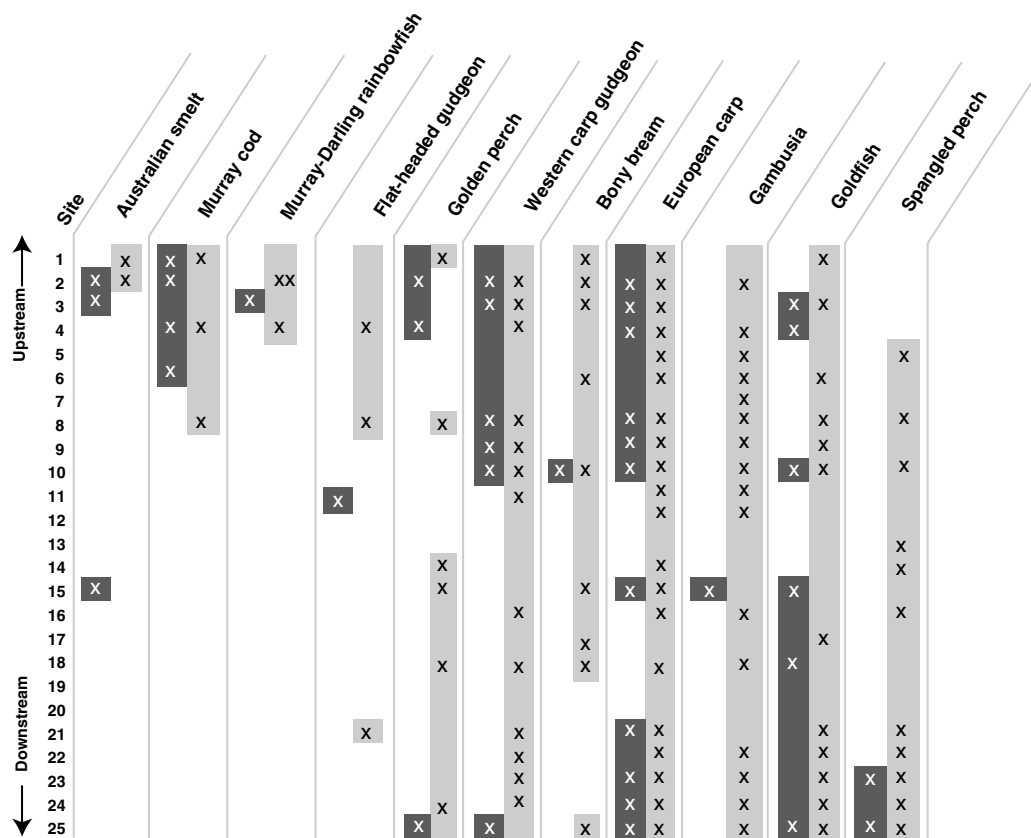


Figure 4. Longitudinal distribution of fish species in the study area before (October 2007; black) and after (March 2008; grey) sampling rounds, from site 1 at Warren to site 34 at Brewon. 'x' symbols indicate species' presence data and are boxed together if they lie within a range of 10 sites. Species are ordered according to their distribution from upstream to downstream.

large-bodied species. After the environmental flow, however, native fish continued to use mid-depth and deep habitats, but were joined by alien species. The only native species which appeared to utilize shallow habitats were small-bodied (Figure 9).

The population structure of most species differed before and after the environmental flow. Before the flow event, few juveniles of any species were collected and populations were dominated by a single adult cohort, with the possible exception of European carp (Figure 10). This pattern was reversed following the flow, with substantial increases in the abundance of juveniles of all species. Strong recruitment was most evident in European carp, goldfish, *Gambusia*, bony bream, *Hypseleotris* gudgeons, spangled perch and golden perch. Comparison of data from the 15 sites sampled before and after the environmental flow (i.e., excluding the additional sites) revealed the same patterns described above for community composition, habitat use, spatial distribution and recruitment.

DISCUSSION

Native fish populations in the lower Macquarie River are in poor health—native species richness is low and alien species dominate fish abundance and biomass. Using a range of gear types in the most comprehensive survey effort to date, this study caught only eight native species. This assessment is consistent with the Sustainable Rivers

Audit [(SRA); Davies *et al.*, 2008], a regional-scale monitoring program, which described fish community health as 'very poor' in the Macquarie River valley as a whole and 'poor' in the lowland zone. The SRA collected six native species from seven lowland sites (<200-m elevation) out of a potential 12 native species predicted under reference conditions (Davies *et al.*, 2008; Table I). In that study, Murray cod were conspicuously absent, but unspotted hardyheads (*Craterocephalus stercusmuscarum fulvus*) were caught. The latter species was not encountered in the present study, nor in fyke net surveys of the Marshes in 2003 (four sites $\times$ two dates) and 2006 (eight sites $\times$ four dates), when seven species were found in low numbers (Jenkins *et al.*, 2004, 2007). Surprisingly, the SRA prediction list included purple-spotted gudgeon, typically considered a slopes or upland species, but did not include flat-headed gudgeon, a lowland species (Lintermans, 2007). Further refinement of 'reference condition' for this river reach is recommended.

Three alien species dominate fish assemblages and biomass in the lower Macquarie River. In this study, European carp, goldfish and *Gambusia*, outnumbered native species by more than 3 : 1 both before and after the environmental flow event. This ratio is much higher than the 0.71 : 1 and 0.82 : 1 reported for main-channel habitats by the SRA (Davies *et al.*, 2008) and NSW DPI (unpublished data), respectively. However, these results are consistent with findings from other carp recruitment hotspots

SMALL FLOWS, DROUGHT REFUGIA AND FISH IN THE MACQUARIE MARSHES

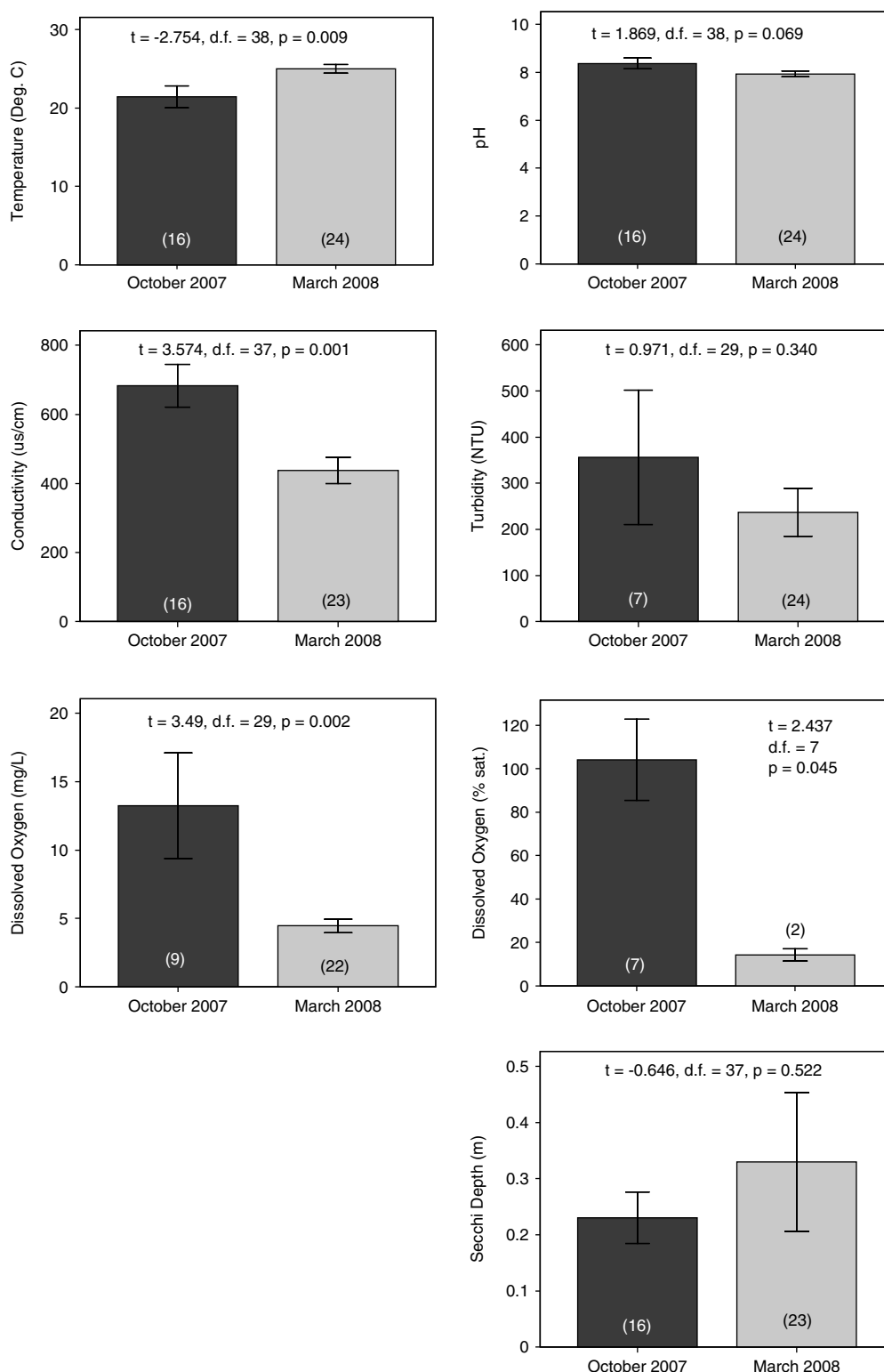


Figure 5. Mean ($\pm$ S.E) water quality variables for sites surveyed in October 2007 (black) and March 2008 (grey), together with two-tailed *t*-test results assuming equal variances. Sample sizes are provided in parentheses.

in the Murray-Darling Basin, such as the Great Cumbung Swamp on the lower Lachlan River and Barmah-Millewa Forest on the Murray River where European carp outnumber native fish $\sim 4:1$ (Driver *et al.*, 2005). These large, low-relief wetlands with shallow, relatively warm semi-permanent water and dense aquatic vegetation (e.g., *Phragmites*, *Carex* and *Paspalum distichum*) provide

ideal spawning and nursery habitats for alien species (Driver *et al.*, 2005), unlike habitats in upland areas (Gilligan and Rayner, 2007).

Freshwater fish in arid-zone rivers depend largely on low-flow refugia during dry periods (Arthington *et al.*, 2005; Balcombe *et al.*, 2006). The persistence of these refuge habitats is regulated primarily by factors which

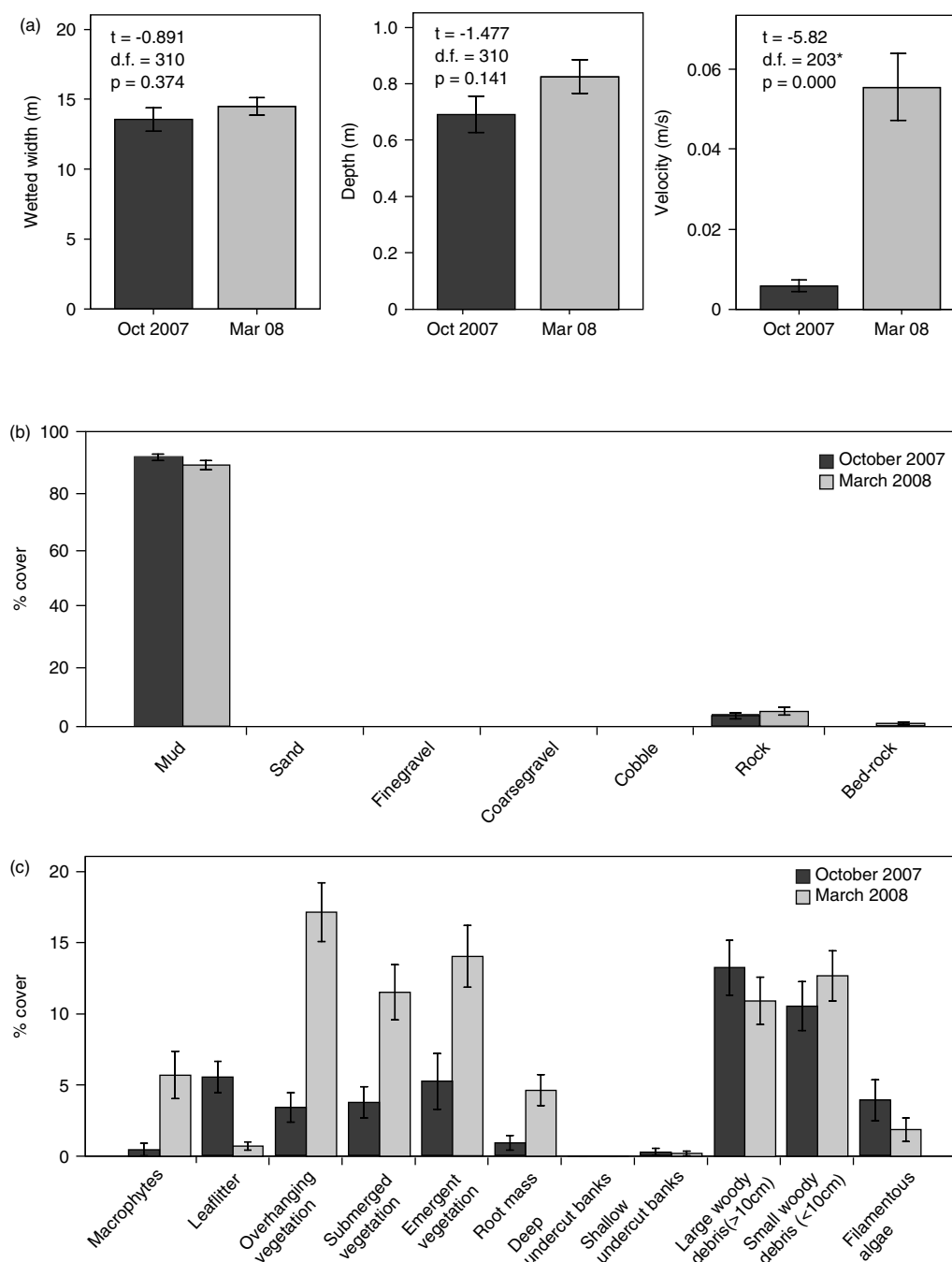


Figure 6. (a) Mean ($\pm$ S.E.) values of hydrologic (a), substrate (b) and vegetation (c) variables during October 2007 (black, $N = 119$) and March 2008 (grey, $N = 193$) with sample sizes in parentheses and two-tailed t -test results assuming equal variances (*except for water velocity). Substrate and vegetation variables were not statistically tested due to extreme non-normality and skewing (e.g., substrate was typically 100% mud or 100% rock).

determine the rate of water loss due to evaporation (~ 1.5 – 2.5 m per annum), including waterhole depth, effective width for wind action, degree of channel incision and height and width of riparian vegetation (Arthington *et al.*, 2005; Hamilton *et al.*, 2005; Costelloe *et al.*, 2007). Inevitably, fish are most dependent on such habitats during the driest conditions, but whether a waterhole acts as a refuge or not will also be regulated by water quality, habitat structure and the intensity of biotic interactions (Magoulick and Kobza, 2003). In waterholes on the unregulated Cooper Creek in arid Australia, the abundance and species richness of fish assemblages

significantly decreased as time since the last flood extended (Arthington *et al.*, 2005). The range in species richness fell from 7 to 11 species down to 4 to 8 species, although 19 months after inundation all 15 waterholes were still wet (Arthington *et al.*, 2005). Similarly, over the period 2001 to 2004, fish assemblages in four of the waterholes were similar soon after flooding, but diverged within 100 days after flows (Balcombe and Arthington, 2009).

These patterns were reflected in the Macquarie Marshes where abundances and species richness were significantly reduced during low flows, with the range per

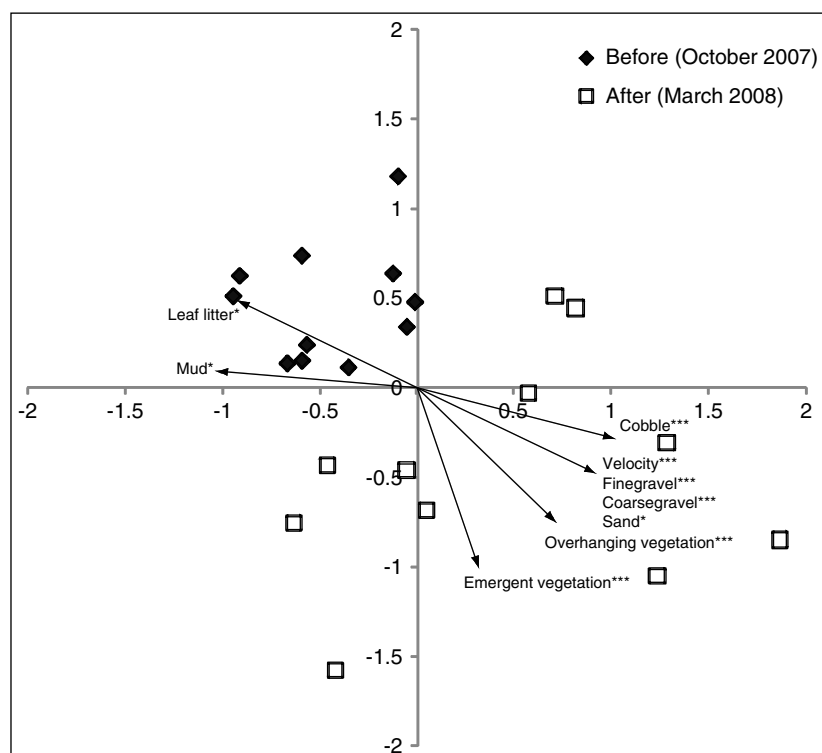


Figure 7. Two-dimensional ordination of fish habitat use before and after the environmental flow event. Each point on the plot represents 1 of the 11 fish species. Stress = 1.7206.

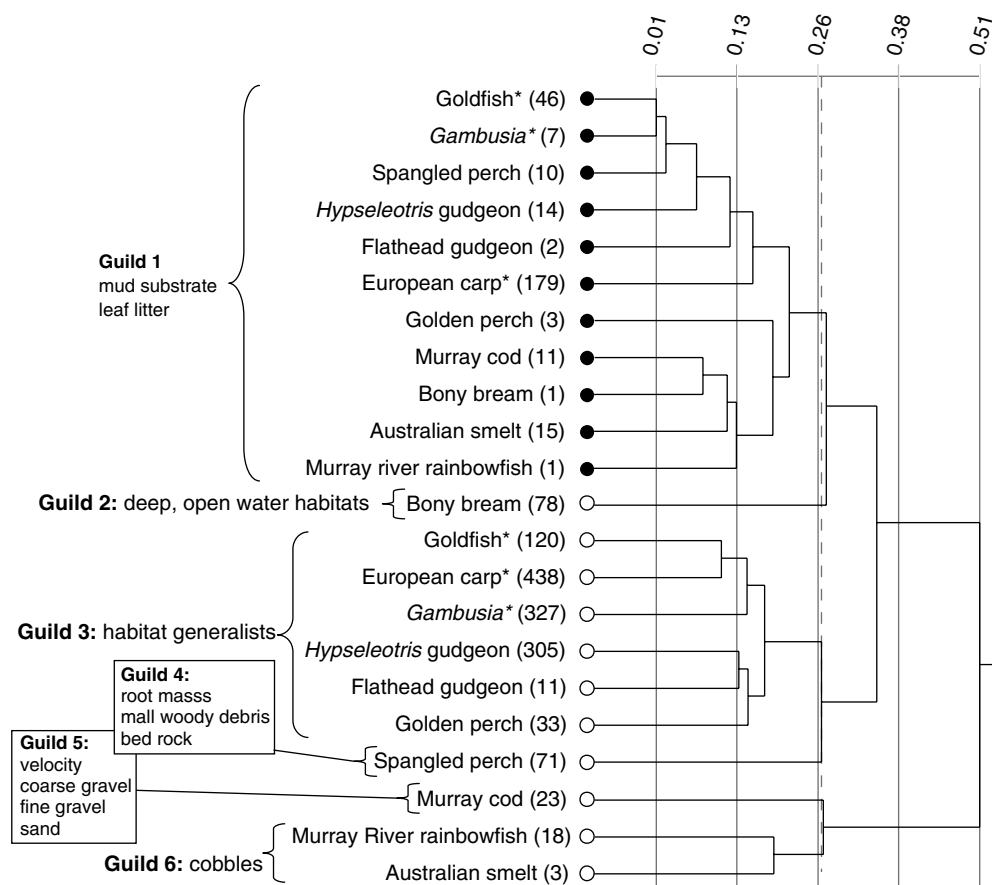


Figure 8. UPGMA classification dendrogram of fish habitat use before (October 2007; ●) and after (March 2008; ○) the environmental flow event. The number of individuals of each species included in the analysis is provided in parentheses. * alien species.

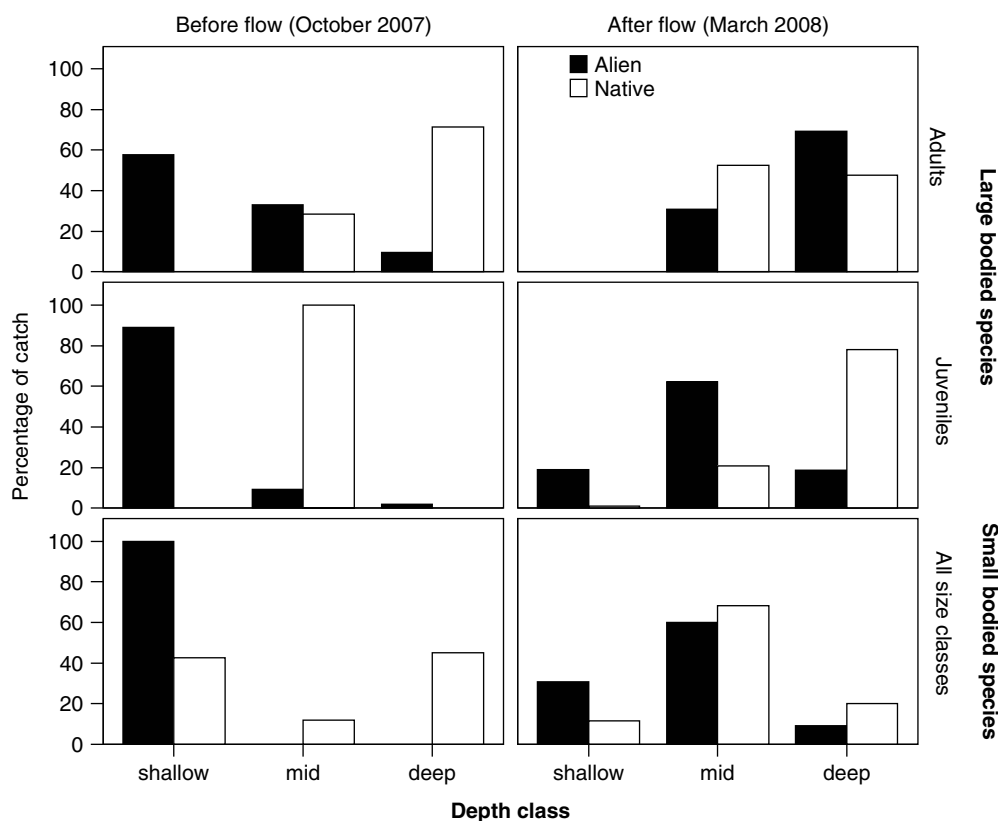


Figure 9. Distribution of native and introduced fish species in the Macquarie Marshes according to water depth before and after the delivery of an environmental flow event. Small-bodied species with poorly defined cohorts (*Gambusia**, *Hypseleotris* gudgeon, flat-headed gudgeon, Australian smelt, spangled perch and rainbow fish) and large-bodied species with distinct juvenile and adult populations (European carp*, goldfish*, bony bream, golden perch and Murray cod) are plotted separately. * = alien species. See Figure 10 for length–frequency data. Bars in each of the six plots sum to 100%.

waterhole only 0 to 5 species compared to 1 to 9 after an environmental allocation (Figure 4). When flows recede after floods, aquatic habitats in the Macquarie Marshes are gradually disconnected, but distinct hydrological stages exist along this gradient (Figure 11). For example, the main channel becomes disconnected from nearby creek habitats before individual pools within the main channel are disconnected from one another. Fish respond to these hydrologic changes according to their ability to disperse and to withstand harsh environmental conditions. Some species/individuals may retreat to refuge habitats as soon as flows begin to recede, whereas others may remain on the floodplain and move later or become stranded (Cucherousset *et al.*, 2007b). If large predatory fish are present, then deep pools may not act as refugia for small-bodied species (Schlosser, 1987; Magoulick and Kobza, 2003).

Determining the exact order of species loss due to drying is difficult without experimental data on species-specific environmental tolerances. However, based on our results, historical records (NSW DPI unpublished data) and the published literature (e.g., Treadwell and Hardwick's (2003) review of fish habitat associations in the Murray-Darling Basin), silver perch and freshwater catfish are likely lost in the earliest stages of drying. These species were once among the most common in the Murray-Darling Basin (Clunie and Kohen, 2001a,b), but have declined substantially across their ranges (Harris

and Gehrke, 1997; Lintermans, 2007). They are likely to be followed by un-specked hardyhead, Australian smelt (possibly prefer flowing waters; Lintermans, 2007), bony bream (possibly susceptible to predation; Pusey *et al.*, 2004), Murray rainbow fish and flat-headed gudgeon (both patchily distributed in the Murray-Darling Basin; Lintermans, 2007) and *Gambusia* (prefer shallow water habitats; Rowley *et al.*, 2005). The remaining species (spangled perch, Murray cod, golden perch, carp gudgeons, goldfish and European carp) may better survive droughts in refuge habitats due to relatively broad environmental tolerances. For example, native carp gudgeons were observed persisting in relatively shallow habitats and adult European carp (~450 mm) surviving in water less than 15 cm deep with dry, cracked mud on their exposed backs.

Since 2001, conditions for native fish in the Macquarie Marshes have been suboptimal at best. This has likely contributed to the ongoing decline of fish communities in the system (Figure 2; NSW DPI unpublished data). In particular, native fish recruitment is likely to have been compromised by large-scale loss of ecological function and hydrologic connectivity in the system (Kingsford and Thomas, 1995; Jenkins and Wolfenden, 2006; S. Ren unpublished data), leading to loss of shallow wetland habitats, reductions in water quality and reduced production of food for juvenile fish (Jenkins and Boulton, 2007). This is supported by the analysis of larval

SMALL FLOWS, DROUGHT REFUGIA AND FISH IN THE MACQUARIE MARSHES

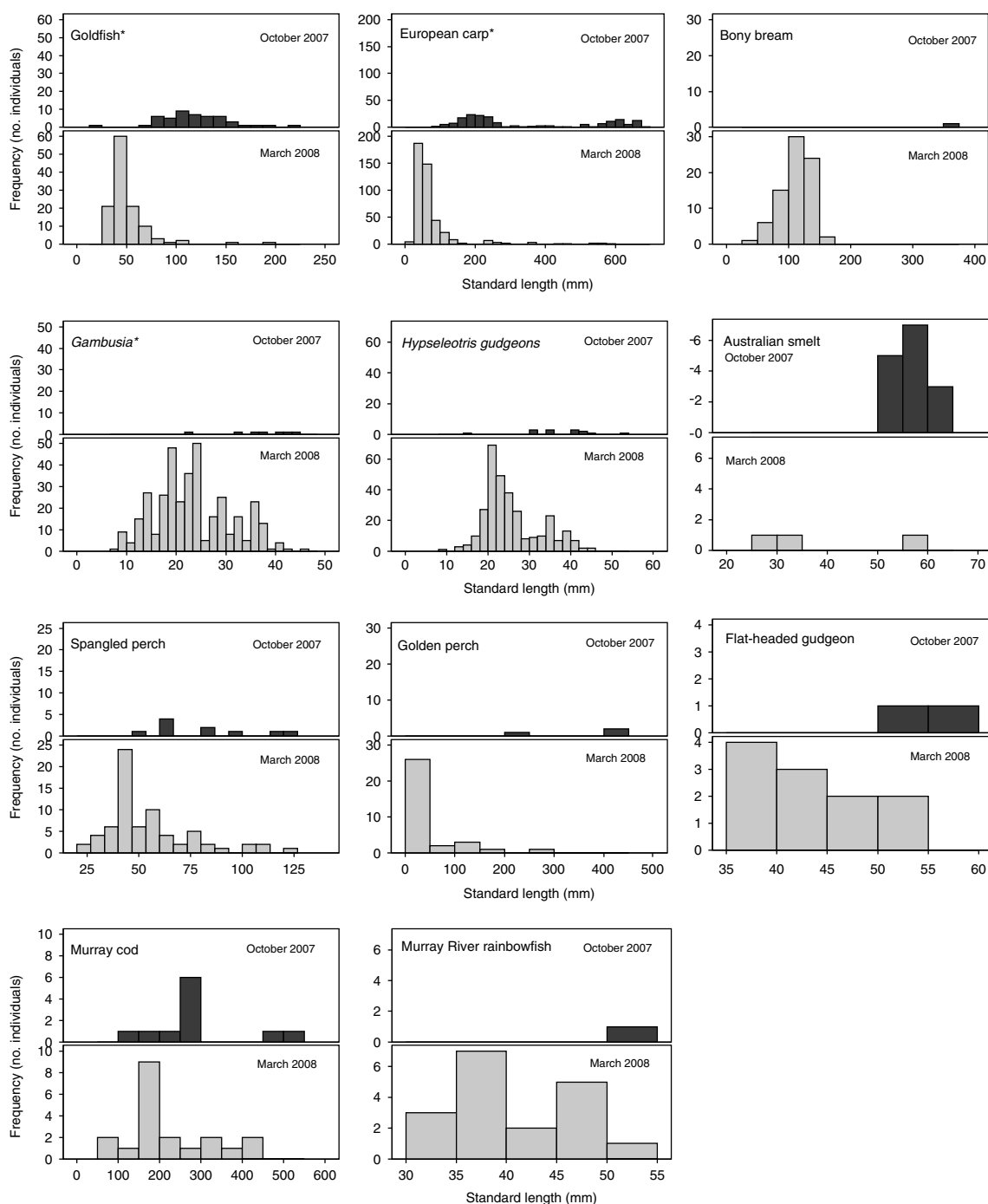


Figure 10. Length–frequency histograms for each fish species caught before (October 2007; black) and after (March 2008; grey) the environmental flow event. * alien species. Note the differences in scales of y-axes.

fish abundance and distribution in the Campaspe River, Victoria (Humphries *et al.*, 2002). Like the Macquarie River, the Campaspe is heavily regulated and about 50% of the mean annual flow is diverted for off-stream use (Smith and Humphries, 1997). Humphries *et al.* (2002) found that most species spawned each year, despite large interannual variation in flow and temperature, and concluded that poor recruitment over several decades, rather than a failure to spawn, was the most likely explanation for the poor health of adult native fish communities.

More recent research from unregulated rivers in south-west Queensland and the Lake Eyre Basin confirms that

most native fish species can recruit in the absence of large floods (A. Keresey *pers. comm.*; Balcombe and Arthington, 2009), but that floodplain habitats are used by almost all native species during various stages of their life history, including late-stage larvae of six species (Balcombe *et al.*, 2007). For example, numbers of larvae and juveniles of four native fish species dramatically increased when each flood (five across 5 years) inundated wetlands of Cooper Creek (Puckridge *et al.*, 2000). The abundant supply of invertebrates in floodplain habitats (Sheldon *et al.*, 2002; Jenkins and Boulton, 2003) improves recruitment outcomes (*sensu* the flood pulse advantage; Bayley,

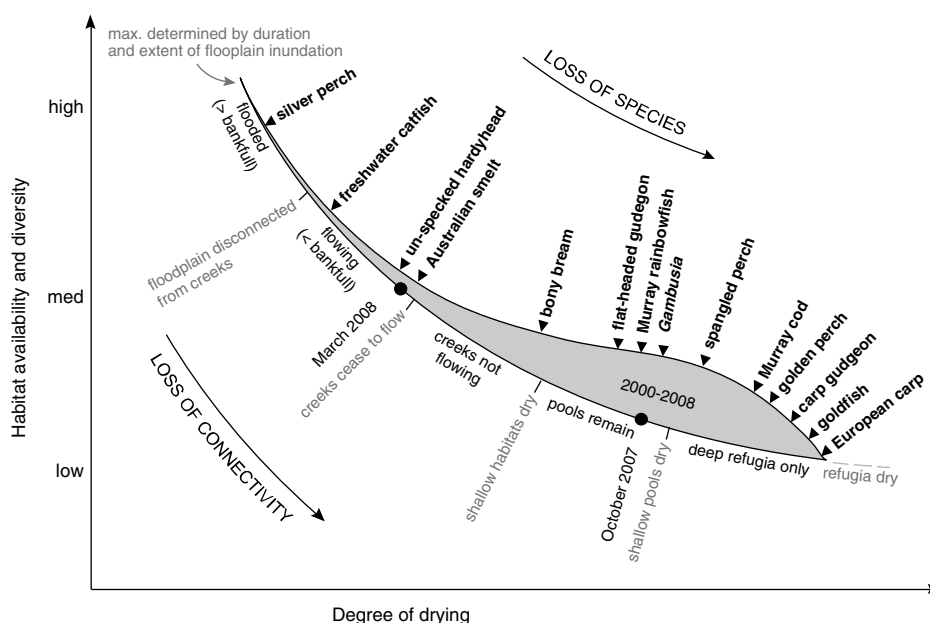


Figure 11. Conceptual diagram of the relationship between species' loss and hydrologic connectivity in the Macquarie Marshes. Distinct hydrologic thresholds are identified, as fish species are lost according to their ecological needs and environmental sensitivities/tolerances. The thickness of the shaded area represents the time spent in each hydrological phase during the period 2000–2008.

1991), even in species that spawn in main-channel habitats (King *et al.*, In press). We hypothesize that large floods, which would allow fish to access the highly productive and extensive floodplains of the lower Macquarie catchment (~420 000 ha; Kingsford *et al.*, 2004), have the potential to support fish spawning and recruitment events are many orders of magnitude greater than those that could be achieved in main channels alone. In the present study, recruitment was observed in a range of species following a 23-GL environmental flow event. However, because this flow did not inundate extensive areas of floodplain, several questions remain unanswered. How much of the observed recruitment was due to seasonal factors? Were fish responding to an increased availability of specific microhabitat types within channels (i.e., spawning habitats with suitable substrates etc; Figure 7) rather than flow *per se*? If so, do small environmental flows simply act as habitat rewatering exercises? Would floodplain inundation stimulate stronger recruitment in native species or merely benefit alien species?

The ecological benefits of environmental flows in arid-zone wetlands depend on the extent, depth, duration, timing and frequency of flooding (Bayley, 1991; Kingsford *et al.*, 1999; Jenkins and Boulton, 2007; Kingsford and Auld, 2005). While the delivery of simple, large flow events may be the vision of conservation managers, low flows, antecedent conditions, overall catchment health, interactions with local habitat conditions and natural patterns of flow variability must be considered, particularly if specific biotic groups are targeted for rehabilitation. For example, consistent low flows may give an impression of ecological health, but in fact dampen biotic responses to larger events (Jenkins and Boulton, 2007). Similarly, small flow events may disproportionately benefit alien fish species, if native species do not utilize

floodplain habitats until water quality conditions have stabilized (Figure 9; Gehrke, 1991; Jenkins and Wolfenden, 2006) and water depths are suitable (Cucherousset *et al.*, 2007a). Given these constraints, the wisest use of small environmental flows for native fish outcomes in arid-zone rivers might be to target specific refuge habitats which sustain fish through droughts, rather than inundating shallow floodplain areas for shorter time periods. This technique could be particularly effective if combined with measures aimed at improving aquatic habitat quality (e.g., providing alternative watering points for stock and increasing the amount of cover from overhead predation; Fausch *et al.*, 2002), but requires baseline information upon which to set goals for rehabilitation (Ward *et al.*, 2001; Moyle *et al.*, 2003).

CONCLUSION

This study has provided an update on the status and structure of fish communities in the Macquarie Marshes, together with a discussion of how these communities may be influenced by the hydrologic dynamics of refuge habitats and patterns of floodplain wetting and drying. The data presented here establish a baseline for future research and several hypotheses for further investigation. It is suggested that these efforts focus on the following: fish movements through arid-zone wetland systems; fish movements out of individual waterholes with the onset of elevated flow conditions; patterns of biotic exchange between the arid-zone wetlands and adjacent riverine systems; fish mortality rates and densities in waterholes and the role of predation in regulating fish community structure in these habitats; larval dynamics in these systems; and the use of floodplain versus waterhole habitats by fish for reproduction and feeding during

flow events. This study encourages management actions that help limit and reverse the decline of native fish communities in arid-zone rivers.

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